

OLLI 497: Ancient DNA

Session 5: October 26th

Summary and Observations

Chapter 5: The Making of Modern Europe

Strange Sardinia

Reich begins with a description of some of the studies comparing the DNA of ancient European hunter-gatherers with early farmers of Europe. These studies showed substantial differences between them, but surprisingly the ancient farmers seem to have a link to Sardinia.

First a study of mtDNA: “Nearly all ancient hunter-gatherers carried one set of mitochondrial DNA types. But the farmers who succeeded them carried no more than a few percent of those types, and their DNA was more similar to that seen today in southern Europe and the Near East. It was clear that the farmers came from a population that did not descend from European hunter-gatherers.”

Going beyond mtDNA, “... the whole-genome studies that followed delivered strange results. In 2012, a team of geneticists sequenced the genome of the “Iceman,” a natural mummy dating to approximately fifty-three hundred years ago.” Reich goes on to describe Otzi and the analyses done. There was a big surprise. “... the ancient DNA data showed that his closest genetic relatives are not present-day Alpine people. Instead, his closest relatives today are the people of **Sardinia**, an island in the Mediterranean Sea.”

Another Sardinia surprise: “In the same year that the Iceman’s genome was published, Pontus Skoglund, Mattias Jakobsson, and colleagues at the University of Uppsala published four genome sequences from individuals who lived about five thousand years ago in Sweden.... Instead of being genetically close to each other, the farmers and hunter-gatherers were almost as different from each other as Europeans are from East Asians today. And the farmers once again had that strange link to **Sardinians**.”

“Skoglund and Jakobsson proposed a new model to explain these findings—that migrating farmers whose ancestors originated in the Near East spread over Europe with **little mixture** with the hunter-gatherers they encountered along the way, a sharp contrast to Luca Cavalli-Sforza’s model for the farming expansion into Europe that had been popular until this time and that emphasized extensive mixture and interaction with the local hunter-gatherers during the expansion.” Reich goes on to show how this model would also explain the link to Sardinia “But Skoglund and Jakobsson also went further and proposed that these two sources—hunter-gatherers and farmers—might have contributed almost all the ancestry of Europeans living today. Here they missed something extraordinarily important.”

A Cloud on the Horizon

Reich begins by reminding us of his and Nick Patterson’s discovery of a ghost population, the Ancient North Eurasians, who contributed to the populations of both Northern Europeans and Native Americans. He asks: “How could the finding of an Ancient North Eurasian contribution to present-day northern Europeans be reconciled with the two-way mixture of indigenous European hunter-gatherers and incoming farmers from Anatolia that had been directly demonstrated through ancient DNA studies?” He points to additional ancient DNA studies

OLLI 497: Ancient DNA

which supported the two-way mixture. How to defend the influence of the Ancient Northern Eurasian? “Something profound must have happened later—a new stream of migrants must have arrived, introducing Ancient North Eurasian ancestry and transforming Europe.”

In 2024-15, data from more than two hundred ancient European DNA samples were published. This led to the solution of how Ancient Northern Eurasian ancestry entered Europe. “Our initial approach was to carry out a principal component analysis, which can identify combinations of mutation frequencies that are most efficient at finding differences among samples.” Reich offers further details on the analysis. The result: “On the scatterplot we obtained for close to eight hundred **present-day West Eurasians**, two parallel lines appeared: the left containing almost all Europeans, and the right containing almost all Near Easterners, with a striking gap in between. By placing all the ancient samples onto the same plot, we could watch their positions shift over time, and the last eight thousand years of European history unfurled before our eyes, offering a time-lapse video showing how present-day Europeans formed from populations that had little resemblance in their ancestry to most Europeans living today.”

Without going into a lot of detail, Reich’s analysis showed that:

- After 14,000 YA, hunter-gatherers contributed some ancestry to present-day Europeans, but not to present-day Near Easterners.
- Between 8800 and 4500 YA, ancient farmers migrated from Anatolia and spread across southern Europe to Iberia, and then north to Germany. They retained 90% of their DNA derived from that ancestral source; they mixed minimally with the hunter-gatherers they encountered.
- Between 6000 and 4500 YA, there was a shift in farmers DNA to a 20% hunter-gatherer ancestry, indicating some mixing between the previously established populations.

Given the fact of so little intermixing, Reich asks: “How did the farming and hunter-gatherer cultures coexist? Hints come from the Funnel Beaker culture, which is named for decorated clay vessels in graves dated after about sixty-three hundred years ago. The Funnel Beaker culture arose in a belt of land a few hundred kilometers from the Baltic Sea, which was not reached by the first wave of farmers, probably because their methods were not optimized for the heavy soils of northern Europe.” This meant that these northern hunter-gatherers had more than a thousand years to adapt to the challenge of farming, while keeping much of their hunter-gatherer ways. In addition: “The people of the Funnel Beaker culture were among those who built megaliths, the collective burial tombs made of stones so large it would have taken dozens of people to move them.” But, new waves of migration proved difficult to resist: “The genetic data may bear witness to this interaction, as there was clearly a stream of new migrants into the mixed population. Between six thousand and five thousand years ago, most of the northern gene pool was overtaken by farmer ancestry, and it was this mixture of a modest amount of hunter-gatherer-related ancestry and a large amount of Anatolian farmer-related ancestry—in a population that retained key elements of hunter-gatherer culture—that characterized the Funnel Beaker potters and many other contemporary Europeans.”

Reich sums up this period: “Europe had reached **a new equilibrium**. The unmixed hunter-gatherers were disappearing, persisting only in isolated pockets like the islands off southern Sweden. In southeastern Europe, a settled farmer population had developed the most socially stratified societies known up until that time, and rituals that as the archaeologist Marija Gimbutas showed featured women in a central way—a far cry from the male-centered rituals that followed. In remote Britain, the megalith builders were hard at work on what developed into the greatest man-made monument the world had seen: the standing stones of Stonehenge, which became a national place of pilgrimage as reflected by goods brought from the far corners of Britain. People like those at Stonehenge were building great temples to their gods, and tombs for their dead, and could not have known that within a few hundred years

OLLI 497: Ancient DNA

their descendants would be gone and their lands overrun. The extraordinary fact that emerges from ancient DNA is that just five thousand years ago, the people who are now the primary ancestors of all extant northern Europeans **had not yet arrived.**”

The Tide From the East

Reich begins by describing the situation on the steppes around 5000 YA. The peoples of the steppes lived close to rivers and other sources of water, giving rise to a hodgepodge of local cultures. “All this changed with the emergence of the Yamnaya culture around five thousand years ago, whose economy was based on sheep and cattle herding. The Yamnaya emerged from previous cultures of the steppe and its periphery and exploited the steppe resources far more effectively than their predecessors. They spread over a vast region, from Hungary in Europe to the foothills of the Altai Mountains in central Asia, and in many places **replaced** the disparate cultures that had preceded them with a more homogeneous way of life.”

“One of the inventions that drove the spread of the Yamnaya was the wheel, whose geographic origin is not known because once it appeared—at least a few hundred years before the rise of the Yamnaya—it spread across Eurasia like wildfire.... for the people of the steppe, ... it made possible an economy and culture that were entirely new. By hitching their animals to wagons, the Yamnaya could take water and supplies with them into the open steppe and exploit the vast lands that had previously been inaccessible. By taking advantage of another innovation—the horse, which had recently been domesticated in a more eastern part of the steppe,... the Yamnaya also became vastly more productive.”

“The increase in the intensity of the human use of the steppe lands coincided with a nearly complete disappearance of permanent settlements—almost all the structures that the Yamnaya left behind were graves, huge mounds of earth called kurgans.... The wheel and horse so profoundly altered the economy that they led to the abandonment of village life. People lived **on the move**, in ancient versions of mobile homes.”

Reich recounts the disagreement that arose among archaeologists about the spread of Yamnaya culture through mass migration. “Our analysis of DNA from the Yamnaya—led by Iosif Lazaridis in my laboratory—showed that they harbored a combination of ancestries that did not previously exist in central Europe. The Yamnaya were the missing ingredient, carrying exactly the type of ancestry that needed to be added to early European farmers and hunter-gatherers to produce populations with the mixture of ancestries observed in Europe today. Our ancient DNA data also allowed us to learn how the Yamnaya themselves had formed from earlier populations. From seven thousand until five thousand years ago, we observed a steady influx into the steppe of a population whose ancestors traced their origin to the south—as it bore genetic affinity to ancient and present-day people of Armenia and Iran—eventually crystallizing in the Yamnaya, who were about a one-to-one ratio of ancestry from these two sources. A good guess is that the migration proceeded via the Caucasus isthmus between the Black and Caspian seas. Ancient DNA data... have shown that the populations of the northern Caucasus had ancestry of this type continuing up until the time of the Maikop culture, which just preceded the Yamnaya.”

“The evidence that people of the Maikop culture or the people who preceded them in the Caucasus made a genetic contribution to the Yamnaya is not surprising in light of the cultural influence the Maikop had on the Yamnaya. Not only did the Maikop pass on to the Yamnaya their technology of carts, but they were also the first to build the kurgans that characterized the steppe cultures for thousands of years afterward. The penetration of Maikop lands by Iranian-

OLLI 497: Ancient DNA

and Armenian-related ancestry from the south is also plausible in light of studies showing that Maikop goods were heavily influenced by elements of the Uruk civilization of Mesopotamia to the south, which was poor in metal resources and engaged in trade and exchange with the north as reflected in Uruk goods found in settlements of the northern Caucasus. Whatever cultural process allowed the people from the south to have such a demographic impact, once the Yamnaya formed, their descendants expanded in all directions.”

How the Steppe Came to Central Europe

“On the eve of the arrival of steppe ancestry in central Europe around five thousand years ago, the genetic ancestry of the people who lived there was largely derived from the first farmers who had come into Europe from Anatolia beginning after nine thousand years ago, with a minority contribution from the indigenous European hunter-gatherers who mixed with them. In far eastern Europe also around five thousand years ago, the genetic structure of the Yamnaya reflected a different mixture of ancestries: an Iranian-related population along with an eastern European hunter-gatherer population, in approximately equal proportions. Populations that were **mixes of European farmers and steppe groups related to the Yamnaya had not yet formed.**”

The leading edge of the Yamnaya were the Corded Ware peoples: “The genetic impact of steppe ancestry on central Europe came in the form of peoples who were part of the ancient culture known to archaeologists as the **Corded Ware**, so named after its pots decorated by the impressing of twine into soft clay. Beginning around forty-nine hundred years ago, artifacts characteristic of the Corded Ware culture started spreading over a vast region, from Switzerland to European Russia. The ancient DNA data showed that beginning with the Corded Ware culture, **individuals with ancestry similar to present-day Europeans** first appeared in Europe.... in Germany, people buried with Corded Ware pots derive about three-quarters of their ancestry from groups **related** to the Yamnaya and the rest from people related to the farmers who had been the previous inhabitants of that region. **Steppe ancestry has endured**, as we also found it in all subsequent archaeological cultures of northern Europe as well as in all present-day northern Europeans.”

“The genetic data thus settled a long-standing debate in archaeology about linkages between the Corded Ware and the Yamnaya cultures. The two had many striking parallels, such as the construction of large burial mounds, the intensive exploitation of horses and herding, and a strikingly **male-centered culture that celebrated violence**, as reflected in the great maces (or hammer-axes) buried in some graves.” Reich notes there were differences as well; however “... the genetics showed that the connection between the Corded Ware culture and the Yamnaya culture reflected major movements of people. The makers of the Corded Ware culture were, at least in a genetic sense, a **westward extension of the Yamnaya.**”

Reich notes: “The discovery that the Corded Ware culture reflected a **mass migration** of people into central Europe from the steppe was not just a sterile academic finding.” He then proceeds to a lengthy discourse on the misuse of archaeological data in the first half of the 20th Century, and the influence this had on Nazi ideology and strategy. I won’t attempt to summarize it here, but please read it.

Reich then returns to his main thesis: “Corded Ware culture demonstrates the **disruptive power** of ancient DNA. It can prove past movements of people, and in this case has documented a magnitude of population replacement that no modern archaeologist, even the most ardent supporter of migrations, had dared to propose. The association between steppe

OLLI 497: Ancient DNA

genetic ancestry and people assigned to the Corded Ware archaeological culture through graves and artifacts is not simply a hypothesis. It is now a **proven fact**.”

But there remain issues, such as: “How was it that the low-population-density shepherds from the steppe were able to **displace** the densely settled farmers of central and western Europe?” Reich recounts an argument that such an event was impossible. “But ancient DNA shows definitively that **major population replacement** happened in Europe after around forty-five hundred years ago.”

He goes on to ask: “How were people with steppe ancestry able to have such an impact on an already settled region?” He offers two possible explanations.

First: “A possible answer is that the farmers who preceded them may not have occupied every available economic niche in central Europe, giving the steppe peoples an opportunity to expand.” In support of this answer, he notes that “... studies of pollen records in Denmark and elsewhere show that around this time, large parts of northern Europe were transformed from partial forest to grasslands, suggesting that the Corded Ware newcomers may have cut down forests, reengineered parts of the landscape to be more like the steppe, and carved out a niche for themselves that previous peoples of the region had never fully claimed.”

Second: “Eske Willerslev and Simon Rasmussen, working with the archaeologist Kristian Kristiansen, had the idea of testing 101 ancient DNA samples from Europe and the steppe for evidence of pathogens. In seven samples, they found DNA from *Yersinia pestis*, the bacterium responsible for the Black Death, estimated to have wiped out around one-third of the populations of Europe, India, and China around seven hundred years ago. Traces of plague in a person’s teeth are almost a sure sign that he or she died of it. The earliest bacterial genomes that they sequenced lacked a few key genes necessary for the disease to spread via fleas, which is necessary to cause bubonic plague. But the bacterial genomes did carry the genes necessary to cause pneumonic plague, which is spread by sneezing and coughing just like the flu. That a substantial fraction of random graves analyzed carried *Y. pestis* shows that this disease was endemic on the steppe.”

“Is it possible that the steppe people had picked up the plague and built up an immunity to it, and then transmitted it to the immunologically susceptible central European farmers, causing their numbers to collapse and thereby clearing the way for the Corded Ware culture expansion? This would be a great irony. One of the most important reasons for the collapse of Native American populations after 1492 was infectious diseases spread by Europeans who plausibly had built up some immunity to these diseases after thousands of years of exposure as a result of living in close proximity to their farm animals. But Native Americans, who by and large lacked domesticated animals, likely had much less resistance to them. Was it possible that, in a similar way, northern European farmers after five thousand years ago were decimated by plagues brought from the east, paving the way for the spread of steppe ancestry through Europe?”

How Britain Succumbed

“After the wave of steppe ancestry crashed over central Europe, it kept rolling. Beginning around forty-seven hundred years ago, a couple of centuries after the Corded Ware culture swept into central Europe, there was an equally dramatic expansion of the Bell Beaker culture, probably from the region of present-day Iberia. The Bell Beaker culture is named for its bell-shaped drinking vessels that rapidly spread over a vast expanse of western Europe...” Reich

OLLI 497: Ancient DNA

notes that isotopic analysis of their teeth revealed that "... some people of the Bell Beaker culture moved hundreds of kilometers from their places of birth. Bell Beaker culture spread to Britain after forty-five hundred years ago."

Reich recounts that analysis his lab did to resolve the question of Bell Beaker culture spread by migration of people or the spread of ideas. He concluded that "... in contrast to what happened with the spread of the Corded Ware culture from the east, the initial spread of the Bell Beaker culture across Europe was mediated by the movement of ideas, not by migration."

However, "Once the Bell Beaker culture reached central Europe through the dispersal of ideas, though, it spread further through migration. Prior to the spread of Beaker culture into Britain, not a single ancient DNA sample from among the many dozen we analyzed had any steppe ancestry. But after forty-five hundred years ago, each one of the many dozens of ancient British samples we analyzed had **large amounts of steppe ancestry** and no special affinity to Iberians at all. Measured in terms of its proportion of steppe ancestry, DNA extracted from dozens of Bell Beaker skeletons in Britain closely matches that of skeletons from Bell Beaker culture graves across the English Channel. The genetic impact of the spread of peoples from the continent into the British Isles in this period was permanent. British and Irish skeletons from the Bronze Age that followed the Beaker period had at most around 10 percent ancestry from the first farmers of these islands, with the other 90 percent from people like those associated with the Bell Beaker culture in the Netherlands. This was **a population replacement** at least as dramatic as the one that accompanied the spread of the Corded Ware culture."

"What made it possible for people practicing the Beaker culture to spread so dramatically into northwestern Europe and outcompete the established and highly sophisticated populations previously established there? Archaeologists view the Bell Beaker culture as extremely different from the Corded Ware culture, which was in turn extremely different from the Yamnaya culture. Yet all three participated in the massive spread of steppe ancestry from east to west, and perhaps they shared some elements of an ideology despite their very different features."

"Prior to the genetic findings, any claim that a new way of seeing the world could have been shared across cultures as archaeologically different from one another as the Yamnaya, Corded Ware, and Bell Beaker could confidently be dismissed as fanciful. But now we know that these people were linked by major migrations, some of which overwhelmed earlier cultures, providing evidence that these migrations had profound effects.... That almost all Europeans today speak closely related languages is proof that there was strong dissemination of a new culture across Europe at one time. Could the spread of shared languages across Europe have been propelled by the spread of people documented by ancient DNA?"

The Origin of Indo-European Languages

Reich tackles one last issue about the making of Modern Europe: "A great mystery of prehistory is the origin of **Indo-European languages**, the closely related group of tongues that today are spoken across almost all of Europe, Armenia, Iran, and northern India, with a great gap in the Near East where these languages only existed at the periphery for the last five thousand years—a fact known to us because writing was invented there."

He goes on to recount the theory put forth in 1987 by Colin Renfrew, namely that the vast spread of near homogeneous languages across a wide swath of Eurasia could be accounted for by the migration of farmers out of Anatolia.

OLLI 497: Ancient DNA

Reich counters that “... the argument that the spread of farming from Anatolia drove the spread of Indo-European languages into Europe has been undermined by the findings from studies of ancient DNA, which showed that a mass movement of people into central Europe occurred after five thousand years ago in association with the Corded Ware culture.... the data show that the Yamnaya also made a major demographic impact—in fact, it is clear that the single most important source of ancestry across northern Europe today is the Yamnaya or groups closely related to them. This suggests that the Yamnaya expansion likely spread a major new group of languages throughout Europe. The ubiquity of Indo-European languages in Europe over the last few thousand years, and the fact that the Yamnaya-related migration was more recent than the farming one, makes it likely that at least some Indo-European languages in Europe, and perhaps all of them, were spread by the Yamnaya.”

“The main counterargument to the Anatolian hypothesis is the **steppe hypothesis**—the idea that Indo-European languages spread from the steppe north of the Black and Caspian seas. The best single argument for the steppe hypothesis prior to the availability of genetic data may be the one constructed by David Anthony, who has shown that the shared vocabulary of the great majority of present-day Indo-European languages is unlikely to be consistent with their having originated much earlier than about six thousand years ago. His key observation is that all extant branches of the Indo-European language family except for the most anciently diverging Anatolian ones that are now extinct (such as ancient Hittite) have an elaborate shared vocabulary for wagons, including words for axle, harness pole, and wheels. Anthony interpreted this sharing as evidence that all Indo-European languages spoken today, from India in the east to the Atlantic fringe in the west, descend from a language spoken by an ancient population that used wagons. This population could not have lived much earlier than about six thousand years ago, since we know from archaeological evidence that it was around then that wheels and wagons spread. This date rules out the Anatolian farming expansion into Europe between nine thousand and eight thousand years ago. The obvious candidate for dispersing most of today’s Indo-European languages is thus the Yamnaya, who depended on the technology of wagons and wheels that became widespread around five thousand years ago.”

Reich notes that this hypothesis seems implausible for India. “Yet the steppe pastoralists broke through to India too.”

This leaves Reich with one last issue, “... the question of the **homeland** of the original Indo-European languages, the place where these languages were spoken before the Yamnaya so dramatically expanded.” Reich suggests that “... the most likely location of the population that first spoke an Indo-European language was south of the Caucasus Mountains, perhaps in present-day Iran or Armenia, because ancient DNA from people who lived there matches what we would expect for a source population both for the Yamnaya and for ancient Anatolians. If this scenario is right, the population sent one branch up into the steppe—mixing with steppe hunter-gatherers in a one-to-one ratio to become the Yamnaya as described earlier—and another to Anatolia to found the ancestors of people there who spoke languages such as Hittite.”

Reich sums up: “By tracing possible migration paths and ruling out others, ancient DNA has ended a decades-old stalemate in the controversy regarding the origins of Indo-European languages. The Anatolian hypothesis has lost its best evidence, and the most common version of the steppe hypothesis—which suggests that the ultimate origin of all Indo-European languages including ancient Anatolian languages was in the steppe—has to be modified too. DNA has emerged as central to the new synthesis of genetics, archaeology, and linguistics that is now replacing outdated theories.”