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ZOOARCHAEOLOGY AND ANCIENT DNA, PART 2: NEW SUBSTRATES AND PERSPECTIVES[1]

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The last decade has seen important technological and methodological advances in the field of palaeogenomics, constantly pushing back the time boundary and broadening our understanding of past human-animal interactions. As well as the development of sequencing technologies, a variety of organic material is being (re)evaluated as potential substrates for DNA analyses. The authors here review a selection of these, including collagenous (leather and parchment), keratinous (hair and feather) and calcified (shell and eggshell) material, and environmental DNA including coprolite. The authors focus on the biological structure of these materials in relation to DNA preservation, highlighting their singularity in comparison to bones and teeth, and inform on some of their direct applications. Finally, the authors consider some of the new perspectives these substrates can bring to our understanding of the past, notably surrounding manufacturing practices and health.

Keywords: Palaeogenomics, zooarchaeology, metagenomics, methodological advances, manufacturing practices, health.

Introduction

The era of ancient DNA (aDNA) research began in the early 1980s with the sequencing of two mitochondrial DNA fragments from dried muscle tissue of a quagga museum specimen (Higuchi et al., 1984). Since, this biomolecular technique has gained in popularity (though not without its challenges) and seen both technological and methodological breakthroughs, adding another arrow to the quiver of tools used in researching past human-animal interactions, from the individual to populations (see Manin, Lebrasseur, this volume). This was accompanied with the pioneering of novel archaeological substrates beyond the usual suspects that are bones and teeth (see Green, Speller, 2017), allowing for a broader range of themes to be explored besides those surrounding the host species, including health and palaeoenvironments. We here explore a selection of new substrates, focusing primarily on their biological structure and the resulting survival potential of DNA molecules through time, before considering the new perspectives these materials may contribute to our understanding of the past.

New Substrates

Leather and Parchment

Hide-derived products are often found in historical and archaeological collections (provided good preservation; Cameron et al., 2006), and contain a unique wealth of information on past peoples' manufacturing processes of everyday items, husbandry practices and past economies.

Animal skin quickly decays if left without treatment for several days. Consequently, skins are processed into 'leather' so as to prevent their putrefaction under warm moist conditions (Vuissoz et al., 2007). Unfortunately, this treatment also damages endogenous DNA. Curing stops putrefaction through salting (Vuissoz et al., 2007) creating a constant salt environment favourable to

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DNA stability and hydrolysis prevention (Reed, 1972; Migliore et al., 2017). However, the European practice can involve stacking these salted fresh skins atop one another thus facilitating movement of DNA molecules between them and potentially resulting in cross-contamination (Campana et al., 2010). Immersing the skins in basic (liming) and acidic baths (deliming) (Vuissoz et al., 2007) is both a blessing and a curse: DNA degradation (including acidic hydrolysis) increases rapidly as the skin's pH moves away from neutral values (Vuissoz et al., 2007; Lindahl, 1993), yet residual lime in the skin can also act as a DNA preservative and contribute to countering attacks by microorganisms and acidic ink (Bower et al., 2010). Following tanning, the processed hide is softened with an oils and/or greases treatment (Vuissoz et al., 2007) which can introduce contamination. Despite these challenges, several studies have successfully extracted DNA from leather (O'Sullivan et al., 2016; Schröder et al., 2016; Bastian et al., 2018).

Parchment undergoes a similar treatment to leather (Teasdale et al., 2015) but its manufacturing process differs between geographical regions, with some local practices consisting of a more 'natural' treatment of the hides which may contribute to DNA preservation. For instance, in Ethiopia, salt-curing is generally not undertaken (Winslow, 2015; Selassie, 1981). Similarly, hair removal through corrosive substances is uncommon; the climatic conditions are such that the skins can be left to soak in clean water for several days (Phillipson, 2013; Winslow, 2015). Furthermore, the use of parchment as writing material for legal and evidential purposes has usually led to careful curation transgressing centuries, protecting them from environmental factors such as high temperatures and fluctuating humidity (Teasdale et al., 2015). Of additional value is the fact that legal documents often carry a date (Teasdale et al., 2015). If not, palaeography and codicology can be used to assign a broader date based on script style (Santos et al., 2010). This provides parchment with a unique dating resolution. Several studies have successfully recovered high-quality endogenous DNA (e.g Shepherd et al., 2019; Teasdale et al., 2015, 2017; Anava et al., 2020).

Keratinous tissues – hairs and feathers

Keratinous tissues such as hair, feathers, nails, claws or horns are another important, albeit challenging, reservoir for genomic materials. They are found in large quantities in taxonomic collections comprising both extant and extinct animals, and, under specific burial conditions impairing microbial decay, they can also survive in the archaeological record (Hofreiter et al., 2012). Here, we focus on hairs and feathers which have a naturally low DNA content (Allen et al., 1998; Olsen et al., 2012), most likely due to their formation process called keratinisation. In hair, this process leads to the cell death of keratinocytes, resulting in loss of cell cytoplasm, a catabolic breakdown of cell organelles and nucleic acids, and dehydration. The hair is fully keratinised about 1mm from the bulb (Bengtsson et al., 2012). Thus, DNA in keratinised cells in the hair shaft is inherently damaged compared to that in the root. Studies have however shown mitochondrial (mt)DNA can be successfully recovered from hair shafts thousands of years old, allowing the recovery of near-complete to full mitochondrial genomes (Gilbert et al. 2004, 2008, 2007; Bengtsson et al., 2012). Hair, even degraded, is also not prone to the same

contamination level as bones. Even when handled by multiple people, in contact with human sweat, or immersed in blood or saliva, keratinous material can be efficiently decontaminated. This may be due to the hydrophobic nature of keratins which provide a water-tight barrier around the hair cortex, and dehydration during keratinisation which reduces hydrolytic damage of the DNA (Gilbert et al., 2006, 2004).

Although several studies have explored the preservation of DNA in feathers from taxonomic collections (e.g. Ellegren, 1991; Sefc et al., 2003; Shepherd et al., 2012), it is not the preferred approach as their sampling can strongly impact the plumage details from a specimen while yielding a relatively low amount of DNA (Billerman, Walsh, 2019). Feather artifacts are also a characteristic component of multiple cultures, in particular in Polynesia and the Americas, and their genomic study has an immense potential (Hartnup et al., 2011). Two studies have highlighted the preservation of mtDNA in archaeological feather shafts and barbs through targeted PCR (Rawlence et al., 2009; Speller et al., 2011) and, given the results that have been obtained on hairs, the potential for whole genome approaches is promising.

Other calcified remains

Many other calcified remains can be found in archaeological sites, in particular eggshells and mollusc shells, but their use as genetic reservoirs is still largely overlooked. The first studies extracting DNA from dry mollusc shells have shown that the genetic material was often very degraded and fragmented and would benefit from an aDNA approach to limit contamination (Geist et al., 2008; Villanea et al., 2016; Zhang et al., 2012). However, it is only in 2017 that the first large scale study on ancient mollusc shells was published, successfully retrieving mitochondrial and nuclear DNA from samples as old as 7,000 years old (Der Sarkissian et al., 2017). The authors of the study also recover microbial DNA from the marine environment, trapped in the biomineral structure of the shell, allowing them to study more broadly the environmental archive. Since then, different studies have been published, pushing the temporal limit for successful DNA recovery to 100,000 years old and extending the geographical range to tropical America (Der Sarkissian et al., 2020; Ferreira et al., 2020; Sullivan et al., 2020).

Contrary to most biominerals including mollusc shells, the biological structure of avian eggshells presents several advantages to DNA preservation. Bird eggshells consist primarily of calcium carbonate (95%), as well as water (1.5%) and an organic matrix (3.5%) (Von Schirnding et al., 1982). Even at high temperatures, the intracrystalline nature of the latter provides the eggshell with a relatively ‘closed-system’ when compared to bones and molluscs. This prevents the migration of organic content in or out, and the entry of microbes (Montanari, 2018; Oskam et al., 2010). Such unique characteristics make eggshells good endogenous DNA reservoirs in environments usually considered unfavourable to long-term DNA preservation, as demonstrated by Oskam et al. (2010) who successfully recovered both mitochondrial and nuclear DNA from archaeological ratite eggshells dating up to 19,000 years ago and originating from New Zealand, Australia and Madagascar. They also showed bacterial load to be 125x lower in moa eggshells than in bones. Since, aDNA analyses have permitted species identification and reconstruction of population struc-

ture/ecology (Jain et al., 2017; Huynen et al., 2010; Oskam et al., 2011), deepened our knowledge on the phylogeny and evolution of extinct species (Grealy et al., 2017; Allentoft et al., 2011), and have been successfully applied on museum material including thinner eggshells (0.2–0.5 mm compared to 4mm for ratite species; Grealy et al., 2019).

Environmental DNA

According to Thomsen and Willerslev (2015), environmental DNA (eDNA) can be defined as the genetic material obtained directly from environmental samples such as soil, sediment and water, without any obvious signs of biological source material. Apart from the micro-organisms naturally occurring in the environment, the macro-organisms will expel DNA in their surroundings though urine, faeces, shed hairs and feathers, and more generally after their death, through the on-site decay of their body (Pedersen et al., 2015; Thomsen, Willerslev, 2015). This approach has particularly benefited from Next Generation Sequencing (NGS) as it now has the power of revealing information on the biotic composition of entire ecosystems (Cristescu, Hebert, 2018; Taberlet et al., 2012). eDNA is present in a particularly degraded form, often as extracellular DNA, which means that it does not benefit from the protection of the cell walls and its preservation is particularly variable (Thomsen, Willerslev, 2015). While some experiments have shown that it would not be preserved more than a month in fresh, temperate water (Dejean et al., 2011; Thomsen et al., 2012), the identification of extinct megafauna in permafrost core samples proves that it can survive several thousands of years in the sediment, if the conditions are favourable (Haile et al., 2009; Willerslev et al., 2003).

However, eDNA is also subject to a number of pitfalls, in particular possible contaminations in time and space. Sediment particles can be quite mobile in the environment, in particular if they are part of a river system, and so is eDNA (Cristescu, Hebert, 2018). Leaching of the DNA molecules (Haile et al., 2007), as well as the (micro-)perturbations affecting a site stratigraphy (Pedersen et al., 2015) will also impact the relative dating of eDNA molecules.

Coprolite

Often found in arid environments, the rapid desiccation of coprolites - desiccated or mineralised faeces from palaeontological and archaeological contexts - means not only a good preservation of the macro and micro remains, but also of the cells and its molecular content (Hagan, 2017). Since the first study in 1998 (Poinar et al., 1998), aDNA analyses have tackled questions beyond that of characterising the depositing species, including diet, gut microbiomes and the environment (see complete review in Shillito et al., 2020). However, these investigations are not without their pitfalls. Coprolites are open systems and are likely subjected to DNA leaching from excretions even if this is dependent on soil structure and sediment conditions (Shillito et al., 2020; Hebsgaard et al., 2009). Nevertheless, the range of sources from which ancient DNA can be recovered through non-targeted metagenomic approach combined with the high temporal resolution makes coprolite a truly unique biological archive.

The animal and its environment: towards renewed perspectives

Palaeogenomics and more specifically metagenomics (the complete genetic makeup of a sample, comprising both endogenous and exogenous DNA content) have offered the opportunity

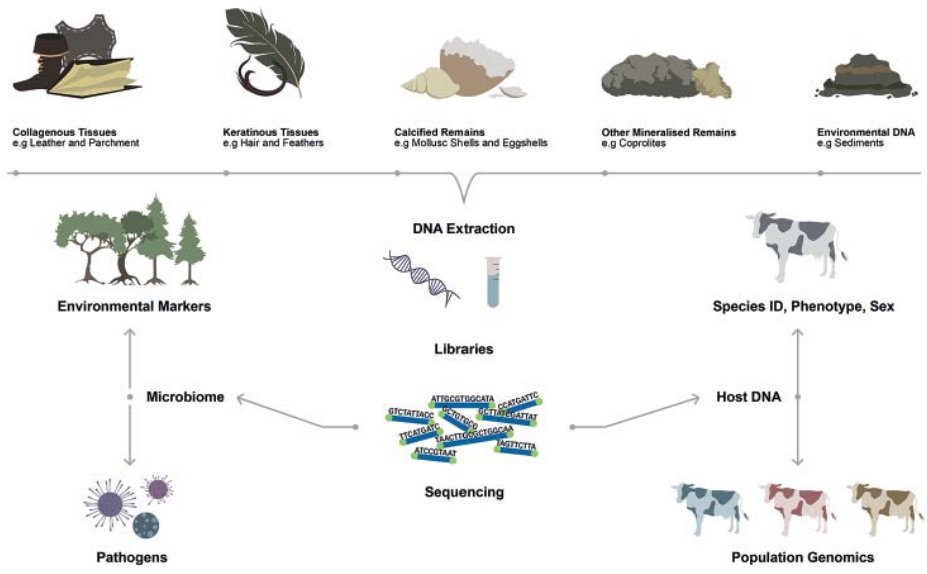

Fig. 1. A depiction of the substrates here discussed and the type of data that can be obtained (Figure by M. Lebrasseur).

Рис.1. Изображение обсуждаемых здесь субстратов и тип данных, которые могут быть получены (Рисунок М. Лебрассер).

to delve into themes beyond those surrounding the host species. Closely linked to the animal is the cultural knowledge of working local products and the resulting manufacturing processes. For instance, palaeogenomics conducted on parchment issued from manuscripts can inform on the source animal, which in turn can point towards the selection of specific species for a particular medium (Winslow, 2015). Coat-colour identification can inform on cultural preferences (Winslow, 2015), and phylogeographic analyses on local and long-distance trade. Palaeogenomics is not without its challenges; for instance, DNA lacks tissue-specificity and may thus offer a partial truth. A common stage in parchment-making is the use of lime, flour, egg whites and/or milk to smoothen its surface (Cicero et al., 2018; Fiddyment et al., 2019). Unless combined with proteomics, these subtleties in species identification would go unnoticed (Fiddyment et al., 2019).

The last decade has seen a tremendous increase in ancient pathogen genomics from bones and teeth which has been summarised and reviewed by Spyrou et al. (2019). Pathological lesions have long been used as indicators of diseases in archaeological specimens, but they may be problematic when given diseases result in resembling pathologies (i.e. tuberculosis and brucellosis). In such occurrences, aDNA can help differentiate between the two (e.g. Mutolo et al., 2012). The sequenced data can also hold valuable insights on the disease's origin and evolutionary history as well as its emergence among human populations. This was illustrated by Bos et al. (2014) who recovered and sequenced three *Mycobacterium tuberculosis* genomes from pre-contact Peruvian coastal populations and revealed tuberculosis was first introduced to the New World by infected seals through their exploitation as a food source by human groups on the South American coast. This only represents the

tip of the iceberg as to the potential of genetic material recovered from ancient pathogens, though it remains important that for such studies, the sampling is carefully targeted to a skeletal region likely to contain the pathogen in question (Margaryan et al., 2018).

Conclusive remarks

This paper addressed only a selection of the novel substrates currently under investigation and the new perspectives they can bring. Our aim here was to showcase the potential of organic material in answering specific research questions, especially in environments where bone and teeth extractions have failed to generate conclusive data. The new perspectives are a particularly important aspect of these new substrates not only for broadening the range of archaeological research questions we can ask, but also in relation to new themes and questions of direct relevance to our modern world, and impactful contributions these findings can make to addressing current global challenges.

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ЗООАРХЕОЛОГИЯ И ДРЕВНЯЯ ДНК, ЧАСТЬ 2: НОВЫЕ СУБСТРАТЫ И ПЕРСПЕКТИВЫ

Офелия Лебрассер, Аурелия Манин

Последнее десятилетие стало свидетелем важных технологических и методологических достижений в области палеогеномики, постоянно раздвигающих временные рамки и расширяющих наше понимание прошлых взаимодействий человека и животных. Наряду с развитием технологий секвенирования, различные органические материалы (пере)оцениваются как потенциальные субстраты для анализа ДНК. Авторами здесь рассматриваются некоторые из них, включая коллагеновые (кожа и пергамент), кератиновые (волосы и перо) и кальцинированные (раковины и яичная скорлупа) материалы, а также ДНК окружающей среды, включая копролиты. Авторы фокусируются на биологической структуре этих материалов с точки зрения сохранения ДНК, подчеркивая их особенность по сравнению с костями и зубами, и рассказывают о некоторых из их непосредственных применений. Наконец, авторами рассматриваются некоторые из новых перспектив, которые могут привнести эти субстраты в наше понимание прошлого, особенно в отношении мануфактурной деятельности и здоровья.

Ключевые слова: палеогеномика, зооархеология, метагеномика, методические достижения, мануфактурная деятельность, здоровье.

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