

## Tooth in the spotlight: exploring the integration of archaeological and genetic data to build multidisciplinary narratives of the Past

Francesco D'ERRICO, Luc DOYON, Joao ZILHÃO & Jack BAKER





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ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

# Tooth in the spotlight: exploring the integration of archaeological and genetic data to build multidisciplinary narratives of the Past

## Francesco D'ERRICO

De la Préhistoire à l'Actuel : Culture, Environnement et Anthropologie (PACEA),  
Université de Bordeaux, CNRS, MCC, Allée Geoffroy Saint Hilaire,  
CS 50023, F-33615 Pessac Cedex (France)  
and Centre for Early Sapiens Behaviour (SapienCE),  
Department of Archaeology, History, Cultural Studies and Religion,  
University of Bergen, Postboks 7805, 5020 Bergen (Norway)  
[francesco.derrico@u-bordeaux.fr](mailto:francesco.derrico@u-bordeaux.fr) (corresponding author)

## Luc DOYON

De la Préhistoire à l'Actuel : Culture, Environnement et Anthropologie (PACEA),  
Université de Bordeaux, CNRS, MCC, Allée Geoffroy Saint Hilaire,  
CS 50023, F-33615 Pessac Cedex (France)  
and Shandong University, Institute of Cultural Heritage,  
72 Jimo-Bilhai Highway, 266237 Qingdao (China)

## Joao ZILHÃO

Centro de Arqueologia da Universidade de Lisboa (UNIARQ), Faculdade de Letras,  
Universidade de Lisboa, Alameda da Universidade, 1600-214 Lisboa (Portugal)

## Jack BAKER

De la Préhistoire à l'Actuel : Culture, Environnement et Anthropologie (PACEA),  
Université de Bordeaux, CNRS, MCC, Allée Geoffroy Saint Hilaire,  
CS 50023, F-33615 Pessac Cedex (France)

Submitted on 5 June 2023 | Accepted on 26 September 2023 | Published on 22 January 2024

[urn:lsid:zoobank.org/pub:F7E7A7CD-49A2-4DB7-929A-64082A5B80C6](https://zoobank.org/pub:F7E7A7CD-49A2-4DB7-929A-64082A5B80C6)

d'Errico F., Doyon L., Zilhão J. & Baker J. 2024. — Tooth in the spotlight: exploring the integration of archaeological and genetic data to build multidisciplinary narratives of the Past. *Comptes Rendus Palevol* 23 (2): 31-43. <https://doi.org/10.5852/cr-palevol2024v23a2>

## ABSTRACT

The article addresses the challenges posed by the interdisciplinary collaboration that led to the recent *Nature* article presenting results of the extraction of ancient human DNA from a perforated deer tooth found in Denisova Cave. We provide a critical analysis of the contextual data that directly impacts the interpretation of the genetic data and the evaluation of the potential of the new DNA extraction technique for future studies. We discuss in greater detail Denisova, the only site that has produced truly exploitable palaeogenetic results. We highlight major unresolved dating inconsistencies at Denisova that need inquiry and explanation. We also emphasize the lack of an appropriate theoretical framework in the analysis of the tooth, of information on the lateralization, sex, age, perforation technique, wear, on the ochre residues, and the release of erroneous information on the associated faunal assemblage. We conclude that quality archaeological data and their sound evaluation should complement palaeogenetic data to create unified, reliable, and verifiable narratives about human history.

## KEY WORDS

Paleogenetics,  
beads,  
personal ornaments,  
Denisova Cave,  
Upper Palaeolithic,  
<sup>14</sup>C dating.

## RÉSUMÉ

*Une dent sous les feux de la rampe : explorer l'intégration des données archéologiques et génétiques pour construire des récits multidisciplinaires du passé.*

Cet article aborde les défis posés par la collaboration interdisciplinaire qui a conduit au récent article de *Nature* présentant les résultats de l'extraction d'ADN humain ancien à partir d'une canine de cervidé perforée trouvée dans la grotte de Denisova. Nous proposons ici une analyse critique des données contextuelles, qui a un impact direct sur l'interprétation des données génétiques et l'évaluation du potentiel de la nouvelle technique d'extraction de l'ADN pour les études futures. Nous approfondissons la discussion en particulier pour Denisova, seul site qui a produit des données paléogénétiques exploitables. À travers une synthèse des précédentes publications et des données récentes, nous mettons en évidence des incohérences de datation non résolues sur le site, qui nécessitent une explication. Nous soulignons également l'absence d'un cadre théorique approprié pour l'analyse de la dent perforée, le manque d'informations sur sa latéralisation, le sexe et l'âge de l'animal sur lequel la dent a été prélevée, la technique de perforation de la dent, l'usure et l'analyse des résidus, ainsi que la diffusion d'informations erronées sur l'assemblage faunique associé. Nous concluons que des données archéologiques de qualité et leur évaluation rigoureuse devraient compléter les données paléogénétiques afin de créer des récits unifiés, fiables et vérifiables sur le passé humain.

**MOTS CLÉS**  
Paléogénétique,  
perles,  
objets de parure,  
grotte de Denisova,  
Paléolithique supérieur,  
datation <sup>14</sup>C.

## INTRODUCTION

One can only be stunned by the technical achievement reported in the recent article by Essel *et al.* (2023). Palaeogenetics has advanced by great strides over the last three decades, including the extraction of DNA from isolated ancient fossil remains (Meyer *et al.* 2012; Pääbo 2014; Prüfer *et al.* 2014), the reconstitution of the genome of a fossil human population (Hajdinjak *et al.* 2018), the identification of hybridisation phenomena between fossil populations (Fu *et al.* 2015; Harris & Nielsen 2016; Kuhlwilm *et al.* 2016; Sankararaman *et al.* 2016; Hajdinjak *et al.* 2018), and the study of the consequences of hybridisation for the epidemiology of current human populations (Silvert *et al.* 2019; Koller *et al.* 2022; Reilly *et al.* 2022). Of late, achievements have concerned the extraction of DNA, including human DNA, from the sediments of caves and shelters occupied by our ancestors (Slon *et al.* 2017; Vernot *et al.* 2021; Massilani *et al.* 2022), and the production of models for the Upper Palaeolithic peopling of Europe (Posth *et al.* 2016, 2023; Villalba-Mouco *et al.* 2023).

These developments have revealed the potential of paleogenetics to further our understanding of the evolutionary history of our lineage and the history of its adaptation to past environments. However, these advances seem to pale, at least from a technical point of view, in comparison with the performance of Essel *et al.*, who succeeded in extracting ancient human DNA from a perforated deer tooth found in Denisova Cave. They attribute a radiocarbon age of 19 000–25 000 years BP to the pendant, identify the individual who would have produced or worn it as a woman and recognize in her genome affinities to a group of ancient inhabitants of northern Eurasia previously found only further east, in Siberia. Based on their results, the authors conclude that their work

redefines how the cultural and genetic archives can be linked to prehistoric archaeology and that it may become possible to systematically combine genetic and cultural analyses to study the use of Palaeolithic artefacts and to ask questions about task specialization, e.g. by sex or genetic ancestry.

These findings and statements caught our attention in several respects because they highlight, in our opinion, certain difficulties that exist in establishing a constructive dialogue between archaeologists and palaeogeneticists. We feel it is important to discuss them here because they are different from the concerns raised in the context of the debates that have animated the dialogue between these disciplines in recent years. Such debates have focused on issues related to the assimilation of genetics, linguistic and cultural data and the ethical and epistemological implications of such assimilations (Pluciennik 2006; Eisenmann *et al.* 2018; Lebrasseur *et al.* 2018; Hakenbeck 2019; Frieman & Hofmann 2019). A good example is the debate between geneticists and archaeologists over the interpretation of Bell Beaker pottery as a signature of an invasion of Europe 4500 years ago by a steppe people speaking an Indo-European language (Szécsényi-Nagy *et al.* 2017; Eisenmann *et al.* 2018; Olalde *et al.* 2018; Anthony 2019; Brace *et al.* 2019; Riede *et al.* 2019). Much of the work published on this and similar issues (Rothhammer & Dillehay 2009; Veeramah 2018; Kristiansen 2022) emphasizes the importance of interdisciplinary collaboration and communication, and the need for researchers to be transparent about their methods and assumptions. The authors often call for increased dialogue between archaeologists, geneticists, and other stakeholders and argue that archaeogenetic data should be used in combination with other sources of information, such as archaeology, linguistics, and historical records, to create a more complete understanding of the past.

## MATTERS OF CONCERN

Here we want to address another, no less sensitive but related aspect of this interdisciplinary collaboration, which is the role of archaeologists and archaeological data in collaborations like the one just published by Essel *et al.* Many archaeologists, archaeozoologists, palaeoanthropologists and dating experts are among the authors of this work. What was and what should have been their contribution to the published research? In this brief contribution we will address two specific concerns. Firstly, we will delve into the stratigraphic and chronological context surrounding the discovery of the tooth, and secondly, we will examine what we perceive as the limited integration of the paper's new genetic evidence with available archaeological data.

Logically, the participation of paleoanthropologists in a paleogenetics study is justified primarily because they have excavated, stratigraphically assessed or dated the sites in which the analysed objects were found, or because they are responsible for the study of certain categories of artefacts discovered at these sites that are relevant for the discussion of the paleogenetic evidence. In short, the archaeologists who participate in the study should be in the best position, after years of intensive work, to propose an informed view of the contextual data and thus enable their geneticist colleagues to interpret their results based on reliable stratigraphic, cultural, and chronological attributions. Peer-reviewers with archaeological expertise should play the role of authoritative devil's advocates to identify inconsistencies in or with the evidence derived from other sites analysed or discussed in the paper. It is legitimate to question, however, whether this role of guarantor and critical analyst of background data has been played satisfactorily here, at least for Denisova, the only site among those studied by Essel *et al.*, that has produced truly exploitable palaeogenetic results and on which we will therefore focus our attention. Admittedly, a chronological attribution of the perforated tooth is also proposed in the article in question based on the palaeogenetic results (3.6 to 31.6 ky), but the margin of error is far too wide to consider that it frees us from the obligation to assess the chronological setting based on the stratigraphic analysis, the cultural attribution, and the radiometric dating of the archaeological layers. Yet, it is the interpretation of the stratigraphic sequence and the dating of these layers that would have required a critical appraisal by archaeology co-authors.

## THE DENISOVA CAVE STRATIGRAPHY AND DATING

According to the information provided by Essel *et al.*, the perforated tooth was found in square E3, at the back of the South Chamber of Denisova, in the upper part of layer 11. It is said that the piece was 3D plotted, but Essel *et al.* provide neither the respective coordinates and find number nor the location of the find on a map with the grid they use. It is also said that the thickness of layer 11 does not exceed 50 cm in the

area in which the tooth was found, and that it ranges in depth from -150 to -230 cm due to a substantial slope, at an angle ranging from 20-25° to 50°, toward the southwestern rock wall of the chamber; however, it is claimed that such a slope would not have affected the integrity of the layers. According to the authors, the age of the tooth can be constrained by two <sup>14</sup>C ages obtained on charcoal samples discovered in the proximity of the tooth (square Z3, c. 1.5 m away) and in the same layer: OxA-X-3089-11, 19 990 ± 61 BP, i.e., 24 200-23 830 cal BP (calibrated years before present), and OxA-X-3089-12, 33 500 ± 220 BP, i.e., 39 180-37 560 cal BP (95.4% probability calibrated ranges).

However, the younger sample comes from the middle rather than from the upper part of layer 11, in which the tooth was found, while the older sample comes from the layer's lower part. This means that the two <sup>14</sup>C ages are not stratigraphically associated with the tooth and therefore can at best provide an estimate of its maximum age. This is all the more so considering that a 15 000-year difference between the two ages in a less than 50 cm thick sedimentary sequence suggests the layer is far from being chronologically homogenous. In addition, Essel *et al.*'s reasoning is predicated on the assumption that, within layer 11, age and depth correlate well, which we find hard to accept given the wide scatter observed in the radiocarbon dates previously published for this stratigraphic unit across Denisova as a whole (Reich *et al.* 2010; Douka *et al.* 2019; Jacobs *et al.* 2019).

In sum, in absence of more <sup>14</sup>C determinations and precise sample depth information, which Essel *et al.* do not provide, all that can be drawn from the reported dating evidence is that the tooth is likely to be younger than the sample from the middle portion of layer 11, i.e., younger than c. 24 000 years ago. Surprisingly, when discussing the age of the tooth, Essel *et al.* fail to consider the other <sup>14</sup>C ages, many of them published in the same source they used, that are available for the Denisova sequence and layer 11 specifically. Indeed, when putting the chronological attribution proposed by Essel *et al.* in the context of previous radiometric determinations and ensuing narratives, several striking inconsistencies emerge.

Two other <sup>14</sup>C ages are available for layer 11 of the South Gallery (Reich *et al.* 2010): a *Hyaena* bone produced an age of 48 650 ± 2 380 BP (KIA-25285) for unit 11.2, and a charcoal sample from the interface between layers 11 and 10 produced an age of 29 200 ± 360 BP (AA-35321). In their 2010 article, Reich and colleagues interpreted the discovery in the South Gallery of a Denisovan molar (Denisova 4), retrieved in the upper portion of layer 11, the same one in which the perforated deer tooth was found, and the associated <sup>14</sup>C ages, as proof that Denisovans inhabited the cave for more than 50 000 years and were followed, around 30 ka, by modern humans. The presence of Denisovans at the site during the accumulation of layer 11 was later supported by the palaeogenomic proximity between Denisova 4 and the Denisova 3 phalanx found in the same layer, but in the East Chamber (Douka *et al.* 2019). Although it is difficult to assess the relevance of these observations without a graphical representation of both the limits between layers and the position of the <sup>14</sup>C dated samples and



finds, they nevertheless reveal that, potentially, the  $^{14}\text{C}$  ages for the South Gallery that Essel *et al.* fail to consider are as pertinent to chronologically attribute the perforated tooth as the ages that they used with that intent. This is all the more so since Denisova 4 came from square G2, i.e., was found at most 2 m away from the tooth pendant. Yet, this previously published information does not appear to have played any role in the chronological attribution of the perforated tooth.

This summary leaves us with several important questions that we would have expected Essel *et al.* to discuss. To what do the authors attribute a discrepancy of at least 15 000 years between the age they obtained for layer 11 and the  $^{14}\text{C}$  ages previously obtained for this same layer in this same part of the cave? How do they explain a 10 000-year inversion between the age they obtained for the middle part of layer 11 and the age previously attributed to the interface between this layer and layer 10? What conclusions do they draw from the fact that, apparently, the upper part of layer 11 has yielded both Denisovan remains, and a pendant impregnated with modern human DNA?

From a cultural standpoint, two subunits have been distinguished in layer 11. The first, found in its lower and middle parts, comprises an Early Upper Palaeolithic stone tool industry characterized by parallel knapping aimed at producing elongated flakes, large blades and small bladelets. The second, found in the layer's upper part, presents a high concentration of small bladelets and microblades, including backed pieces. Interestingly, according to Essel *et al.* most of the non-utilitarian objects, i.e., beads, pendants, and ornaments made of animal teeth, bone, mammoth tusk, soft stone, ostrich eggshells and freshwater shells, and bone tools, such as bone eyed-needles, points, polishers, awls, etc., would have been found in the lower part of layer 11.

When describing the pendant, Essel *et al.* point out that pendants of this type are common in the Initial and Early Upper Palaeolithic at Denisova Cave as attested by some specimens found in the East Chamber, layers 11.2 and 11.1, and directly dated to 41 900–38 400 cal BP (OxA-30005) and 32 660–31 100 cal BP (OxA-30006). In the original article reporting these ages, the authors cautioned that the determinations should be considered minimum ages owing to the small size of the objects and the marginal collagen yields, ranging between 1.0 and 1.6 w% collagen, which prevented the application of robust chemical pre-treatment methods (Douka *et al.* 2019). Yet, when used on different subsamples of the same sample, no statistically significant difference exists between the results obtained with the more and the less robust methods used by Douka *et al.* (2019: table S2). There is therefore little reason to suppose that the ages reported by Essel *et al.* are underestimates, the more so since their samples were processed with the AOx-SC technique. Accepting both the accuracy of Essel *et al.*'s charcoal dates and their stratigraphic relevance to assess the age of the perforated deer tooth, as Essel *et al.* do, it is clear that the cultural relationship between the bearers of the pendants found in the East and the South Chambers becomes an open issue, and the homogeneity and/or stratigraphic integrity of the deposit must be interrogated.

In sum, the stratigraphy of Denisova Cave is extremely complex, and there can be no question that the sequence underwent significant post-depositional disturbance, as originally argued by Zilhão (2007) and since corroborated by the geological and archaeological work carried out at the site (Zwyns 2012; Morley *et al.* 2018, 2019; Kuzmin & Keates 2020). Any ground-breaking discovery would benefit from a critical in-depth appraisal of the sequence to clarify rather than muddle its understanding, including detailed geoarchaeological analyses, taphonomic study of faunal remains, and systematic re-dating of cultural and non-cultural material. Considering the above, the proposed agreement between the dating based on genetic evidence and the new  $^{14}\text{C}$  ages published in the paper must be considered as unsurprising and of little significance without resolving the major inconsistencies revealed by the site's dating record. It is the responsibility of the archaeologists to carry out this critical analysis and to propose interpretations that are acceptable to the scientific community. The application of new and increasingly sophisticated DNA extraction techniques cannot solve these problems.

#### COMBINING ARCHAEOLOGICAL AND GENETIC RESULTS TO BUILD A UNIFIED NARRATIVE

The second question that arises from the Essel *et al.* article is why the representatives of the different disciplines did not set about developing, as far as possible, the dialogue and cross-fertilization process that they call for in the conclusion of their article. If the aim is to combine the results of different disciplines to create a better informed narrative of our past and not only to show that techniques common in forensic medicine can be perfected and applied to the Palaeolithic, the integration of archaeological and palaeogenetic data represents an epistemological imperative, and all the more so when the results of the research are published in a high ranking multidisciplinary journal such as *Nature*. A supplementary reason for the need to contrast results is, as will be shown below, that the inclusion of pertinent archaeological data in the scientific discourse would have had a direct impact on the interpretation of the genetic data and the discussion of the potential of the technique for future applications.

The bodily fluids of the human who wore this pierced tooth left a genetic signature that was identified by the researchers, but the analysis of this genetic material does not inform us about the duration of the object's use. We have no way of knowing at present whether it took a day, a week, or a much longer period of time for this ornamental object to become impregnated with said fluids, nor whether this process erased previous traces left by other individuals of the same or the other sex. This question is relevant because the anthropological implications of the information provided by palaeogenetics would not be the same. For instance, in the case of objects worn for a single day or by a single person, how might paleogenetic data be used, as the authors explicitly contemplate in their conclusions, to obtain information on task specialization by sex?



FIG. 1. — Pictorial representation of an exchange of ornaments between two women living in Siberia during the Upper Palaeolithic. Creation by NightCafe Studio free AI (<https://creator.nightcafe.studio>) after a text of Fd'E.

One way of approaching the lifespan of an object of adornment, which also provides information on its social life, is to study the wear over its surface and, in particular, the wear of the perforation, the area that is often the most worn due to friction against the thread used to sew the pendant onto a garment or thread it into a necklace, bracelet or diadem. Archaeologists have investigated and experimentally reproduced this wear, and tools exist to document and quantify it (d'Errico 1993; d'Errico *et al.* 1993, 2022; Vanhaeren *et al.* 2013; Martisius *et al.* 2018; Falci *et al.* 2019). No steps seem to have been taken in the study to identify these traces and to

integrate the results of a functional analysis with those provided by paleogenetics. This is surprising because an analysis of the surface condition of the object, carried out with a confocal microscope, is presented in the article, but it was carried out with the sole aim of showing that the surface of the object had not been substantially damaged by the sampling intended to test for the presence of DNA. The same microscope could have been used, in combination with optical and scanning microscopy, to assess the degree of wear of the perforation and thus contribute with archaeological data to the generation of a unified interpretation of its paleoanthropological significance.



There is ample evidence that adornment objects were exchanged over great distances during the Palaeolithic and we know for certain that in some cases deer canines travelled several hundred kilometres and were worn by individuals living in cold regions where this species was not present (Vanhaeren & d'Errico 2003a, 2005; Rigaud *et al.* 2019). The canine in question may have arrived in Denisova following exchanges with populations living in eastern Siberia and been lost in Denisova before losing the genetic imprint of the individual that originally made and carried it and before absorbing the genetic material of the individual that may have carried it to Denisova (Fig. 1). This is true considering that ornaments were often not worn in contact with the skin as necklaces or bracelets but sewn onto clothing (Vanhaeren & d'Errico 2001; d'Errico *et al.* 2021). The object may therefore have been impregnated with the body fluid of the individual who handled it during its manufacture rather than the one who wore it as a result of exchange. Taking this into account, it is problematic to draw conclusions from the genetic analysis of this object in terms of population dynamics. Creating a dialogue between disciplines is therefore essential.

One way that archaeology contributes to weighing up such hypotheses is to verify whether deer remains are present in the archaeological layer that yielded the ornamental object. If absent or rare, several hypotheses about how the canine was acquired must be considered. For instance: 1) cultural exchange rather than acquisition from an animal that the cave's inhabitants hunted; 2) scavenging from frozen carcasses exposed by erosion of permafrost deposits; and 3) on-site acquisition of reworked wapiti remains (provided the species is present in underlying deposits, as indeed it is; Vasiliev *et al.* (2021)). Essel *et al.* (2023, SI: 5-6) claim that remains of a deer, the wapiti (*Cervus elaphus sibiricus* sp.), were found in layer 11 and cite Vasiliev *et al.* (2021) in support of this statement. That paper, however, tells a different story, namely, that layer 11 is the only one of the eleven archaeological layers analysed that yielded no deer remains. Considering the large time span covered by the accumulation of this stratigraphically complex unit this is quite remarkable and strongly supports scenarios where the ornament is an exotic good acquired by Denisova inhabitants through exchange or a fossil whose age, regardless of it being established by genetic or radiometric techniques, differs from the age of the archaeological event of interest (its modification and use as an item of jewellery).

Essel *et al.* argue that their extraction technique makes it possible to systematically combine genetic and cultural analyses in the study of Palaeolithic artefacts. The study of ornaments used by traditional societies shows that they can provide different types of information to archaeologists. Through the raw material from which they are made, their morphology, their colour, their association and arrangement on the body, ornaments make it possible to express, depending on the human group, the individual's belonging to an ethnic, linguistic or social group or to an age class (Kinietz 1972; Wiessner 1984; Joyce 2005; Micheli 2012; Nowell & Cooke 2021). But Palaeolithic ornamental objects are also the result of techniques used to transform natural materials

into cultural objects and attach them to an individual's body. It is known that the materials chosen (e.g. shell, tooth, ivory, antler, bone, eggshell, etc.), the animal species preferred, and the techniques of shaping and attaching, differ among prehistoric human groups (Vanhaeren & d'Errico 2006; Rigaud *et al.* 2015; d'Errico *et al.* 2021; Baker *et al.* in press).

It is therefore necessary to characterise these behaviours when publishing objects of adornment. This naturally requires adequate photographic documentation, which for an object as important as this ornament requires photos of all four sides of the object, as well as microscopic photographs to document and identify the techniques of perforating the tooth on both sides. Documenting the location of the wear on the perforation is important in order to know, for example, whether the perforated tooth was part of a necklace or was sewn onto a garment (Vanhaeren & d'Errico 2001; Vanhaeren *et al.* 2013; Märgärit *et al.* 2018; Falci *et al.* 2019; d'Errico *et al.* 2021). This information is essential if we are to use DNA extracted from personal ornaments to find out whether individuals of different sexes perhaps wore different ornaments or perhaps the same but attached or displayed differently. In addition, when present, such as it is the case for the pendant described by Essel *et al.*, mineral pigments and residues should be chemically characterised as this information is crucial to document what raw materials were involved in the manufacture and use of the object and where they came from (Cristiani *et al.* 2014; Rigaud *et al.* 2014; Martí *et al.* 2017; Collins *et al.* 2020; d'Errico *et al.* 2021; Velliky *et al.* 2021). All this documentation is missing in the Essel *et al.* paper.

But there is more to consider here. Genetic analysis of the tooth identifies it as belonging to the Asian wapiti (*Cervus canadensis* Erxleben, 1777). Like the European red deer (*Cervus elaphus* Linnaeus, 1758), this species has two non-functional canines in its jaw that do not have opposing teeth and therefore gradually wear away over the course of the individual's life against the gums covering the mandible in the space between the incisors and the premolars (Greer & Yeager 1967; d'Errico & Vanhaeren 2002). Archaeologists who have studied the use of these teeth as personal ornaments have shown that they are characterized by both strong sexual and inter-individual dimorphism (Fig. 2) and that it is possible, by relying on qualitative and metric parameters (Fig. 3), to identify the sex and age of a deer from their canines, and to know whether two canines originally belonged to the same deer (Greer & Yeager 1967; d'Errico & Vanhaeren 2002). These methods have been repeatedly applied successfully to address issues such as exchange networks and social inequality during prehistory (Vanhaeren & d'Errico 2005; Rigaud *et al.* 2010; Rigaud 2013). An analysis of the available photographs of the perforated deer canines discovered at Denisova (Fig. 4) reveals the interest of such an approach. It highlights the use as ornaments of both stag and hind canines of different maturity, including very old hinds and, interestingly, the absence of pairs of canines originating from the same animal. Although this information needs to be confirmed by in-depth analysis, it supports an interpretation of the perforated canines as the result of exchanges (d'Errico & Vanhaeren 2002).





FIG. 2. — **A**, Perforated and incised red deer canines from the late Upper Palaeolithic site of the Avène des Iboussière, Malaverne, France, one of the collections to which methods to detect sex, age and pairs from the same deer were applied; **B**, modern stag (**top**) and hind (**bottom**) canines from the Island of Rum, Scotland, showing from left to right increasing wear of the crown corresponding to aging; **C**, dramatic individual dimorphism in stag canines from the Rum island. Scale bars: 1 cm. Credits: photos of F. d'Errico; B, C, modified after d'Errico & Vanhaeren 2002).

Combined with results provided by a successful paleogenetic analysis of the ornaments, sex attribution of wapiti canines opens the possibility of looking into whether men exclusively or preferentially wore stags' and women hinds' canines or vice versa. It may even be possible to compare the genetic ancestry

of two humans wearing canines originating from the same deer or establish whether a person was wearing two canines of a single deer. Judging from the photo of the tooth presented in the article, the individual who left her DNA on the pendant wore a hind canine. But how can we move forward in

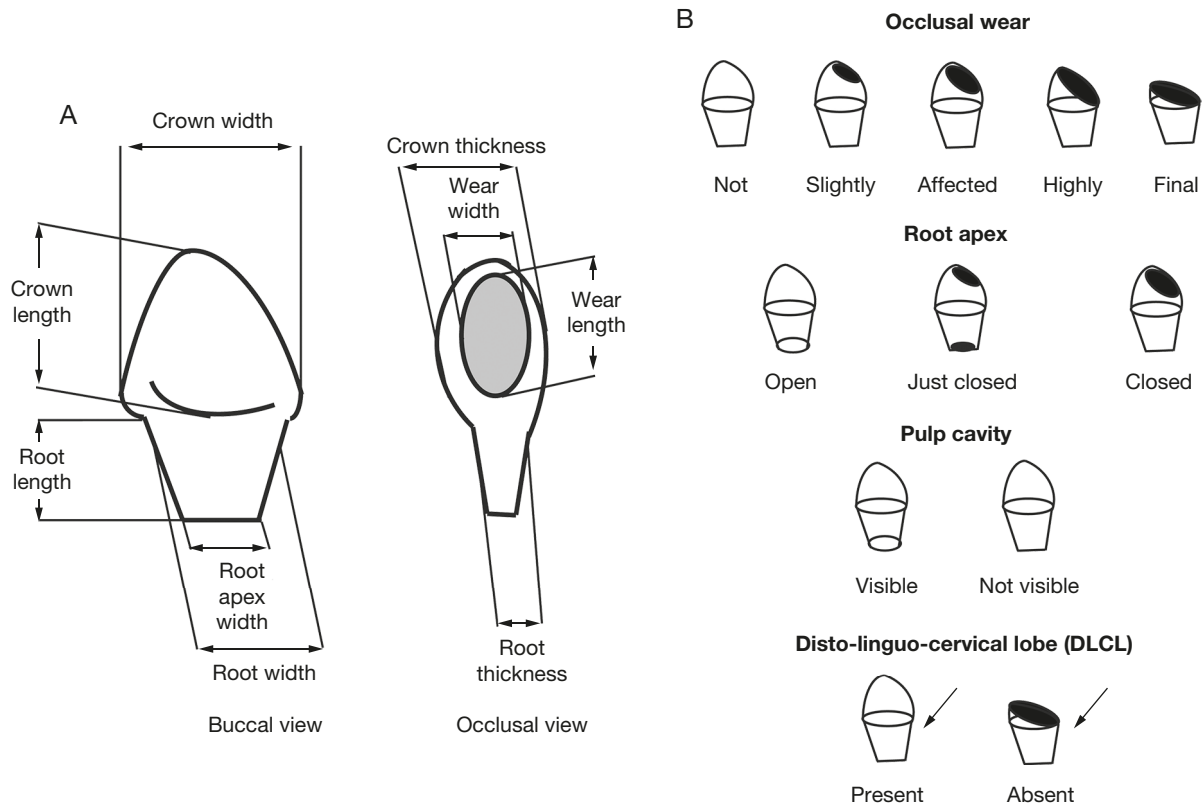


Fig. 3. — **A, B**, Metrical (**A**) and morphological (**B**) variables used to identify sex and age of red deers from their canines (modified after d'Errico & Vanhaeren 2002).

this pursuit if the sex attribution or at least the diagnostic characters and metric data allowing such an attribution are not provided, at least in the accompanying supplementary information of the article?

Among the possible outcomes of such kinds of studies, one might be able, for instance, to show that the canines systematically worn by women were of hinds, thereby opening new horizons for the understanding of the symbolic systems of the populations living in this region of Eurasia during the Upper Paleolithic. Reaching conclusions on this matter requires that archaeologists critically evaluate the genetic results and ask their geneticist colleagues to do the same in light of the archaeological evidence. For instance, Essel *et al.* state that the person who produced or wore the ornament they analysed was a woman. However, judging by their text (Essel *et al.* 2023: extended data table 3), that is not exactly what their data seem to be saying: “Among the mtDNA fragments overlapping these positions, 86.6% (95% CI: 82.2-90.5%) match the state of DCP1, suggesting that the mtDNA fragments recovered in this fraction originate predominantly, but not exclusively, from a single ancient human individual, presumably the user or the maker of the pendant”. So, since they convincingly show that almost all the DNA recovered is ancient, this means that the human DNA extracted from the pendant could in fact have come from more than one ancient individual, which, if consistent with the archaeological analyses that Essel *et al.* failed to carry out, might support its interpretation as evidence

for cultural exchange. In short, the tooth’s archaeological retrieval and analysis, subsequent to its having been lost or disposed of in the cave, is but the last episode in a long string of processes involving different actors, both anthropogenic and natural. Considering all these methodological aspects will in the future help in adequately addressing the multiple avenues of paleoanthropological interpretation raised by such aDNA evidence.

## CONCLUSION

The issues discussed here do not reveal any unbridgeable conflicts between archaeology and paleogenetics, but they do highlight that the integration of rich and reliable archaeological data is an essential prerequisite for the advances in DNA research to be able to make meaningful contributions to our understanding of human history. The potential of these advances is not in question. However, this potential cannot be realized in the absence of reliable chronological and stratigraphic data and quality archaeological observations. In a nutshell: geneticists are ill-advised if they believe that their discipline will one day allow them to reconstruct human history without the support of quality archaeological data; and archaeologists must likewise avoid the temptation to consider that their work ends with the excavation of a site and the transference of samples to their geneticist colleagues.



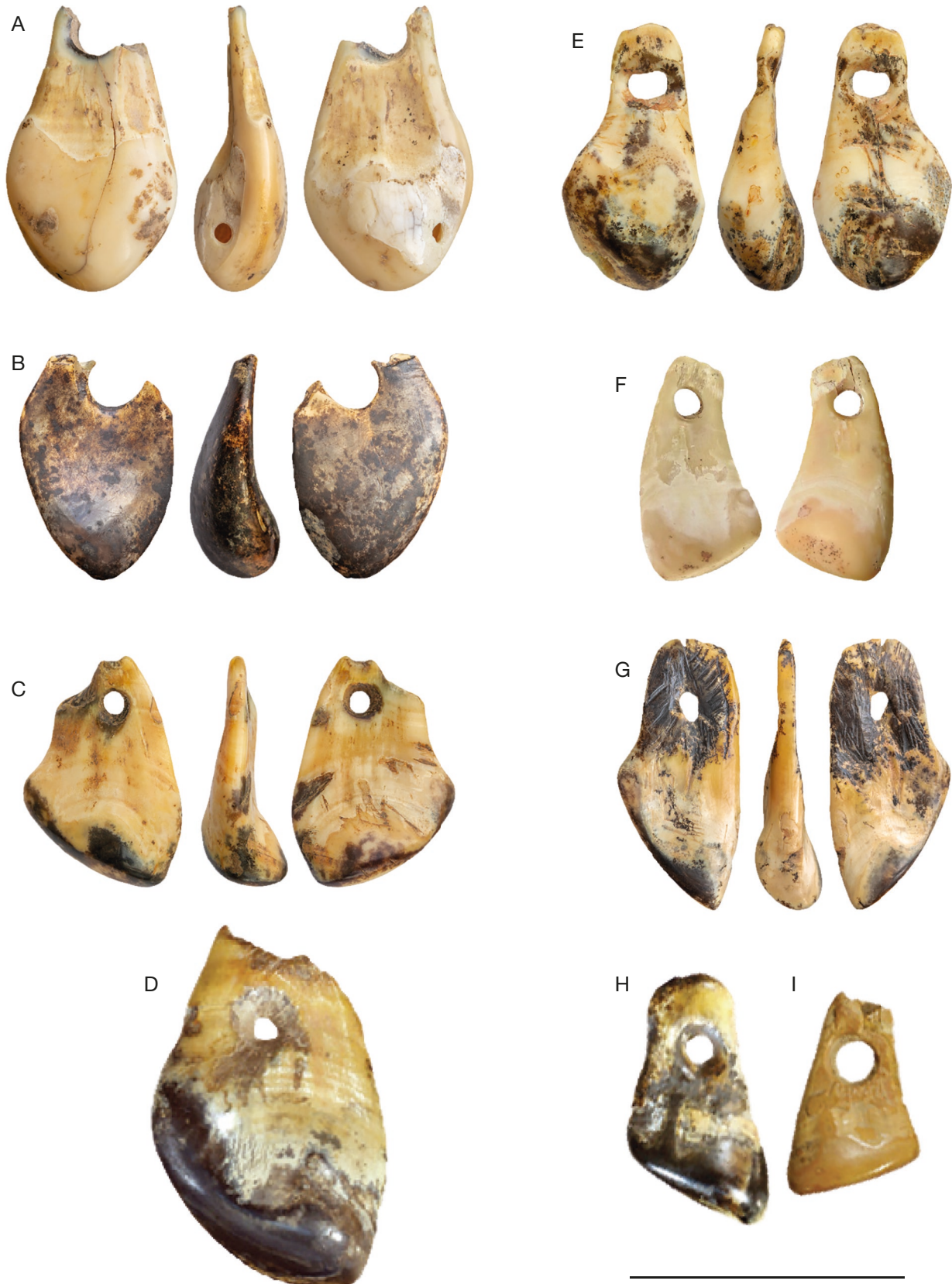


FIG. 4. — A-I, Perforated canines of large cervids found at Denisova cave (modified after Derevianko & Shunkov 2004; Shunkov *et al.* 2020; Essel *et al.* 2023): A-C, E, G: IUP, East Chamber; D, H, I, EUP, Main Chamber; F, IUP, South Chamber. Canines extracted from: A-D, G, male individuals; E, F, H, I, female individuals. Canines are ordered according to the maturity of the individuals, indicated by the degree of use-wear of the occlusal side of the crown (preliminary assessment following the method established by d'Errico & Vanhaeren 2002). A, B, E, younger individuals; C, D, F, G, H, I, older individuals. Scale bar: 3 cm (as shown in the original publications).

### Acknowledgements

We thank Solange Rigaud for the critical reading of the manuscript. This research was funded by the following agencies: Initiative d'Excellence IdEx, University of Bordeaux, Talent program grant #191022-001 (Fd'E, LD); French government in the framework of the University of Bordeaux's IdEx "Investments for the Future" program / GPR "Human Past" (Fd'E, LD); Research Council of Norway, Centres of Excellence (SFF), Centre for Early Sapiens Behaviour, SapienCE grant # 262618 (Fd'E); European Research Council Synergy Grant for the project Evolution of Cognitive Tools for Quantification (QUANTA), No. 951388 (Fd'E); French Ministry of Education and Research (JB). We also thank two reviewers, the associated editor, Nicolas Teyssandier and the chief editor Michel Laurin for their constructive comments.

### Authors' contributions

Fd'E and JZ wrote the article with inputs from the other authors.

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*Submitted on 5 June 2023;  
accepted on 26 September 2023;  
published on 22 January 2024.*