

АКАДЕМИЯ НАУК РЕСПУБЛИКИ ТАТАРСТАН
МАРИЙСКИЙ ГОСУДАРСТВЕННЫЙ УНИВЕРСИТЕТ

ПОВОЛЖСКАЯ
АРХЕОЛОГИЯ

№ 1 (35)
2021

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Индекс ПП753,

электронный Каталог печатных изданий "ПОЧТА РОССИИ"

Выходит 4 раза в год

© Академия наук Республики Татарстан, 2021

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Издательство «Фэн»



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ZOOARCHAEOLOGY AND ANCIENT DNA, PART 1: A BRIEF REVIEW OF THE METHODS AND APPLICATIONS¹

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Ancient DNA (aDNA) analyses from archaeological animal remains is well suited to many of the objectives investigated through zooarchaeological analyses. This paper aims at presenting the field of palaeogenomics, particularly in its application to zooarchaeological questions. While it does not seek for exhaustivity, it focuses on practical issues, hoping to promote trans-disciplinary dialogues. The authors begin with a presentation of the nature of aDNA and the main taphonomic pathways leading to its differential preservation. Then the authors offer a brief historical review of the aDNA techniques, from the early discoveries of 1984–1985 to the advent of next generation sequencing and high throughput approaches at the beginning of the 21st century. The authors describe the main challenges of aDNA research in recent years as it needs to adapt to a new range of methods and how the study of animal remains has been impacted. Finally, the authors highlight the main outcomes of the application of aDNA to describe animals and their populations and future lines of research that could be explored.

Keywords: zooarchaeology, palaeogenomics, domestication; translocation, biodiversity, ancient DNA.

Introduction

Zooarchaeology is a growing field, at the crossroads of social archaeology and archaeological science. By focusing on the remains of the animals that shared the environment and life of past societies, it aims at reconstructing palaeoenvironments and how human groups have been interacting with them, from early hunting and scavenging, to domestication and the development of husbandry practices, to complex market economies.

The recovery of DNA sequences from archaeological bones and teeth is particularly well suited to many of the objectives investigated through zooarchaeological analyses, such as taxonomic and sex identification, phenotypic reconstructions and phylogenetic relationships (e.g. Lebrasseur et al., 2018). Palaeogenetic data has thus been increasingly integrated to zooarchaeological interpretations, until the establishment of joint research programmes. The rapid

and constant development of the field of palaeogenomics, whether it be laboratory protocols, sequencing technologies or bioinformatic analyses, offers a growing body of possibilities for the investigation of past human-animal relationships. In this paper, we offer a brief overview of the field of palaeogenomics, its major developments and how these have been beneficial to zooarchaeological studies, as well as some caveats in sampling strategies. We finally highlight some research orientations that could be deepened in the future.

Nature and challenges of aDNA

Ancient DNA (aDNA) is by definition a degraded molecule. While, during the life of an individual, the cell is subjected to chemical attacks provoking mutations in the genetic sequence, specific enzymatic mechanisms are in place to repair the damages and maintain the genomic stability. However, these mechanisms stop following the organism's

¹ AM was funded by a NERC Standard Grant (NE/S00078X/1). OL was funded by the Global Challenges Research Fund (GCRF) One Health Regional Network for the Horn of Africa (HORN) Project, from UK Research and Innovation (UKRI) and Biotechnology and Biological Sciences Research Council (BBSRC) (project number BB/P027954/1).

death, allowing irreversible mutations to occur and build up. Observations on cell content have also shown DNA molecules start to break into increasingly smaller fragments within a few hours after death (Johnson, Ferris, 2002). Other factors, such as salinity or pH, may influence the alteration of the tissues, and thereby DNA degradation, by inducing differential chemical and microbial attacks (Shved et al., 2014). Systematic studies of DNA taphonomy however lack to clarify the relative impact of such attacks in different substrates (Geigl, Grange, 2014).

Early works have shown that the overall biomolecular preservation of a sample is generally better in cold environments than in temperate or warm climates (Smith et al., 2003). Based on the comparative DNA preservation of a large number of samples submitted to different environmental factors, two main taphonomic pathways have been identified (Kistler et al., 2017): on the one hand, the ratio of deamination of cytosine into uracil is strongly correlated with time and on-site mean temperature, leading to an increasing number of miscoding lesions in older samples and warmer sites. On the other hand, the degree of DNA fragmentation increases with local precipitation (i.e. humidity) and temperature fluctuation, while the age of the sample is not significant.

Retrieving usable genomic data from archaeological remains is thus particularly challenging, especially as the samples increase in age. Moreover, most of early human history happened in warm environments, that are not the most favourable to DNA preservation. Although some tests have been done to correlate DNA yield and bone structural preservation through less invasive methods (Sosa

et al., 2013), it is difficult to predict the success rate of a given analysis. Therefore, aDNA analyses are often considered as high-risk approaches, an aspect reinforced by their destructive nature that requires a thoughtful and balanced decision between the destruction of archaeological remains and the extent of information that could possibly be obtained.

Historical overview of aDNA techniques

Since the successful recovery of preserved DNA in the skin of a 140 years old quagga, in 1984 (Higuchi et al., 1984), the field of aDNA has been rapidly evolving to incorporate new technological and methodological developments. Tedious and hardly replicable bacterial cloning was soon replaced by Polymerase Chain Reaction (PCR), making it possible to produce a virtually unlimited amount of copies of a single DNA fragment, targeted through unique primers (Saiki et al., 1988) (fig.1). While laboratory procedures were strengthened and homogenised to limit modern contaminations and ensure the authenticity of the ancient sequences (Cooper, Poinar, 2000; Hofreiter et al., 2001), DNA extraction protocols were progressively refined to increase molecules recovery and reduce PCR inhibitors (Hagelberg, Clegg, 1991; Höss, Pääbo, 1993; Yang et al., 1998). For two decades, the field of ancient genomics relied mostly on Sanger sequencing (Sanger, Coulson, 1975), particularly well suited to the sequencing of PCR products.

The advent of Next Generation Sequencing (NGS), during the first decade of the 21st century has revolutionised the field of aDNA (Knapp, Hofreiter, 2010; Linderholm, 2016). While Sanger sequencing was limited to one sequence at a time, these high throughput platforms

allow the sequencing of billions of sequences in parallel (Mardis, 2008). NGS techniques are based on the sequencing of short fragments of DNA, typically shorter than 300 bp, which is particularly well adapted to the study of fragmented aDNA. While most of the early applications of NGS to aDNA focused on Neanderthal fossils (e.g. Green et al., 2006), in 2005 an international team used it on a 30,000 years old woolly mammoth bone fragment and managed to sequence its full mitochondrial genome and parts of its nuclear DNA (Poinar et al., 2006). By successfully retrieving long parts of the genomes of extinct species, it marked the beginning of a new era in data generation and opened new research perspectives.

Overview of aDNA research in the era of NGS

Moving from Sanger sequencing to NGS approaches led to multiple adaptations in the protocols (fig.1). Most of the research effort has focussed on bones and teeth, given their prevalence in the archaeological record and their reliability as aDNA reservoirs. Extraction protocols have been updated to retrieve the smaller fragments (Dabney et al., 2013) and increase the proportion of host (i.e. endogenous) DNA in contrast to microbial and environmental contaminants, using a pre-digestion step, a chemical wash or a combination thereof (e.g. Schroeder et al., 2019).

In order to be sequenced on a NGS instrument, the DNA fragments need to be prepared in 'libraries', which includes the repairs of their ends, the addition of platform-specific adapters and indexes, and their amplification through a few cycles of PCR. Here again, multiple methods have been proposed to improve the recovery of the most degraded fragments, with varying degrees of complex-

ity and laboratory constraints (e.g. Wales et al., 2018).

Another leap forward in the field of aDNA has been the recurrent evidence that some bones preserve DNA better than others. The petrous part of the temporal bone is a dense and non-vascularised element that allows for good preservation and low environmental contamination, yielding particularly high rates of host DNA (Hansen et al., 2017; Pinhasi et al., 2015).

However, the surge in targeting petrous bones has recently raised a wave of ethical concerns amongst archaeologists, anthropologists and zooarchaeologists alike (Alberti et al., 2018; Charlton et al., 2019; Evin et al., 2020; Pálssdóttir et al., 2019; Sirak, Sedig, 2019). On the one hand, this bone carries invaluable taxonomic, ageing and sexing information that will be lost after its destruction for analysis (Pálssdóttir et al., 2019), although this pitfall can be mitigated through three-dimensional models built prior to sampling (Evin et al., 2020). On the other hand, by targeting exclusively petrous – in other words, selecting only skulls – the investigators may introduce a significant bias in their research (Charlton et al., 2019). While this issue has only been explored from the perspective of human remains, a parallel idea can be drawn from zooarchaeological assemblages, where skeletal representation is a direct consequence of animal exploitation strategies. Amongst hunter-gatherer groups, skulls are predominant in kill sites and where the early body processing took place, whereas they are in minority in consumption sites (e.g. Binford, 1978). It is impossible to know if the decision of transporting some skulls to the residential sites was made on a favourable concurrence of circumstances, as suggested by Lupu (2006), or on par-

ticularly impressive attributes carried by the animal that would have made it an interesting trophy; but this selection could have an impact on the population diversity represented in a certain assemblage. While this vision should be smoothed in analysis of domestic animals in early agricultural societies, with the on-site processing of the entire body (e.g. Blaise, 2009: 369; Sierra et al., 2019), the development of market economies and long-distance trading networks, certainly involving meat products (e.g. Thornton, 2011), is likely to once again distort the distribution of the skeletal parts.

In order to mitigate these biases, investigations have been carried out on other parts of the skeleton to identify other suitable elements. Using CT-scanning, Alberti et al. (2018) identify a high-density layer on the outermost part of long bones cortical. By targeting this layer in a range of different large mammals, they retrieved a significantly higher amount of endogenous DNA compared to the trabecular bone. This approach highlights the potential to successfully recover ancient DNA from the least diagnostic areas of the bones.

Moving towards NGS also strongly impacted data processing and analysis, and the toolbox of the palaeogeneticist now includes a full suite of dedicated bioinformatic programmes. Although the proportion of endogenous DNA expected for a given sample can be enhanced through the selection of a specific anatomical part and the use of improved laboratory protocols, it remains relatively low (typically 0.1-10 % of the library) and needs to be sorted informatically (fig.1). The results of a NGS run require relatively heavy processing to map the millions of reads of each sample to the genome of interest, further complicated by the degraded nature of aDNA. The

pipelines need to be well calibrated to accurately consider the very short size of the fragments, the recurrent presence of post-mortem damages and the large amount of duplicated sequences arising from libraries preparation.

One of the striking contrasts between the sequencing of PCR positive amplicons and the unsupervised approach of shotgun sequencing allowed by NGS is that while the first approach is generally expected to provide immediate relevant information, the shotgun sequencing may offer discouraging results when the DNA is too degraded and too fragmented to evenly cover the host reference genome. Moreover, the result of an alignment to a genome other than that of the host will mimic a poorly preserved sample, as only the conserved regions between the two genomes will be covered. Multiple tools of competitive alignments have been used to nuance an a priori identification based on morphoscopical characters (e.g. Harris et al., 2020; Teasdale et al., 2015) but it can limit the use of aDNA as a dedicated method for species identification. This downside can be partly overcome by the implementation of enrichment methods such as targeted or whole genome captures that have proven to be well suited to aDNA and efficient throughout related taxa (e.g. Popović et al., 2020) (fig.1). However, the shotgun approach has also paved the way to whole new lines of investigation such as past health and ancient metagenomics which we will describe further (Lebrasseur, Manin, this volume).

Answering zooarchaeological questions through aDNA

With the ability to consider full ancient mitochondrial genomes and even nearly-complete genomes of the host species, the targets considered by aDNA

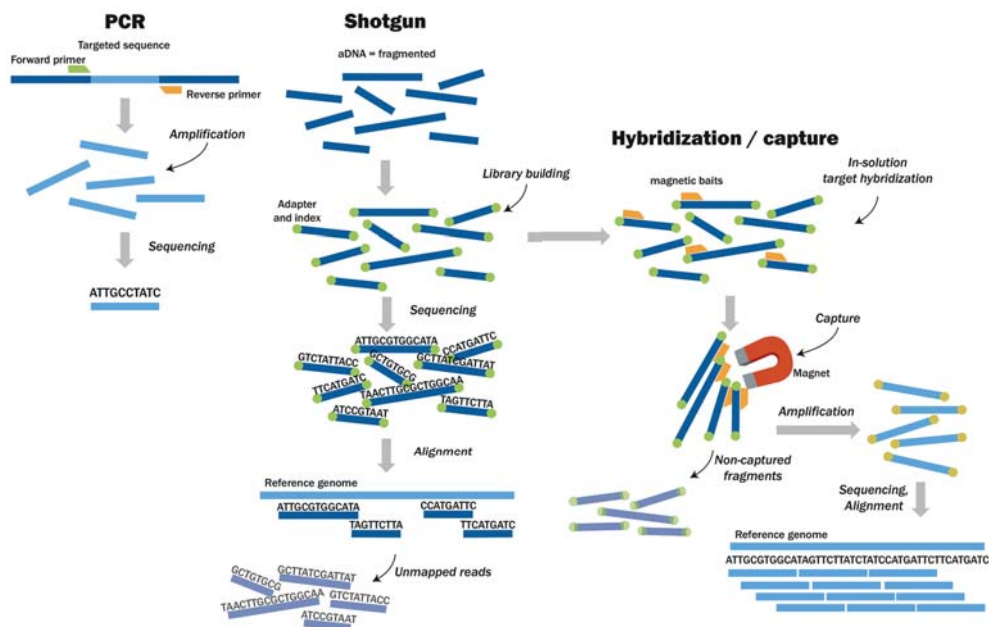


Fig. 1. A description of the three main methods used for the amplification and the sequencing of aDNA (DAO: A. Manin).

Рис. 1. Описание трех основных методов, используемых для амплификации и секвенирования древней ДНК (Абстрактный интерфейс базы данных: А. Манин).

studies have evolved in many directions. Along with the development of NGS, PCR-based approaches and Sanger sequencing are still valuable tools to answer specific questions, such as taxonomic identification, phylogeny and haplogroup attributions. Moreover, it often allows the incorporation of larger comparative datasets, including from regions of the world where DNA preservation is particularly low. There is thus a large set of tools available to question the role of animals and their use at different scales, from the populations to the individuals.

Most of the zooarchaeological applications of aDNA have dealt with domestic animals. Apart from the in-depth analysis of horse, dog, pig, cattle and goat genomes (see review in Frantz et al., 2020), a large range of animals are being investigated, such as sheep (e.g.

Dymova et al., 2017; Rannamäe et al., 2016), reindeer (e.g. Bjørnstad et al., 2012; Rosvold et al., 2019), chickens (Girdland Flink et al., 2014; Lebrasseur et al., paper from this volume), turkeys (e.g. Manin et al., 2018; Speller et al., 2010) or geese (e.g. Heikkinen et al., 2020; Honka et al., 2018). This focus has been encouraged by the extensive analysis of these species for agronomic purposes and their use as models in medical research leading to the availability of numerous comparative genomes and a relatively good understanding of the existing genes, their alleles and what they code for. Several studies have thus been able to reconstruct ancient dogs, horses and pigs coat colour (Linderholm, Larson, 2013; Ludwig et al., 2009; Ollivier et al., 2013), or metabolic changes, such as starch digestion in ancient dogs (Ollivier et al., 2016) and laying productivity in

chickens (Loog et al., 2017), highlighting how fast the animals have adapted to human environment.

Another aspect stemming from genomic analyses is the ability to identify the sex of the animals. Although this element is not often used in archaeological interpretations, it is a powerful tool for constructing culling profiles (Speller, Yang, 2016) and it would gain in being more widely considered.

In contrast, very few studies have been carried out on non-domestic animals. Human-induced translocations have recently been investigated in different parts of the world (e.g. Cucchi et al., 2020; George et al., 2018; Stanton et al., 2016) and it is a promising field to understand animal dispersions. Since the early stages of aDNA, many works have focused on extinct fauna, which have been very helpful in understanding population dynamics preceding their extinction or how they relate to modern species (e.g. Baca et al., 2016; Lynch et al., 2015; Stanton et al., 2020). Very few parallels exist interrogating the population dynamics of extant wild species (but see e.g. Abbona et al., 2019; Heino et al. 2019) although the archaeological

record would be a fantastic reservoir of genomic data to improve our understanding of long-term population dynamics, in particular for endangered species (e.g. Fordham et al., 2020).

Conclusion

In this paper, we presented a short overview of the history of ancient DNA and its applications specifically in regard to answering zooarchaeological questions. Rather than seeking for exhaustivity, we focused on selected practical issues and we hope it will help in promoting dialogue between zooarchaeologists and geneticists in the future. While we focused here on the study of the animals through the aDNA analysis of their bones and teeth, other substrates are available to offer complementary perspectives. Moreover, the development of metagenomic analyses, encompassing all the environmental and microbial genetic material accompanying the host DNA, has opened new lines of investigation into the integration of the animal in its environment. Details on these two elements and their integration in the zooarchaeological context will be the object of another paper (Lebrasseur, Manin, this volume).

REFERENCES

1. Abbona, C., Lebrasseur, O., Johnson, J., Giardina, M., Neme, G., Wolverton, S. 2019. In *Journal of Archaeological Science: Reports* 25, 624–31.
2. Alberti, F., Gonzalez, J., Paijmans, J., Basler, N., Preick, M., Henneberger, K., Trink, A., Rabeder, G., Conrad, N., Münzel, S., Joger, U., Fritsch, G., Hildebrandt, T., Hofreiter, M., Barlow, A. 2018. In *Molecular Ecology Resources* 18 (6), 1196–1208.
3. Baca, M., Popović, D., Stefaniak, K., Marciszak, A., Urbanowski, M., Nadachowski, A., and Mackiewicz, P. 2016. In *Die Naturwissenschaften* 103 (92), 1–17.
4. Binford, L. R. 1978. *Nunamiut ethnoarchaeology*. New York: Academic Press.
5. Bjørnstad, G., Flagstad, Ø., Hufthammer, A. K., Røed, K. H. 2012. In *Journal of Archaeological Science* 39 (1), 102–108.
6. Blaise, E. 2009. *Economie animale et gestion des troupeaux au Néolithique Final en Provence: approche archéozoologique et contribution des analyses isotopiques de l'émail dentaire*. PhD Diss. Aix-en-Provence.
7. Charlton, S., Booth, T., Barnes, I. 2019. In *World Archaeology* 51 (4), 574–585.
8. Cooper, A., Poinar, H. N. 2000. In *Science* 289 (5482), 1139.
9. Cucchi, T., Papayianni, K., Cersoy, S., Aznar-Cormano, L., Zazzo, A., Debruyne, R., Berthon, R., Bălăşescu, A., Simmons, A., Valla, F., Hamilakis, Y., Mavridis, F., Mashkour, M., Darvish, J., Siahsharvi, R., Biglari, F., Petrie, C. A., Weeks, L., Sardari, A., Maziar, S., De-

- nys, C., Orton, D., Jenkins, E., Zeder, M., Searle, J. B., Larson, G., Bonhomme, F., Auffray, J.-C., Vigne, J.-D. 2020. In *Scientific Reports* 10 (1), 8276.
10. Dabney, J., Knapp, M., Glocke, I., Gansauge, M.-T., Weihmann, A., Nickel, B., Valdiosera, C., García, N., Pääbo, S., Arsuaga, J.-L., Meyer, M. 2013. In *Proceedings of the National Academy of Sciences of the United States of America* 110 (39), 15758–15763.
11. Dymova, M. A., Zadorozhny, A. V., Mishukova, O. V., E. A. Khrapov, E. A., Druzhkova, A. S., Trifonov, V. A., Kichigin, I. G., Tishkin, A. A., Grushin, S. P., Filipenko M. L. 2017. In *Animal Genetics* 48 (5), 615–618.
12. Evin, A., Lebrun, R., Durocher, M., Ameen, C., Larson, G., Sykes, N. 2020. In *Royal Society Open Science* 7 (3), 192034.
13. Fordham, D. A., Jackson, S. T., Brown, S. C., Huntley, B., Brook, B. W., Dahl-Jensen, D., Gilbert, M. P. T., Otto-Bliesner, B. L., Svensson, A., Theodoridis, S., Wilmschurt, J. M., Buettel, J. C., Canteri, E., McDowell, M., Orlando, L., Pilowsky, J., Rahbek, C., Nogues-Bravo, D. 2020. In *Science* 369 (6507).
14. Frantz, L. A. F., Bradley, D. G., Larson, G., Orlando, L. 2020. In *Nature Reviews Genetics* 21 (8), 449–460.
15. Geigl, E.-M., Grange, T. 2014. In Patou-Mathis, M., Denys, C. (eds) *Manuel de taphonomie*. Arles: Errance, 147–164.
16. George, R. J., Plog, S., Watson, A. S., Schmidt, K. L., Culetton, B. J., Harper, T. K., Gilman, P. A., LeBlanc, S. A., Amato, G., Whiteley, P., Kistler, L., Kennett, D. J. 2018. In *Proceedings of the National Academy of Sciences of the United States of America* 115 (35), 8740–8745.
17. Girdland Flink, L., Allen, R., Barnett, R., Malmström, H., Peters, J., Eriksson, J., Andersson, L., Dobney, K., Larson, G. 2014. In *Proceedings of the National Academy of Sciences of the United States of America* 111 (17), 6184–6189.
18. Green, R. E., Krause, J., Ptak, S. E., Briggs, A. W., Ronan, M. T., Simons, J. F., Du, L., Egholm, M., Rothberg, J. M., Paunovic, M., Pääbo, S. 2006. In *Nature* 444 (7117), 330–336.
19. Hagelberg, E., Clegg, J. B. 1991. In *Royal Society Proc. B.* 244 (1309), 45–50.
20. Hansen, H. B., Damgaard, P. B., Margaryan, A., Stenderup, J., Lynnerup, N., Willerslev, E., Allentoft, M. E. 2017. In *PLoS One* 12 (1): e0170940.
21. Harris, A. J. T., Feuerborn, T. R., Sinding, M.-H. S., Nottingham, J., Knudsen, R., Rey-Iglesia, A., Schmidt, A. L., Appelt, M., Grønnow, B., Alexander, M., Eriksson, G., Dalén, L., Hansen, A. J., Lidén, K. 2020. In *Journal of Anthropological Archaeology* 59, 101200.
22. Heikkinen, M. E., Ruokonen, M., White, T. A., Alexander, M. M., Gündüz, İ., Dobney, K. M., Aspi, J., Searle, J. B., Pyhäjärvi, T. 2020. *Long-term reciprocal gene flow in wild and domestic geese reveals complex domestication history*. G3.
23. Heino, M. T., Askeyev, İ. V., Shaymuratova, D. N., Askeyev, O. V., Askeyev, A. O., van der Valk, T., Pečnerová, P., Dalén, L., Aspi, J. 2019. In *Archaeology of the Eurasian steppes* 4, 179–190.
24. Higuchi, R., Bowman, B., Freiberger, M., Ryder, O. A., Wilson, A. C. 1984. In *Nature* 312 (5991), 282–284.
25. Hofreiter, M., Jaenicke, V., Serre, D., von Haeseler, A., Pääbo, S. 2001. In *Nucleic Acids Research* 29 (23), 4793–4799.
26. Honka, J., Heino, M. T., Kvist, L., Askeyev, I. V., Shaymuratova, D. N., Askeyev, O. V., Askeyev, A. O., Heikkinen, M. E., Searle, J. B., Aspi, J. 2018. In *Genes* 9 (7).
27. Höss, M., Pääbo, S. 1993. In *Nucleic Acids Research* 21 (16), 3913–3914.
28. Johnson, L. A., Ferris, J. A. J. 2002. In *Forensic Science International* 126 (1), 43–47.
29. Kistler, L., Ware, R., Smith, O., Collins, M., Allaby, R. G. 2017. In *Nucleic Acids Research* 45 (11), 6310–6320.
30. Knapp, M., Hofreiter, M. 2010. In *Genes* 1 (2), 227–243.
31. Lebrasseur, O., Ryan, H., Abbona, C. 2018. In Pişkin, E., Marciniak, A., Bartkowiak, M. (eds), *Environmental archaeology: current theoretical and methodological approaches*, Cham: Springer International Publishing.
32. Linderholm, A. 2016. In *Biological Journal of the Linnean Society* 117, 150–160.
33. Linderholm, A., Larson, G. 2013. In *Seminars in Cell & Developmental Biology* 24 (6–7), 587–593.
34. Loog, L., Thomas, M. G., Barnett, R., Allen, R., Sykes, N., Paxinos, P. D., Lebrasseur, O., Dobney, K., Peters, J., Manica, A., Larson, G., Eriksson, A. 2017. In *Molecular Biology and Evolution* 34 (8), 1981–1990.

35. Ludwig, A., Pruvost, M., Reissmann, M., Benecke, N., Brockmann, G. A., Castaños, P., Cieslak, M., Lippold, S., Llorente, L., Malaspinas, A.-S., Slatkin, M., Hofreiter, M. 2009. In *Science* 324 (5926), 485.
36. Lupo, K. D. 2006. In *Journal of Archaeological Method and Theory* 13 (1), 19–66.
37. Lynch, V. J., Bedoya-Reina, O. C., Ratan, A., Sulak, M., Drautz-Moses, D. I., Perry, G. H., Miller, W., Schuster, S. C. 2015. In *Cell Reports* 12 (2), 217–228.
38. Manin, A., Corona-Manrique, E., Alexander, M., Craig, A., Thornton, E. K., Yang, D. Y., Richards, M., Speller, C. F. 2018. In *Royal Society Open Science* 5 (1), 171613.
39. Mardis, E. R. 2008. In *Trends in Genetics* 24 (3), 133–141.
40. Ollivier, M., Tresset, A., Bastian, F., Lagoutte, L., Axelsson, E., Arendt, M.-L., Bălăşescu, A., Mashkour, M., Sablin, M. V., Salanova, L., Vigne, J.-D., Hitte, C., Hänni, C. 2016. In *Royal Society Open Science* 3 (11), 160449.
41. Ollivier, M., Tresset, A., Hitte, C., Petit, C., Hughes, S., Gillet, B., Duffraisse, M., Pionnier-Capitan, M., Lagoutte, L., Arbogast, R.-M., Bălăşescu, A., Boroneant, A., Mashkour, M., Vigne, J.-D., Hänni, C. 2013. In *PloS One* 8 (10).
42. Pálsdóttir, A. H., Bläuer, A., Rannamäe, E., Boessenkool, S., Hallsson, J. H. 2019. In *Royal Society Open Science*. 6, 191059.
43. Pinhasi, R., Fernandes, D., Sirak, K., Novak, M., Connell, S., Alpaslan-Roodenberg, S., Gerritsen, F., Moiseyev, V., Gromov, A., Raczky, P., Anders, A., Pietrusewsky, M., Rollefson, G., Jovanovic, M., Trinhhoang, H., Bar-Oz, G., Oxenham, M., Matsumura, H., Hofreiter, M. 2015. In *PloS One* 10 (6): e0129102.
44. Poinar, H. N., Schwarz, C., Qi, J., Shapiro, B., MacPhee, R. D. E., Buigues, B., Tikhonov, A., Huson, D. H., Tomsho, L. P., Auch, A., Rampp, M., Miller, W., Schuster, S. C. 2006. In *Science* 311 (5759), 392–394.
45. Popović, D., Mendoza España, V., Ziółkowski, M., Weglenski, P., Baca, M. 2020. In *Journal of Archaeological Science: Reports* 31, 102273.
46. Rannamäe, E., Lõugas, L., Niemi, M., Kantanen, J., Maldre, L., Kadõrova, N., Saarma, U. 2016. In *Animal Genetics* 47 (2), 208–218.
47. Rosvold, J., Hansen, G., Røed, K. H. 2019. In *Journal of Archaeological Science: Reports* 26, 101860.
48. Saiki, R. K., Gelfand, D. H., Stoffel, S., Scharf, S. J., Higuchi, R., Horn, G. T., Mullis, K. B., Erlich, H. A. 1988. In *Science* 239 (4839), 487–491.
49. Sanger, F., Coulson, A. R. 1975. In *Journal of Molecular Biology* 94 (3), 441–448.
50. Schroeder, H., Damgaard, P. B., Allentoft, M. E. 2019. In *Methods in Molecular Biology* 1963, 21–24.
51. Shved, N., Haas, C., Papageorgopoulou, C., Akguel, G., Paulsen, K., Bouwman, A., Warinner, C., Rühli, F. 2014. In *PloS One* 9 (10): e110753.
52. Sierra, A., Bréhard, S., Montes, L., Utrilla, P., Saña, M. 2019. In *Archaeological and Anthropological Sciences* 11, 5813–5829.
53. Sirak, K. A., and Sedig, J. W. 2019. In *World Archaeology* 51 (4), 560–573.
54. Smith, C. I., Chamberlain, A. T., Riley, M. S., Stringer, C., Collins, M. J. 2003. In *Journal of Human Evolution* 45 (3), 203–217.
55. Sosa, C., Vispe, E., Núñez, C., Baeta, M., Casalod, Y., Bolea, M., Hedges, R. E. M., Martínez-Jarreta, B. 2013. In *American Journal of Physical Anthropology* 151 (1), 102–109.
56. Speller, C. F., Kemp, B. M., Wyatt, S. D., Monroe, C., Lipe, W. D., Arndt, U. M., Yang, D. Y. 2010. In *Proceedings of the National Academy of Sciences of the United States of America* 107 (7), 2807–2812.
57. Speller, C. F., Yang, D. Y. 2016. In *Journal of Archaeological Science: Reports* 10, 520–525.
58. Stanton, D. W. G., Alberti, F., Plotnikov, V., Androsov, S., Grigoriev, S., Fedorov, S., Kosintsev, P., Nagel, D., Vartanyan, S., Barnes, I., Barnett, R., Ersmark, E., Döppes, D., Germonpré, M., Hofreiter, M., Rosendhal, W., Skoglund, P., Dalén, L. 2020. In *Scientific Reports* 10 (1), 12621.
59. Stanton, D. W. G., Mulville, J. A., Bruford, M. W. 2016. In *Royal Society Publishing. Proceedings B* 283 (1828), 20160095.
60. Teasdale, M. D., van Doorn, N. L., Fiddyment, S., Webb, C. C., O'Connor, T., Hofreiter, M., Collins, M. J., Bradley, D. G. 2015. In *Royal Society Publishing. Proceedings B* 370 (1660), 20130379.
61. Thornton, E. K. 2011. In *Journal of Archaeological Science* 38 (12), 3254–3263.

62. Wales, N., Carøe, C., Sandoval-Velasco, M., Gamba, C., Barnett, R., Samaniego, J. A., Ramos Madrigal, J., Orlando, L., Gilbert, M. T. P. 2018. In *BioTechniques* 59 (6), 368–371.

63. Yang, D. Y., Eng, B., Waye, J. S., Dudar, J. C., Saunders, S. R. 1998. In *American Journal of Physical Anthropology* 105 (4): 539–543.

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ЗООАРХЕОЛОГИЯ И ДРЕВНЯЯ ДНК, ЧАСТЬ 1: КРАТКИЙ ОБЗОР МЕТОДОВ И ПРИМЕНЕНИЙ

Аурелия Манин, Офелия Лебрассер

Анализ древней ДНК (аДНК) из археологических остатков животных хорошо подходит для многих целей, исследуемых с помощью зооархеологических анализов. Эта статья направлена на представление области палеогеномики, особенно в ее приложении к зооархеологическим вопросам. Хотя статья не претендует на полноту, она сосредоточена на практических вопросах, способствуя продвижению трансдисциплинарного диалога. Авторы дают описание природы аДНК и основных тафономических путей, ведущих к ее дифференциальной сохранности. Затем предлагаются краткий исторический обзор методов аДНК, начиная с первых открытий в 1984–1985 годах до появления секвенирования следующего поколения и подходов высокопроизводительного секвенирования в начале 21 века. Авторами описываются основные проблемы исследований аДНК в последние годы, так как решение этих проблем должно быть адаптировано к новому диапазону методов и должно оказать влияние на изучение остатков животных. Наконец, авторами выделяются основные результаты применения аДНК в будущих направлениях исследований, которые могут быть осуществлены для описания животных и их популяций.

Ключевые слова: зооархеология, палеогеномика, доместикация, транслокация, биоразнообразие, древнее ДНК.

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Статья принята в номер 01.12.2020 г.

Исследования А. Манин финансированы за счет стандартного гранта Совета по исследованию окружающей среды (NE/S00078X/1). Исследования О. Лебрассер профинансированы Фондом исследования глобальных проблем Единой региональной сети здравоохранения для стран Африканского Рога (HORN), возглавляемой Ливерпульским университетом (Великобритания) в рамках программы "Исследования и инновации и Исследовательского совета по биотехнологиям и биологическим наукам" (номер проекта ВВ/P027954/1).