Human mobility and the prehistoric spread of farming: isotope evidence from human skeletons
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For over a century, archaeologists, linguists and, more recently, geneticists have debated whether the earliest farmers in Europe and elsewhere were migrants to new regions, whether indigenous hunter-gatherers adopted farming, or whether both processes combined as the two groups intermarried. Now analysis of isotopes in archaeologically recovered skeletons is providing new evidence about the mobility of some of the earliest farmers in central Europe and Southeast Asia.

The aim of this research project is to use isotopic analysis of human skeletons from archaeological sites to investigate the prehistoric spread of agriculture—one of the most remarkable transformations in human history, which changed the world from one of dispersed, mobile hunter-gatherers to one of settled farmers. This complex process left a clear demographic legacy, in geographical patterns of languages and human genes that often reflect the directions in which agriculture spread. By studying evidence from the bones, plant remains, pottery and house structures that the earliest farmers left behind, archaeologists have been able to show that agriculture spread quite rapidly through Europe about 7000 years ago and more slowly through mainland Southeast Asia about 4000 years ago.

One of the most interesting questions about this transition is whether agriculture spread with migrating farmers or as a new way of life adopted by indigenous hunter-gatherers. Unfortunately, current evidence derived from prehistoric artefacts, genes of present-day people, and the distribution of languages, cannot answer this question directly. The archaeological, genetic and linguistic evidence can tell us when and where agriculture spread, but not whether, in any given region, it was spread by migrating farmers or adopted by indigenous hunter-gatherers; nor can it reveal how much intermarriage may have taken place between them.

The research described here approaches these questions in a new way, by using a novel but proven scientific method to elucidate the geographical basis of this prehistoric expansion of human settlement. The project is designed to acquire evidence of human mobility directly from the skeletons of prehistoric individuals involved in the transition from hunting and gathering to agriculture. I have selected two geographical regions for comparison from the many archaeologically recorded prehistoric agricultural expansions, one in central Europe and the other in Southeast Asia. By comparing evidence for human mobility during the transition to agriculture in these two widely separated regions, I aim to test, in both regions, two hypotheses about the transition to agriculture: that it involved intermarriage between indigenous and migrant populations, and that the pace of the transition was influenced by the prevailing customs of marital residence. The results will advance our understanding of how and why agriculture spread, and provide valuable parameters that population geneticists can use to refine their continental-scale models of demographic history.

Isotopic analysis of archaeological skeletons

The method involves measuring ratios of isotopes of various elements in human skeletal remains. Isotopes are atoms of the same chemical element that have different masses. The element strontium (Sr), for example, has several naturally occurring isotopes, including ⁸⁶Sr, which represents about 10 per cent, and ⁸⁷Sr about 7 per cent, of the strontium that occurs naturally on the Earth today. The heavier isotope, ⁸⁷Sr, has one more neutron than the lighter isotope, ⁸⁶Sr, but because they both have the same number of protons and electrons, the two isotopes behave chemically in the same way.

In the project we measure isotope ratios of strontium (⁸⁷Sr/⁸⁶Sr) in archaeological tooth enamel, which enables us to identify the geographical area where a person obtained his or her food during childhood, while the enamel was forming. The ⁸⁷Sr/⁸⁶Sr ratio in rock minerals depends on how much rubidium (Rb) was originally in the mineral and how old the rock is. This is because a particular isotope of rubidium, ⁸⁷Rb, changes slowly into ⁸⁶Sr through radioactive decay. The half-life of this process is very long (48 billion years), and so the decay of ⁸⁷Rb into ⁸⁶Sr occurs significantly only on a geological timescale, not on a human (or archaeological) timescale. Unlike lighter elements such as carbon and nitrogen, strontium isotopes are heavy enough to be conveyed, without measurably fractionating (a term used to describe the changing proportions of one isotope to another), through eroded rocks, soils and the food chain into human tooth enamel. Because the ⁸⁷Sr/⁸⁶Sr ratio varies in different types of rock, it serves as a geological, and hence geographical, signature within archaeological tooth enamel.

By comparing the human tooth-isotope values with the local ⁸⁷Sr/⁸⁶Sr range of values for each site, we can infer that individuals with values within the range were local and those with values outside the range were immigrants. However, it is possible that isotopically identified local individuals might have migrated between similar geological provinces, and non-locaals may once have been mobile foragers who obtained their food from extensive, ecologically diverse territories. We hope that a new method we are developing will allow us to differentiate between migrants between permanent agricultural settlements and hunter-gatherers who moved...
seasonally to exploit wild foods – two alternate explanations for a non-local isotope signature at a site.

In the analytical procedure that I follow, several milligrams of tooth enamel from an archaeological skeleton are cleaned and then dissolved in acid. At the Institute of Archaeology, I then extract purified strontium from the dissolved enamel by using a special resin to capture the strontium. The purified Sr solution is then dried on a small tungsten filament (Fig. 1), similar to the filament of a light bulb, which is loaded into a thermal ionization mass spectrometer (TIMS, Fig. 2) in the Isotope Geochemistry Unit, directed by Rex Taylor at the Southampton Oceanography Centre. Inside the TIMS machine, which is kept very nearly at a vacuum, the filament is heated by several amperes of current. As the ions (atoms with a +1 charge) of strontium burn off from the filament, they are accelerated through a curved flight tube by means of an extremely high voltage (8000 volts) and directed around the curve by a strong magnetic field. Being slightly heavier, the 87Sr travels in a slightly wider curve, enabling one detector to catch the 86Sr atoms while a separate detector, positioned at the end of a slightly tighter curve, catches the 87Sr atoms. What is measured is the 87Sr/86Sr ratio, which we use directly for our interpretations.

Results from Neolithic Germany

Much of my recent research, often in collaboration with T. Douglas Price of the University of Wisconsin, has focused on the spread of the Linearbandkeramik (LBK) culture, which comprises the archaeological remains of the first farmers of central Europe and the pottery they introduced some 7500 years ago. Their domesticated plants and livestock clearly derive from Neolithic cultures in southeastern Europe and western Southwest Asia (the Levant), where their large wooden longhouses and so-called shoe-last adzes appear to be novel innovations of the LBK, apparently as an adaptation to life in the deciduous forests of central Europe. The radiocarbon dates from the earliest LBK sites tell us that the culture spread rapidly from the Hungarian plain into central Europe between about 5700 and 5500 BC. From about 5500 to 5375 BC there appears to have been a pause in the LBK expansion, when part of the western LBK boundary lay within the upper Rhine Valley in southwestern Germany (Fig. 3). Because archaeological dates for the earliest LBK sites in the valley overlap with the latest dates for Late Mesolithic sites farther west, in the period from c. 5500 to c. 5200 BC, it was here that we decided to look for evidence of possible interaction between LBK groups and indigenous hunter-gatherers to the west.

Geologically, the upper Rhine Valley in southern Germany is also ideal for strontium-isotope analysis because the Vosges and Black Forest uplands, underlain by gneisses and granites, should have significantly higher 87Sr/86Sr values (>0.715) than the Jurassic and younger sedimentary rocks (<0.710) of the lowlands. Having previously determined that, for prehistoric Germany, archaeologically recovered pig teeth represent the local values well,8 and my colleague Corina Knipper (University of Tübingen) then mapped the biologically available strontium, carbon and oxygen isotopic signatures of prehistoric southern Germany by analyzing tooth enamel from the remains of pigs from archaeological sites distributed around the region.9 The mapping confirmed our expectations of a marked upland/lowland difference in biologically available 87Sr/86Sr values. Furthermore, carbon isotopes in the carbonate fraction of pig enamel were generally slightly more enriched in 13C in the samples from the uplands.

The cumulative results from southern Germany, that we have obtained over the past four years are beginning to provide a very informative picture of the changes in human mobility patterns over time in the early Neolithic. They indicate that shortly after 5500 BC, when farming began in the region, there were many non-locals at each community, mostly with upland strontium-isotope signatures (Fig. 4). A few centuries later, around 5000 BC, there were fewer non-locals overall, and females are more common among the non-locals with upland signatures.

The burials of non-locals show patterns that are consistent within each site but different between sites. Our studies at two LBK cemeteries, Dillingen and Flomborn (Fig. 3), showed that very few of the non-locals, male or female, were buried with a shoe-last adze, the characteristic early Neolithic artefact that was present with most of the local males.10 However, at Stuttgart-Mühlhausen (Fig. 3) we recently found that males buried with a shoe-last adze have the non-local signatures. Also, at several sites, most non-locals were buried so that the head was oriented towards a certain cardinal direction, with that direction peculiar to each site. At Flomborn and Stuttgart-Mühlhausen, for example, most of the non-locals are buried with the head...
pointing west, whereas at Schwetzingen most of the non-locals point north or northeast. These results indicate that some people, who had subsisted partly on upland resources, were buried in socially distinct ways among communities who subsisted primarily on lowland resources. It may be that some of the former were hunter-gatherers who joined agricultural communities, but as yet we cannot be sure of this.

To address this difficult problem, I initiated last year a collaboration with Tim Atkinson, Director of the new Bloomsbury Environmental Isotope Facility at UCL, to analyze carbon and oxygen isotopes in addition to strontium isotopes. This has added a substantial amount of information from each skeleton, for only 15 per cent additional cost per sample analyzed. For example, at Talheim (see Fig. 3), the site of a village massacre about 4900 BC, a few females have $^{87}$Sr/$^{86}$Sr values that are only slightly (although significantly) higher than those from the rest of the village population. But, by measuring $^{18}O/^{16}O$ ratios in the same samples, we have discovered that a sample from one of these women differs greatly from the rest, and we can tell more about her origin by comparing the sample with the regional isotope data obtained from archaeological pig teeth. Although the values for the rest of the community fall within the range for the Neckar Valley, where Talheim is located, this one female $^{18}O/^{16}O$ ratio is higher than any of our samples from the region. One probable explanation is that she came from farther west, towards the Atlantic, an inference based on the fact that $^{18}O/^{16}O$ ratios in precipitation are progressively higher in that direction (because the heavier oxygen tends to fall out first from the rain clouds as they move inland from the Atlantic). If we find similar oxygen-isotope outliers in samples from earlier Neolithic sites when hunter-gatherer territory lay to the west of the Rhine Valley, they may provide the best evidence for the presence of hunter-gatherer immigrants within farming communities.

**A new comparative study in Southeast Asia**

In order to undertake a second case study, independent of the first, I recently began to investigate the spread of agriculture into Southeast Asia by analyzing samples from two Neolithic sites in Thailand. Current evidence points to the swampy lakelands of the middle Yangtze River as the home of the first rice farmers about 10,000 years ago. Although somewhat more recent, this mirrors the process of wheat and barley domestication in Southwest Asia. In both regions, agricultural communities multiplied and spread. Just like the Neolithic sites of Europe with respect to the origins of their agricultural complex in the Levant, the earliest agricultural sites in Southeast Asia show a pattern of decreasing age away from a central China heartland, and for Southeast Asia we are asking essentially the same question: how much was the spread of rice farming the result of migration by farmers, and how much was it the result of indigenous hunter-gatherers adopting agriculture? Interestingly, in contrast to the rapid and almost complete spread of agriculture in prehistoric Europe, hunting and gathering persisted in parts of prehistoric Southeast Asia for many centuries after agriculture became established. By comparing the results from Thailand and Germany, we hope to gain a better understanding of the spread of agriculture in both regions.

With funding from a small grant from the British Academy, I accepted a once-in-a-lifetime opportunity to undertake a Neolithic investigation of the first isotope analyses ever carried out of samples from the two most substantial and well-documented Neolithic human skeletal collections from Thailand (Fig. 5): Khok Phanom Di (2000-1500 BC) and Ban Chiang (2100 BC to 200 AD). I found that, at each of these important sites, the range of $^{87}$Sr/$^{86}$Sr values for males remains the same through time, but the range of female values compresses dramatically to within the local range at a particular mortuary phase. This may indicate a cultural shift to matrilocality in Southeast Asia. If so, there are anthropological grounds for hypothesizing that matrilocality slowed the conversion to farming.

This preliminary project is now in the process of being expanded, in collaboration with other archaeologists and skeletal biologists, including Charles Higham and Nancy Tayles of the University of Otago, and Michael Pietrusewsky and Miriam Stark of the University of Hawaii, with the aim of analyzing over 300 human skeletons from multiple sites in Thailand and Cambodia that span the period 2100 BC to AD 400. As in Germany, I am first mapping the biologically available isotopic signatures around the study region using archaeological tooth enamel from local animals such as rats and domestic pigs.

A site of particular interest is Ban Non Wat (Fig. 5), from which Professor Higham and Dr Tayles will provide over 100 human skeletal samples for analysis. Here, a Neolithic settlement and cemetery, stratified below Bronze and Iron Age layers, provides a rare opportunity to examine the evidence of early farmers and also the marriage and migration practices of a prehistoric village community over the ensuing 2000 years. Excavations at Ban Non Wat

![Figure 4](image_url)  
**Summary of $^{87}$Sr/$^{86}$Sr in human tooth enamel from Neolithic Germany:**  
$\sigma$ = female, $\square$ = male, $\Delta$ = sex unknown, + = pig (used to map values). Filled (grey) symbols are burials with a shoe-last adze. Sites ordered chronologically, from the earliest at the left, include Early Milhausen (EM), Flomborn (F), Late Milhausen (LM), Schwetzingen (S), Talheim (T), and Dillingen (D). $^{87}$Sr/$^{86}$Sr above about 0.7108 (horizontal line) indicates significant diet from the uplands.
have already unearthed the largest sample of human remains so far discovered in Southeast Asia. The analysis of strontium isotopic variation in the excavated skeletons will make it possible to ask key questions about the nature of human migration and the spread of agriculture. For example, were the first settlers of Ban Non Wat 4000 years ago born and raised elsewhere or did they come to settle a new environment? Or, alternatively, were some of the population local hunter-gatherers who intermarried with intrusive agriculturalists? Was this an isolated village, or did marriage and descent patterns change over time? These questions will be addressed as I analyze comparative material from the other Neolithic sites in central Thailand.

Implications

The research described in this article is beginning to provide the kind of direct evidence at the scale of the individual that is crucial to understanding the great demographic transition in prehistory. The pace of the transition varied considerably between the presence of non-local females in early agricultural sites in Neolithic Germany and Thailand. This question arises of whether marital residence and social organization change over time? How did social organization change over time? These questions will be addressed as I analyze comparative material from the other Neolithic sites in central Thailand.

Notes

1. The research described in this article is one of the projects at UCL being undertaken under the auspices of the Centre for the Evolutionary Analysis of Cultural Behaviour, directed by Professor Stephen Shennan of the Institute of Archaeology.
7. This method will use a laser apparatus to measure isotopes across the growth layers in tooth enamel, which form over the course of childhood. We expect variable isotopic signatures through time from tooth enamel of samples from farmers who had moved from one fixed settlement to another.
14. The term matrilocality refers to the cultural convention whereby the woman, when marrying, moves to the man's place of residence; patrilocality refers to the converse practice.