

ANCIENT DNA'S IMPACT ON ARCHAEOLOGY: WHAT HAS BEEN LEARNED AND HOW TO BUILD STRONG RELATIONSHIPS

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Note: This article contains images of non-indigenous skeletal material.

In this article I discuss how ancient DNA (aDNA) has the potential to provide powerful new insights into humanity's past. It may seem odd for such comments to come from someone who considers himself an American Southwest archaeologist; however, my role in the Reich Laboratory of Medical and Population Genetics as a liaison between geneticists and archaeologists has allowed me to critically examine the relationship between these two fields and to explore how they work together.

The Power of aDNA

Perhaps the most well-known example of the power of aDNA involves ancient hominins. As is likely the case for many readers of this piece, I initially learned of aDNA's capabilities with the publication of the Neanderthal genome. The ability to recover aDNA from a Neanderthal was astounding in and of itself, but these data also confirmed that Neanderthals and modern humans interbred. Possibly even more astonishing was the discovery of a new group of hominins (Denisovans) from a single finger-bone. These were incredible findings, but they also felt remote. Ancient DNA seemed confined to paleo-anthropological research and not directly relevant to my own archaeological research interests. It soon became apparent, though, that aDNA would permeate archaeology.

Data from a few ancient hominins demonstrated how aDNA can reshape our understanding of human history at the global scale. Once archaic genomes were decoded, it became possible to identify segments of them in modern populations. Researchers discovered that Neanderthal and Denisovan DNA is virtually absent in sub-Saharan African populations, highest in Australo-Papuan populations, and intermediate in European, East Asian, and Native American groups (Reich 2018). The presence of archaic genome segments in non-Africans is interesting in

its own right, but also constrains possible scenarios for the history of the peopling of particular regions. For example, since modern Australian Aborigines have Denisovan/Neanderthal DNA, these populations must have arrived in Australia after intermixing occurred, which is genetically dated to 54–49kya for the Neanderthal admixture and 49–44kya for the Denisovan admixture (Reich 2018). Yet some archaeological studies (Clarkson et al. 2017) claim evidence of human occupation in Australia by at least 65kya, meaning that if the 65kya dates are indeed accurate and correspond to human settlements, then they must reflect people who contributed little if anything to present-day Australian Aborigines. This discrepancy has yet to be resolved, but it is clear that future research into the initial populating of Australia must take aDNA data into consideration.

In addition, aDNA studies in both Remote Oceania and the Americas have demonstrated that there was no single "founding event" from which modern groups solely derive their ancestry. Ancient DNA has revealed that the first inhabitants of Remote Oceania, associated with the Lapita archaeological culture, were almost entirely of mainland East Asian/Taiwan aboriginal related ancestry, and later mixed with groups carrying Papuan ancestry (Lipson et al. 2018a; Skoglund et al. 2016). In the Americas, aDNA from an ~12,600-year-old infant skeleton in Montana (Anzick-1) was found to be more similar to modern-day Central and South American populations (Rasmussen et al. 2014) than to northern North American groups (Cree, Ojibwa, and Algonquin), which suggests that northern-southern lineage population structure in the Americas is at least as old as the Anzick-1 infant. An additional unexpected discovery is that some present-day Amazonian groups have significant genetic similarities to Australo-Papuans and Andaman Islanders (Skoglund and Reich 2016), as well as to a Paleolithic Chinese individual dating to ~40,000 years ago (Yang et al. 2017), a pattern that can only be explained by a genetically diverse

population contributing to the ancestors of present-day South Americans (multiple pulses of movement from Asia). Potential evidence of this “population Y” was only recently found in very ancient individuals (approximately 10,400–9,800 BP) from Lagoa Santa, Brazil (Moreno-Mayer et al. 2018). However, this signal has yet to be found in any other more recent samples, and thus serves as a good example of how genetic data can generate new testable hypotheses.

The power of aDNA is not limited to examinations of the spread of *Homo sapiens* into previously uninhabited areas. Ancient DNA can also shed light on the transformations of specific archaeological cultures through time. One of the starkest examples of this was the virtually complete replacement of English Neolithic farmers by mainland Europeans associated with the Bell Beaker archaeological culture around 2000 BC (Olalde et al. 2018). Ancient DNA has also helped elucidate the spread of farming populations into Europe and southeast Asia (Haak et al. 2015; Lipson et al. 2018b). In each of these instances there is robust genetic evidence of previously distinct local groups mixing with incoming agricultural and/or pastoralist groups.

Such genetic insights add nuance to the archaeological record and can be used to reassess assumptions engrained in archaeology. Pots don't equal people, but aDNA at least allows researchers to examine if the efflorescence of a new type of pottery (or any cultural practice) correlates with the arrival of a new group of people. Ancient populations were not static; people moved, migrated, and interacted with one another constantly. With very little variation, modern groups in a particular area or region are genetically different from the people who lived there one thousand years ago. Thus, we must think of archaeological cultures as fluid, not as homogeneous entities bounded by time and geography.

Although some of the most notable aDNA research has elucidated global- or continental-scale transformations, ancient genomes can be just as powerful for addressing regional or site-specific archaeological questions. Y chromosome and mitochondrial DNA haplogroups, genetically inferred sex, and proportions of ancestry from divergent source populations are all data that are normally generated during aDNA analysis and can be very informative for specific archaeological questions. These data can be used to identify relatives and/or familial lineages at particular sites or in particular regions. Hundreds of first- and second-degree relatives have been identified in data analyzed at the Reich Laboratory. In some instances, we have been able to identify related individuals from sites kilometers apart, such as an English Bell Beaker-associated father-daughter pair (Olalde et al. 2018). There was no prior archaeological indication that these individuals were related—in fact, archaeologists had initially assessed the father-daughter as being from two different

archaeological cultures. Such examples from aDNA demonstrate the truly arbitrary nature of archaeological boundaries. These two individuals, from different sites, previously seemed like bounded, discrete entities. Yet when we consider them as father-daughter, these boundaries melt away.

Combining aDNA with isotopic and archaeological data also allows archaeologists to examine social organization in more detail than ever before. For example, data could be used to determine if individuals from certain room blocks or neighborhoods at a particular site were closely related to each other, or if social organization was more heterogeneous. It could also be used to determine if particular familial lineages had more power than others. Archaeologists can produce rich life-histories for individuals and should now be able to determine if a person lived and died in the same place, who their closest relatives were, what they ate, and multiple other fine-grained details.

A study conducted by Corina Knipper and colleagues (2017) is an excellent example of how multiple techniques can be combined to create new insight into the social organization of a particular place. Using isotopic, genetic, and archaeological data from 84 Late Neolithic Bell Beaker and early Bronze Age individuals of Germany's Lecht Valley, researchers were able to determine that the majority of adult females were non-locals (whereas males and juveniles were locals), that local individuals tended to share mtDNA haplogroups while the mtDNA haplogroups of non-locals were heterogeneous, that non-locals were buried similarly to locals, and that non-local females arrived around the age of 16. Knipper and colleagues used these findings to argue that inhabitants of these Lecht Valley sites practiced a patrilineal residential system with female exogamy. While studies of whether particular groups were patrilineal, matrilineal, exogamous, etc., certainly are not new to archaeology and have been examined without aDNA, at the very least, aDNA can help confirm or deny previous hypotheses. As the work by Knipper and colleagues demonstrates, however, combining aDNA with other techniques can provide powerful new understandings of ancient social practices.

Explaining aDNA Practices

The explosive growth of research in aDNA over the last few years (Figure 1) has been extraordinarily exciting, but it has also justifiably created some anxiety. As an archaeologist embedded in one of the world's most active aDNA laboratories, I would like to speak to some concerns and explain some aDNA practices so that readers can better understand how aDNA laboratories operate and how aDNA research is conducted.

Any insights gained from aDNA undeniably come at a price—a price that is by no means solely financial. Perhaps

BONES AND CHROMOSOMES: THE ANCIENT DNA REVOLUTION IN ARCHAEOLOGY (PART 1)

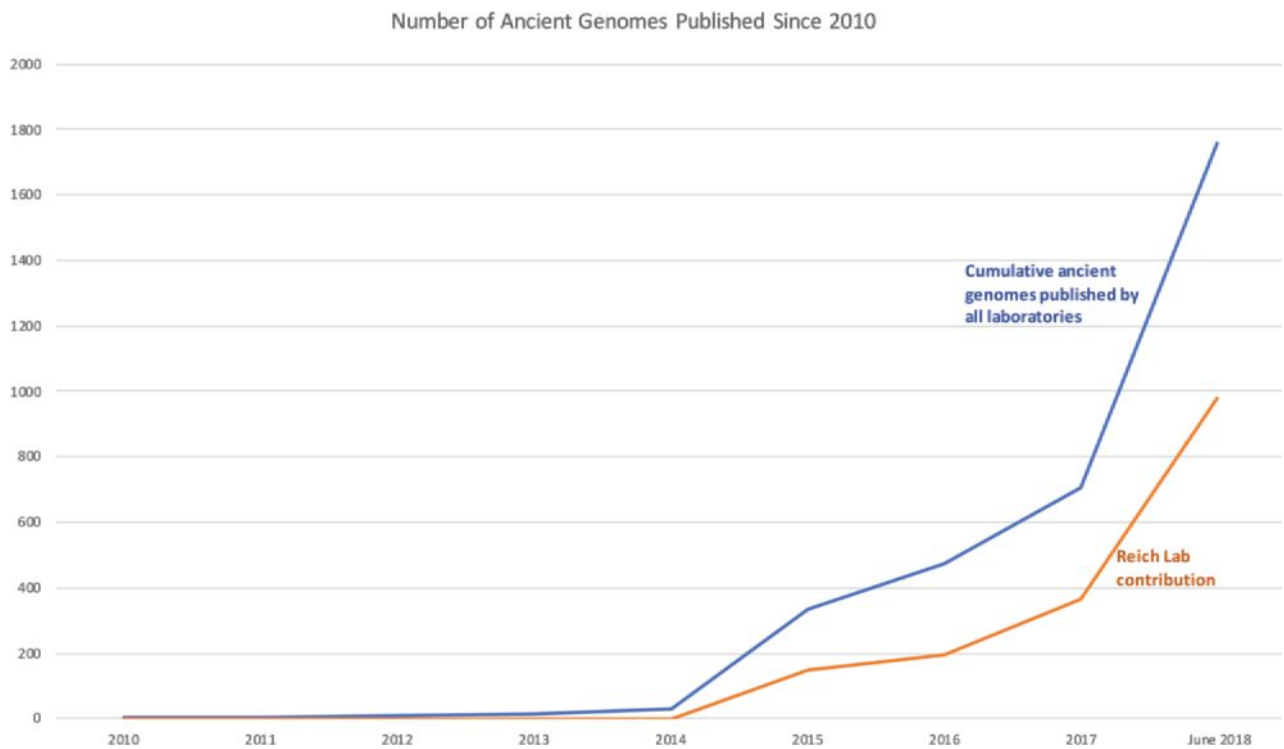


Figure 1. Number of ancient genomes published since 2010.

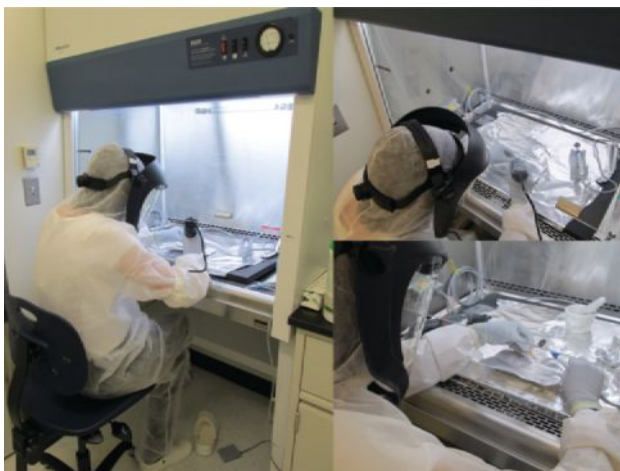


Figure 2. Reich Laboratory technician processing a tooth for aDNA.



Figure 3. Petrosal portion of temporal bone prior to processing. The Reich Laboratory uses a "sandblaster," pictured here, to extract the cochlea.

the most obvious is the conversion of skeletal elements into powder from which aDNA is then extracted (Figure 2). While destructive analysis is required for various biomolecular techniques (e.g., radiocarbon dating and isotopic analysis), much of the trepidation surrounding aDNA largely stems from the processing of the petrosal portion of the temporal bone to access and obtain aDNA from the cochlea (Figure 3). Studies have demonstrated that cochlea

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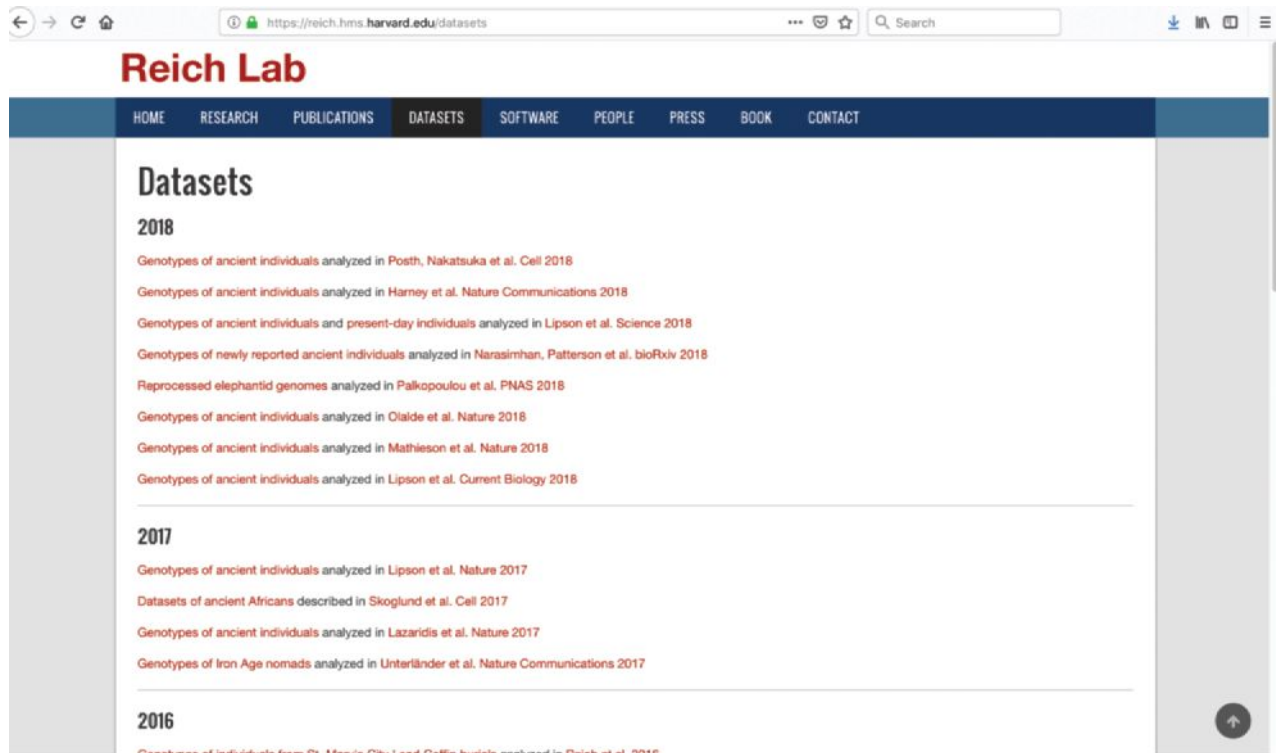


Figure 4. Image from the Reich Laboratory website where published genomic data are open access (<https://reich.hms.harvard.edu/datasets>).

yield up to 100x more endogenous human DNA per unit of powder than other skeletal elements (Gamba et al. 2014; Pinhasi et al. 2015). This has allowed for the acquisition of aDNA from archaeological contexts which were previously virtually unobtainable (particularly in hot, humid regions), and for a higher overall acquisition success rate. Since each person has only two petrous/cochlea, these are much rarer than some other skeletal elements (like ribs or teeth) and destructive analysis is therefore more impactful. Yet the amount and quality of aDNA data that can be recovered from the petrous/cochlea often justifies destructive analysis of this element.

The focus on the petrous/cochlea, along with the exponentially increasing number of aDNA studies, has led to concerns about destructive sampling of these skeletal elements. Ancient DNA labs should take every measure to ensure that destructive analysis is as slight as possible, and we endeavor to do that in the Reich Laboratory. Methods are constantly being refined to minimize destructive impact. We also try, where possible, to analyze individuals who have both petrous/cochlea present, so that one can remain morphologically intact.

A complementary concern that I have seen expressed involves data access. This issue certainly is not limited to aDNA; open access publications, online public databases, and article pre-prints are just a few indicators that sharing of data has become an integral aspect of scholarly work. Regarding aDNA specifically, I have heard archaeologists express worry that genetic data will be kept from them and that skeletal samples will be locked up in aDNA labs, making the samples inaccessible to other archaeologists or paleoanthropologists. Speaking from my experience, however, this is an area where I believe that archaeologists should have few concerns. The aDNA community has extremely high standards of data sharing, and researchers in this community share all data through open access third-party databases as a condition of publication (Figure 4). In fact, gaining access to aDNA data often seems easier than archaeological data, which can be buried in “gray literature,” remain unpublished for decades in incomplete site reports, or is sometimes inaccessible for independent examination even after publication.

There is also a concern that, at this point, most of the world's aDNA data have been produced by a handful of laboratories; for example, about half the world's published human aDNA

data (measured by the number of samples with genome-scale data) have been published by the Reich Laboratory (see Figure 1). It is important that laboratories in this field do not hold skeletal samples longer than is needed to queue and process them. In the Reich Laboratory, we aim to process any skeletal elements we receive and return them to the archaeologists or anthropologists who shared them with us within a year of receipt. This was an aspiration until recently, but it is now a goal that we are achieving for most samples that we process.

Another feature of aDNA research that archaeologists may find odd is that there are (currently) no for-fee service aDNA labs, and thus the laboratory relationships that archaeologists are familiar with (e.g., radiocarbon laboratories) are not the right models. Some of the misunderstandings between archaeologists and aDNA laboratories may stem from this. Similar to for-fee chronometric laboratories, aDNA technicians and analysts process samples provided by archaeologists, and therefore should expediently report those results to them. However, aDNA labs have their own research programs to which the samples they are studying need to contribute, and are not just providing a service to archaeologists. Geneticists in aDNA labs tend to be most interested in population-level research questions that span vast geographic regions and segments of time, whereas the data and results archaeologists most often request from laboratories focus on particular individuals, features, or sites. Thus, archaeologists should expect the collaborations formed with aDNA labs to be atypical of collaborations with other for-fee laboratories, and the goal should be to work with geneticists to generate papers that produce findings of interest to both communities. I have seen multiple positive examples of these kinds of outcomes during my time in the Reich Laboratory.

Concerns with aDNA Analysis

As aDNA studies have become more common, archaeologists have also raised broader questions about the limits of what aDNA can tell us about the past and how data can be applied to the archaeological record; such discussion is absolutely necessary to advance the field.

Some of the most pointed critiques of aDNA, especially from archaeologists who work in Eurasia, have focused on studies that find evidence of migration and significant population transformations over time. Many of these critiques about aDNA and migration have previously been addressed and discussed in public forums, especially European archaeological journals (Furholt 2017; Johannsen et al. 2017; Klejn et al. 2017), but it is valuable to briefly summarize the discussions here. Some archaeologists have argued that it is inappropriate to make strong claims with relatively few samples—data from

a few individuals within a particular archaeological culture are seemingly used to represent everyone from that time and place. Concerns about low sample sizes have been ameliorated, however, as aDNA data from tens or even hundreds of individuals are now examined for regional/continental-scale studies. Other archaeological concerns center on the idea of migration in general. “Migration” was heavily critiqued within archaeology in the 1970s–1990s. During that time, archaeologists became focused on the small-scale and deconstructed the idea that shared material culture represented homogeneous social entities. An obviously related concern is that aDNA studies attempt to link specific archaeological cultures with biological populations. Thus, it may seem that aDNA researchers are chasing the ghosts of archaeology’s past by studying migration, and that aDNA is removing nuance from the archaeological record.

While the field of archaeology may have moved away from migration, the population-level questions geneticists and aDNA analysts address should not be constrained by archaeological theoretical trends. Data cannot be ignored simply because it does not fit *en vogue* theories. However, I do not mean to flip-pantly dismiss archaeological data in favor of aDNA—aDNA alone cannot answer all the questions in which archaeologists are usually most interested. Returning to the English Neolithic-Bell Beaker replacement example, although it is evident genetically that dramatic population replacement occurred, *why* this happened cannot be answered solely with aDNA. Did Neolithic Britons welcome continental Bell Beakers with open arms? Or were the Britons brutally subdued? “Typical” conquest—marauding groups of males killing local adult males and claiming women as their slaves, captives, and wives—seems unlikely, since both Y and mtDNA haplogroups were replaced, but this cannot be ruled out entirely through genetics. Indeed, with this new genetic evidence, archaeologists can reevaluate previous archaeological findings for unnoticed or understudied aspects of the material record that may relate to this replacement. Archaeologists and geneticists therefore must collaborate so that results in both fields can be synthesized.

Another concern that has been articulated regarding aDNA stems from the fact that most of the work in this field has been carried out by European and American researchers, and that aDNA studies of European cultures far outnumber those from the rest of the world (Marciniak and Perry 2017; Prendergast and Sawchuk 2018). This asymmetry largely reflects the fact that it is in Europe where most of the aDNA technology was invented, and it is in Europe where some of the best-preserved skeletal samples are available for research; the field is so new that most of the studies have remained focused on European contexts based on sample sets collected several

years ago. Laboratories, including the one in which I work, increasingly include researchers and samples from non-European contexts, but the imbalances are far from rectified, and addressing these issues will be an important challenge for the aDNA field to solve over the coming years.

Engagement and outreach with indigenous communities is a particular issue in aDNA that needs to be given special consideration and should be an integral aspect of research (Bardill et al. 2018). The question of how best to conduct outreach with indigenous communities—especially when samples cannot be connected in a clear way to any living group—is a challenge, and there is not yet a clear consensus about how best to do it. Studies in the last few years have addressed these issues through approaches ranging from direct and repeated engagements between geneticists and large numbers of local tribal groups, to no direct engagements at the request of museums that felt that any decision to conduct outreach should be entirely directed by the museums that hold the collections (Kennett et al. 2017; Rasmussen et al. 2011; Rasmussen et al. 2014; Rasmussen et al. 2015). It is increasingly clear that some direct engagement between geneticists and indigenous peoples should happen, and aDNA projects do appear to be taking engagement more seriously, as demonstrated by two recent publications on the spread of humans through the Americas (Moreno-Mayer et al. 2018; Posth et al. 2018; see also Malaspina et al. 2016; Scheib et al. 2018; Tobler et al. 2017). Yet continued engagement is necessary—for example, even if a study meets the letter of the law for the Native American Graves Protection and Repatriation Act, that law has not yet had time to catch up to community practice and expectations. The range of reasonable solutions is still being explored and is an issue we all need to work on collaboratively over the coming years.

Conclusion

While some major differences in approaches exist between archaeologists and aDNA specialists, it is incumbent on archaeologists and geneticists to find a shared language that allows them to work together with shared values. Ancient DNA is most powerful when hundreds of individuals from multiple time periods, sites, and regions can be studied in synthesis—this is the population level at which geneticists work. However, this large, population-level scale is not what many archaeologists are accustomed to. Archaeologists, including myself, often research a particular site, or particular features at a site. Thus, researchers on both sides need to better appreciate the different approaches and research questions addressed by the respective fields.

To help ameliorate any tensions, more open communication between archaeologists and geneticists is needed. Fortunately,

efforts to build bridges between genetics and archaeology are occurring more regularly. Along with this issue, there was an excellent SAA Online Seminar on aDNA in December 2017 led by Drs. Christina Warinner and Courtney Hofman, and there is a growing number of aDNA symposia at archaeology and genetic conferences. It is also important to carry out more student training—students interested in population genetics must learn about ancient cultures and about how archaeologists interpret the past, and aDNA research methods must be incorporated into archaeology classes.

Keeping up with the speed of aDNA research can be overwhelming. Some of the research mentioned in this issue will undoubtedly be out of date by the time of publication. Ancient DNA is rapidly revolutionizing what we know about the past, from the spread of our hominin ancestors, to the social organization of specific archaeological groups. As with other technologies that have revolutionized the field (e.g., radiocarbon dating, GIS analysis, LiDAR), it seems likely that future generations will find it difficult to imagine a time when aDNA wasn't an integral part of archaeological research.

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