The Populating of Europe

The purpose of this discussion is to examine the nature of the populating of Europe by modern humans (let's call them Homo Sapiens Sapiens – HSS, to differentiate from Neanderthals, who were undoubtedly 'sapiens' whom I'll label HSN) as revealed using the latest whole genome DNA techniques. In the last decade progress in analysing DNA data has improved beyond all recognition, both in the manner in which DNA data can be captured more quickly, cheaply, and very much more comprehensively, and also in the development of techniques for analysing what such data reveals about population lineages, their mixing and timing. I do not propose to go into the DNA logic in this talk but rather concentrate upon the results as applied to European populations over approximately the last 50,000 years, seeing also how they can be interpreted in the light of multi-disciplinary evidence from archaeology, anthropology, linguistics and geological/environmental studies.

Until July 2019 it was assumed that modern humans first began to populate Europe during warmer interludes in the last Ice Age. However, the finding of the Apidima 1 skull fragments – although heavily distorted by burial damage, suggests that an HSS population had reached at least as far as southern Greece way back ~210 thousand years ago! I'll use the archaeological abbreviation 'ya' for 'years ago' and 'kya' for 'thousand years ago' – so I'll write things like "the discovery of Apidima 1 living in Europe ~210kya & HSS-like skulls in Morocco from over 300kya, shows the inadequacy of just using the tiny mitochondrial DNA, which last month was claimed to show that humans began in the Botswana area ~ 200 kya and did not leave it for 70,000 years". The Apidima skull, if confirmed as HSS, indicates that an early form is living in Greece during the Aveley Interglacial, a warm stage that just precedes the last cold spell of the 2nd last Ice Age, the Wolstonian. The subsequent warm period of the Ipswichian is followed by the start of the Devensian Ice Age around 115kya {I am using UK nomenclature; these geological periods have a host of other names elsewhere!}. We have, as yet, no DNA to see how these very early pioneers, who seem to be then displaced by Neanderthals (HSN) rather than the other way around, relate to those who arrive much later, ~50kya.

I Hunter-Gatherers Populations of Europe

The Devensian glaciations in Western Europe increased to reach a maximum around 22kya - with the de-glaciation commencing around 19 kya (in the Northern Hemisphere at least, later at ~14.5kya in the high latitudes of the southern hemisphere). We have currently learned most about the various more recent pioneers who spanned at least the second half of the Devensian period, from the DNA work of Qiaomei Fu and her colleagues in David Reich's lab in Harvard. They've analysed ~ 50 skeletal remains spanning ~45kya to 7kya using a number of new techniques and analyses of ancient DNA data to enable determination of their different source populations and mixings thereof.

The technique of previous workers, and they themselves when they started, had been to compare such ancient DNA with that of current populations, but the differences among current peoples was clearly of so little relevance to population change and movement back then, that they soon realised they must concentrate on comparing these ancient samples with one another. From this the team was able to group them into 4 clusters plus some outliers amongst the oldest individuals. Using Fu's work we are able to tell a story of the first 35,000 years of human history in Europe in terms of 5 overall phases of Hunter-Gatherer migrations.

I.1 *Devensian Populating By Modern Humans*

The influx of HSS into Europe taking place from around 50kya onwards, is via a population that is spreading from Africa and the Near East, up through the Balkans, and then spreading out both east and west. This influx occurred sometime before 45kya, and we have DNA analysis of human bones from Romania and western Siberia that are this old.

They seem to have been members of a population that initially flourished but then largely disappeared, since their DNA appears no more closely related to that of subsequent Hunter-Gatherer populations coming to occupy both Eastern and Western Europe, than it is to modern East Asians. In terms of archaeology we still see the long lasting Neanderthal (HSN) Mousterian tool culture possibly being adopted by these HSS, who may then produce the briefer (though still somewhat archaeologically controversial) Chatelperronian tool culture. Indeed DNA analysis of a 40kya skeleton found in the Oase cave in Romania, whose form appeared to resemble an HSS-HSN hybrid, has shown that this individual must have had a direct Neanderthal ancestor no more than 6 generations back.

Their collapse seems to have occurred around 39kya, which suggests that a primary cause *may* have been the cataclysmic volcanic event that occurred near Naples around 39.2kya.

The Campanian Ignimbrite Super-eruption Event

This was a very large explosive volcanic 'super-eruption' leaving a huge caldera of ~ 13 km in diameter, known to the Romans as the Phlegraean Fields. Animals within a radius of 100 km were unlikely to have survived, and an overall emission of 680 cubic kilometres of material spread much further {this is over 200 times larger than the eruption of Vesuvius that destroyed Pompeii and Herculaneum 37 thousand years later}. The sudden cooling and the environmental impact (as shown by severe pollen depletion lasting several years), atop an already cold and vegetation-thinning Europe, may have been the last straw for the Neanderthals, who it has long been thought depended upon large animal populations for survival (though recent analysis of Neanderthal faeces indicate a more mixed meat and veg. diet). Deposits of Neanderthal bones and tools essentially disappear above this ash marker. It also seems to have had a similar effect on the above HSS European population; as we said above, the DNA of any human remains subsequent to this event, are unlike the DNA of these previous inhabitants; the post-Campanian European population appears to be the result of another migration.

This event is often taken to mark the transition from the middle Palaeolithic to the upper Palaeolithic.

I.2 *The Aurignacian Expansion*

The DNA identification of these post-Campanian arrivals starts with a 37kya individual in Kosteniki in western Russia, and then we have a 35kya individual from the Goyet caves in Belgium. There is a wonderful collection of remains in these Belgian Caves - they have provided DNA for the populations occupying them over the next 20,000 years, contributing evidence to much of the rest of the Hunter Gatherer cultures appearing in Europe over this time interval. Fu and co-workers used 4-population tests to show these two earliest individuals are members of two separate sub-lineages descended from a single ancestral population, but one that is *not* that which gave rise to the pre-Campanian

Chatelperronian culture, and one that has not appeared to have mixed with any non-European peoples. These new arrivals seemed to have spread up from the Balkans after 39kya. They bring with them the *Aurignacian* Culture.

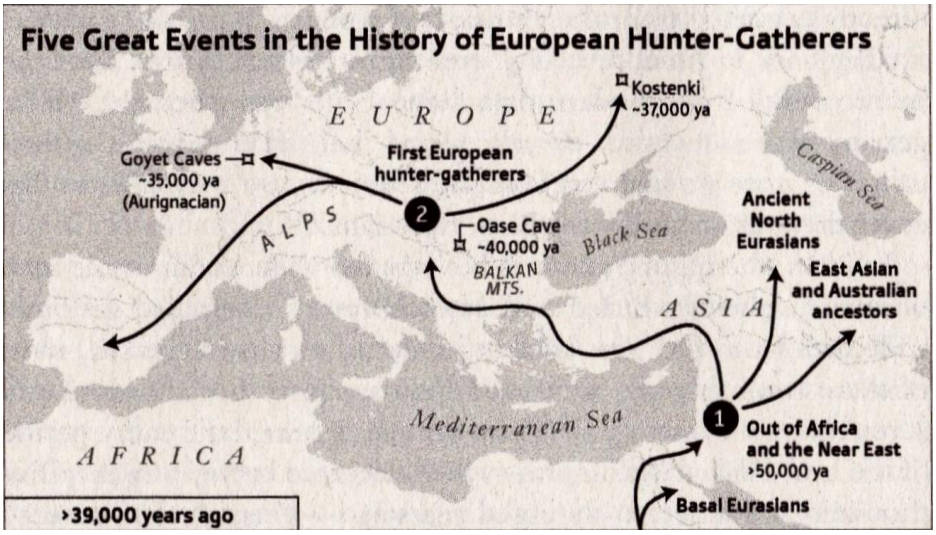


Figure 1: Early Homo Sapiens Spread (1), and the Aurignacians (2)

As well as different tool types, the Aurignacian is associated with a mature cave art of both figurative and abstract patterns. The therianthropic lion-man mammoth ivory carving we have discussed before, and the first known 'Venus' figures and musical instruments, are from these Aurignacian peoples.

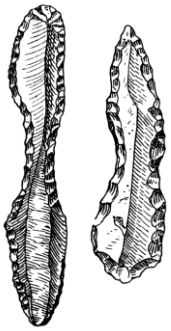


Figure 2 Aurignacian Culture - art and artefacts

We have many indications of ritual – including footprints in a cave system in which apparently children were walking backwards on their heels for 500 metres. Given the apparent disappearance of

the very early pioneers and the pre-Campanian super-eruption peoples, the Aurignacian people can currently claim the title of the founding population of modern Europeans.

I.3 *The Gravettian Expansion*

A change in this widespread culture starts sometime ~ 33kya, spreading west from the region of Kostenki. Production of Venus-type figurines massively increases and induces the highly precocious development of ceramic technology to make even more voluptuous versions of the Venus figures when these people reach Dolne Vestonici~ 31kya, a site of great manufacturing innovation.

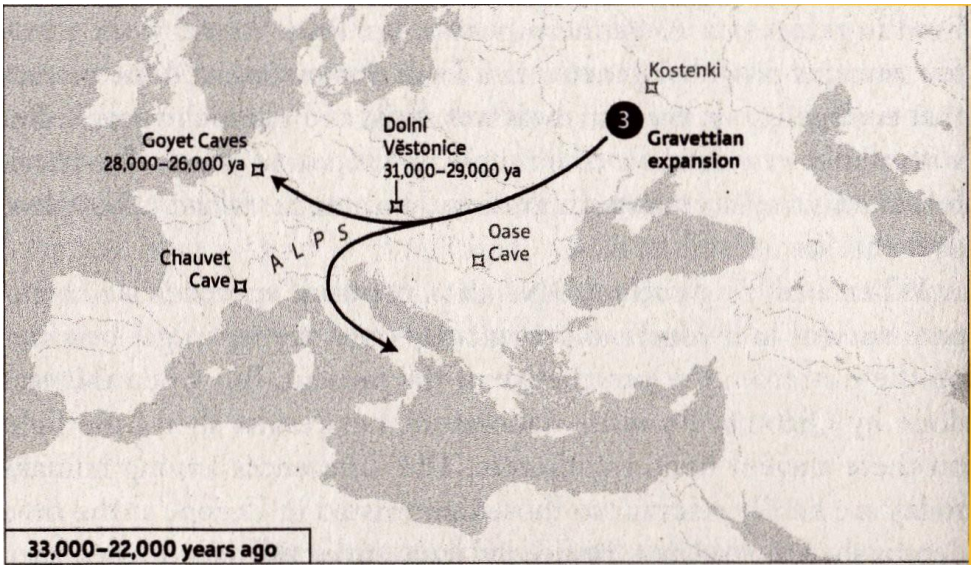


Figure 3 Gravettian Expansion

They gradually spread further west and by ~28 kya we find them represented in the Goyet cave collection. They bring with them new tools - such a barbed arrow points and knives with a flattened edge on one side for pressing on. To some extent its art moves off the cave wall and into sculpture. They are much more deliberate in their burial practices – see the Red 'Lady' of Paviland that we have discussed earlier is Gravettian – so we have many more bones upon which to do DNA analyses.

Figure 4 Gravettian Culture - art and artefacts

Is this cultural change accompanied by another complete change of people within 10,000 years of the post-Campanian change? Not completely new, no: Fu et al's testing has shown that the people carrying this new culture are descendants of the Kostenki sub-lineage of the Aurignacian people – which probably explains the continuance of the significance of things like the Venus figurines; but as they spread west, by around 28kya they appear to have displaced or replaced the sub-lineage of the 35kya Goyet Cave Aurignacian individual during the remains of this pre-glacial maximum phase.

They had a high meat diet which would have helped combat the increasing cold and this was obtained using sophisticated and mobile hunting techniques. The culture continues until we reach the last glacial maximum in Europe which occurs ~ 22 kya. When this happens, we have a retreat of all the population to warmer *refugia*.

I.4 *The Magdalenian Re-Population*

As the climate started to warm again, western Europe sees an expansion of people from the warmer refugia in Spain and the Basque region. The earliest skeleton associated with this new culture dates from ~19 kya in Spain and it held a surprise in its DNA.

It was in fact a descendant, not of the eastern subgroup of the Aurignacians that had led to the Gravettian, but rather of the long removed western Aurignacian subgroup of the 35kya Goyet cave individual. It seems that they had not simply disappeared, as the pre CI eruption peoples appear to have done, but rather had moved south-west, thereby being in a region that would, later on, provide a more viable environment, and from which they would re-emerge successfully as the higher latitudes began to warm up.

They then spread north-east into France, Germany and Central Europe where they hold sway for the next 5 - 7 thousand years. They were a very mobile people moving with herds and seasons; the people who come over Doggerland to spend time in places like Creswell Crags and Farndon in summers are almost certainly of this lineage. Cave art seems to have a resurgence with masterworks like those at Lascaux; we also have intricate bone carving, both artistic and in tools, with great skill in microlith work.

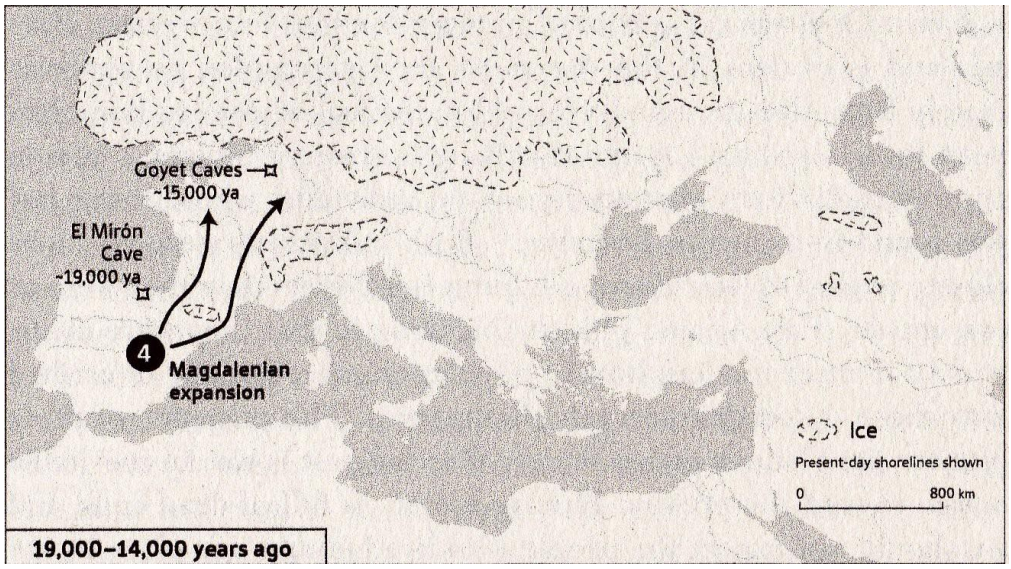


Figure 5 The Magdalenian Expansion

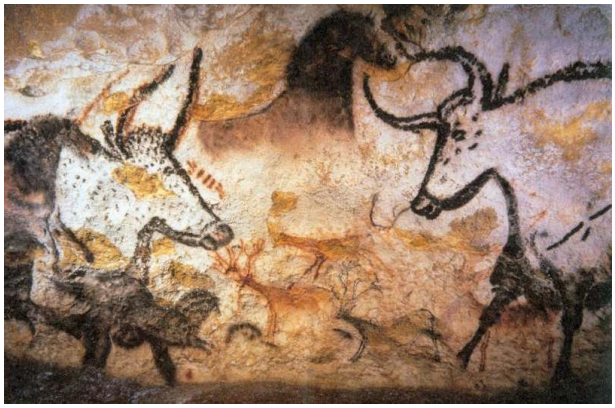


Figure 6 Magdalenian Culture - art & artefacts

At this time the population further south-east in Italy are still exhibiting what might be termed an epi-Gravettian culture. This is almost certainly because during this period there is still an ice wall extending from the Alps to the sea near Nice; a wall that had prevented communication of areas to the west with Italy and the Balkans for at least 10,000 years. We have, as yet no good DNA from those south-eastern European people at this time but, given their archaeology, they may well be related to the descendents of the eastern sub-branch of the Aurignacian that developed the Gravettian culture.

I.5 *The Bølling-Alleröd Expansion*

The Bølling-Alleröd Oscillation is the name given a short climate period involving periods of some strong warming, from ~ 14.5kya following the decline of the Devensian glaciation at the end of the oldest Dryas, and ending abruptly around 2000 years later with the arrival of the younger Dryas {Dryas is an alpine tundra plant that is used by geologists as a temperature indicator}. It was possibly caused by destabilisation of methane clathrates during glacial retreat; we do appear to have a number of explosive eruptions at that time {worryingly, we are currently starting to see small craters of explosive clathrate release in the Siberian tundra}. It caused the final melting of the ice wall that had divided the south-east from western Europe and we get plants and animals migrating in abundance into south western Europe from the south eastern areas.

More 4-population tests showed that along with all the plants and animals, we get a very substantial human expansion taking place, with a large hunter-gatherer population spreading into western Europe. This expansion appears to replace the Magdalenian peoples to a very substantial degree, such that this south eastern Hunter-Gatherer DNA soon dominates the population of western Europe. These people's DNA appears to be closer to that of present day populations in the Near-East (Phoenicians showed continuity with them ~2.5kya). This may indicate the source area of these people, but could equally well mean that, as well as spreading west during the Bølling-Alleröd, they also spread east into Anatolia and beyond. Either way, whereas the Hunter-Gatherers of the Aurignacian, Gravettian, and Magdalenian, are all plausibly descended from a lineage that separated from those of the Near/Middle East several tens of thousands of years earlier, these last Hunter-Gatherer immigrants to western Europe probably diverged more recently from those whose descendants will develop agriculture and eventually bring that technology to the region.

{Note: Palaeolithic cultures tended to develop individual versions on a more regional level – in the Allerød alone at least five can be distinguished – but here I am taking a broad brush approach.}

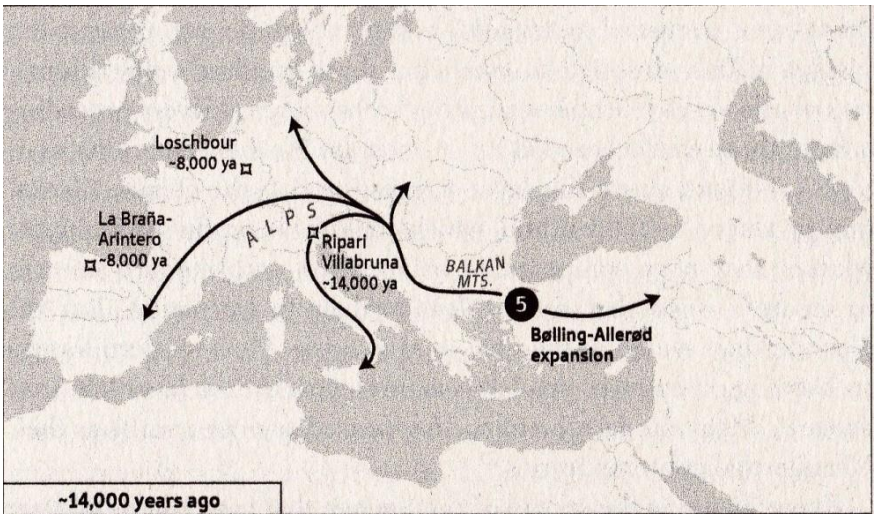


Figure 7 The Bølling-Allerød Expansion

Gobekli Tepe

II The Development of Farming

At about 11-12kya, we see the beginning of the major archaeological change indicating the development of farming and the associated Neolithic cultures. Farming is thought to be initially a two pronged affair with Hunter-Gathers in Anatolia, the Levant, and the Fertile Crescent developing various crops, and a separate Hunter-Gatherer people further east in eastern Iran domesticating a number of animals. These two groups seem to quickly amalgamate the crop and animal farming techniques. Profound archaeological changes spread from these areas, westward into Europe along the Mediterranean, north-west along the Danube, and also eastwards to west Asia. They eventually reach the British Isles and Scandinavia in the northwest, and the Siberian plain and the Indus valley in the east {the development of farming further east in East Asia was an independent creation}.

As with many other archaeological changes we need to ask was this new technology spread by the movement of people, or of ideas, or both. We always knew that it could not be simply be just that of ideas since all the domesticated cereal and animal species were only found in those Near/Middle East regions so people had to have brought them to Europe. {Archaeologists refer to these areas as the Ancient Near East, in modern political geography terminology this is mostly termed the Middle East},

Until three or four years ago DNA data on these initial farmers was of very poor quality – the hot summer climate in the Near East accelerated the breakdown of ancient DNA. However improvements in enriching tiny amounts of intact DNA, eliminating damage and reducing contamination by bacteria and modern humans, developed by Matthias Meyer's group in Svante Pääbo's lab in Germany, and the finding in 2014 by Ron Pinhasi (an anthropologist working in Dublin) that the petrous bones of ancient skeletons (the hard prominence behind the ear) were much richer in preserved DNA then other parts (often by a factor of 2-400x), transformed our ability to obtain good data from small amounts of ancient DNA to help better tackle the problem of Neolithic Near East DNA degraded by warmth {as well as greatly aiding the analysis of our small collection of the much older early Hominin DNA – a topic for another time}.

This has revealed the surprising result that the DNA of the western branch of these farming innovators was in fact as different from the eastern branch by as much as the DNA of modern Europeans differs from that of modern East Asians! Both were derived directly from the Hunter-Gatherers that preceded them in those two areas: the Natufians who built Gobelki Tepe in the case of the western arm in Anatolia & the Fertile Crescent, and the Iranian Hunter-Gatherers in the case of the eastern arm.

In summary, analyses by a team led by Iosif Lazaridis in Harvard shows that we have 4 different populations occupying what we might term West Eurasia during this time of the early development of farming period: – the two different populations developing the plant and animal agricultural techniques, plus the Hunter-Gatherers of Western & Central Europe, and the Hunter-Gatherers of Eastern Europe (who had not been affected by the Bølling-Allerød influx). Each of these peoples differed from the others by as much as Western Europeans differ from East Asians today.

Those inclined to assign racial groupings to people would have had no trouble describing these as the 4 separate races occupying West Eurasia – they are represented by the four groups, A, B, C and D, of black circles shown on the plot of DNA variations shown in Figure 8. However the light grey dots, representing the DNA of present day populations, show that virtually none of these now exist in an unmixed form; the idea of an extant 'pure' ancient European stock is not something that can be supported, even just back to the Neolithic.

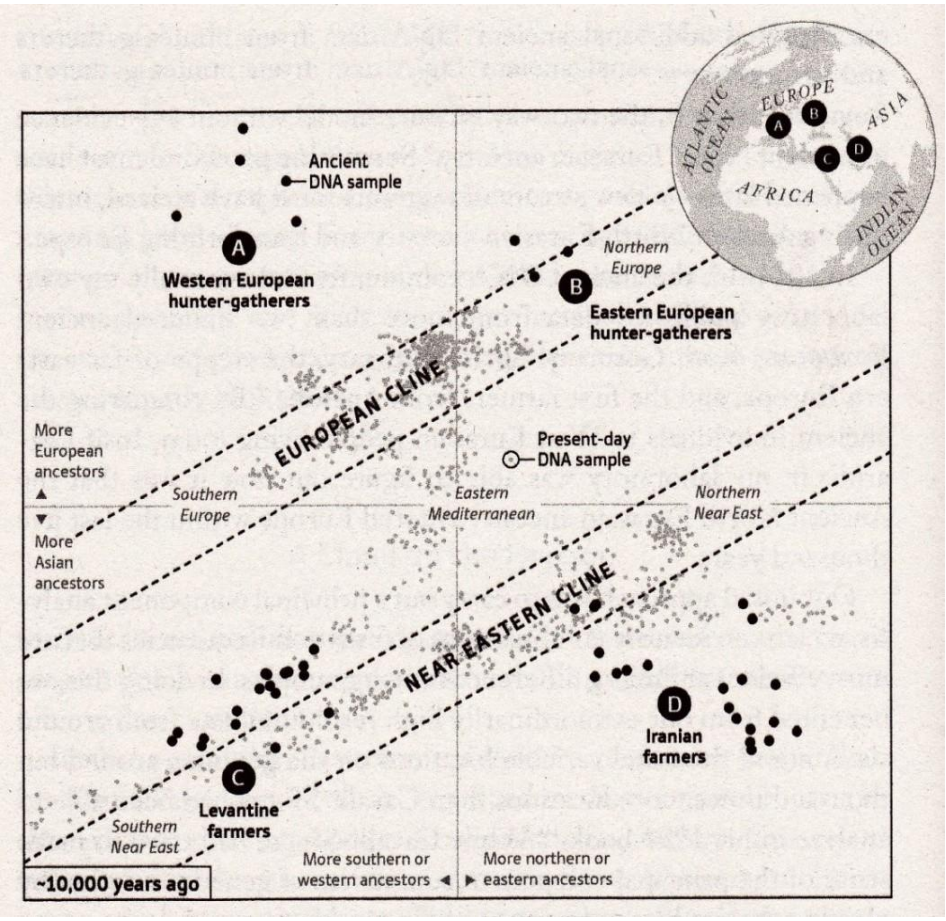


Figure 8: DNA of the 4 populations of west Eurasia ~10kya (black dots); & of Modern Populations (grey dots)

The axes of Figure 8 record the two *principle components of variation* (two combinations describing the collections of DNA sites that are most variable in the samples) for all the DNA analysed, each dot

representing where an individual's DNA lies as far as these two components are concerned - a visualisation technique for DNA variation first applied to ancient DNA studies by Cavalli-Sforza.

III The Spread of Farming

Over the next few thousand years, agriculture spreads northwest via Anatolia. For these new agricultural techniques to arrive, someone had to bring the domesticated grains and animals, since, as we said, none of these was indigenous to western Europe, only to the Near East. It always seemed highly probable that this had to be done by the farmers themselves, so a wave of immigration was assumed to have occurred. However, unlike previous Hunter-Gatherer migrations, we now have newcomers who wish to do something quite different with the land – so the questions presented are not simply ones concerning the eradication, or displacement, or mixing of peoples, but also of lifestyles and land transformations. Clearly a farm is not an area of land in which hunter-gathering and foraging would be welcome, but the majority of the land is not quickly cleared, so did the two lifestyles remain adjacent but separate for some considerable time? Did the Hunter-Gatherers come to arrangements whereby they adopted the farming lifestyle – by, say, allowing access to areas of land in exchange for seed-corn and domesticated animals? Did they mix with these new arrivals?

Since the DNA work of Cavalli-Sforza and co-workers back in the 1970s, the evidence suggested that these farmers spread the technology into western Europe from Anatolia, mixing with the indigenous Hunter-Gatherer populations as, or soon after, they arrived. Thus Europe becomes a mix of the Levantine western Near East farmers with the western Hunter-Gatherers. Cavalli-Sforza also appeared to demonstrate that it was they who spread the Proto-Indo-European language (PIE).

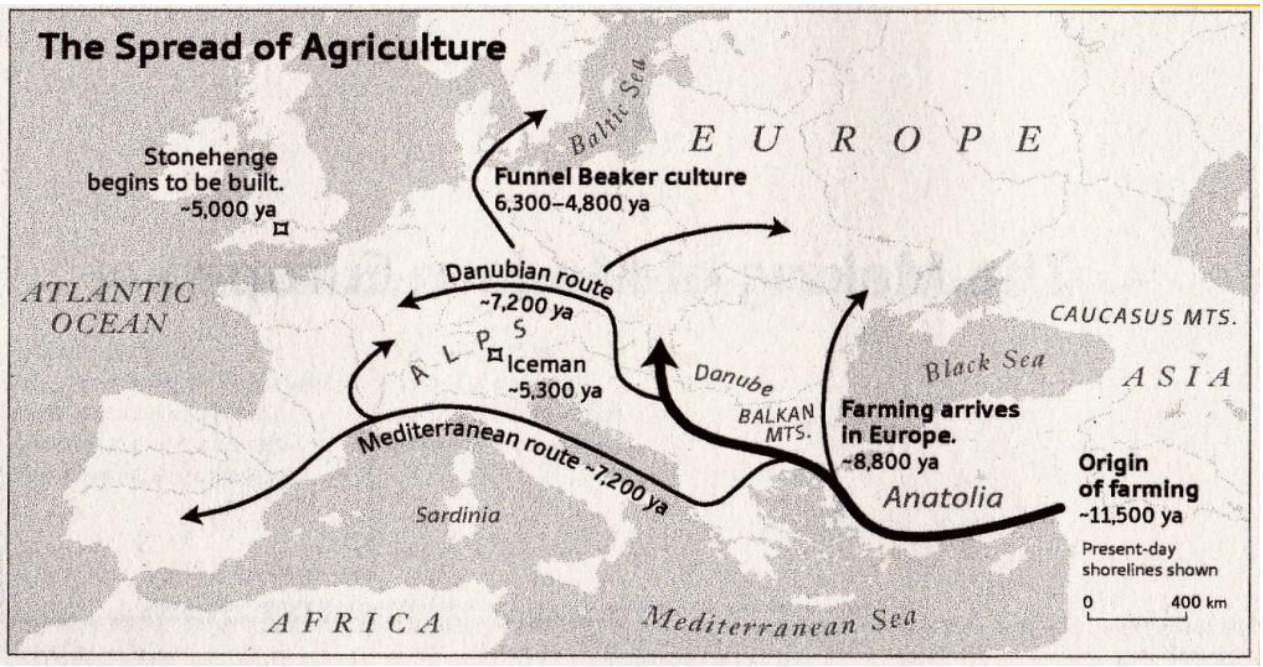


Figure 9: The Spread of Farming

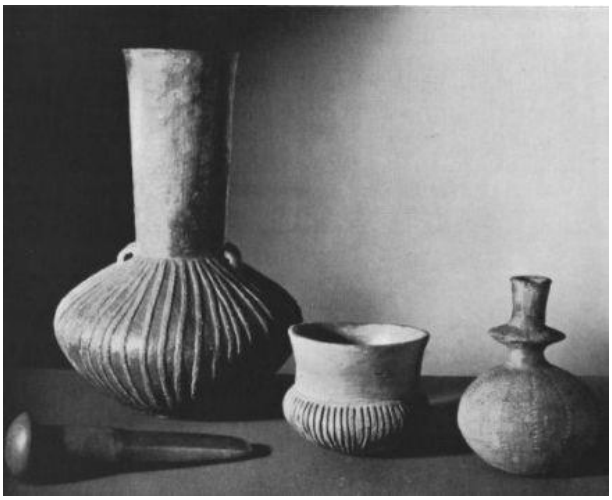
Despite the many difficulties Cavalli-Sforza's pioneering work had to cope with, and the tiny fraction of DNA variation sites he was able to employ, his conclusions remained the accepted view as the technology developed over the next several decades. However in the last decade the number of

markers one can readily use in the DNA has increased by 3 or 4 orders of magnitude and it is not surprising that the detail they reveal is somewhat more complex and supports a somewhat different conclusion. There were also some problems with the palaeo-linguistics links to PIE.

The very first farmers in western Europe appear to be an aceramic culture in Crete and the Peloponnese going as far back as 9 kya; some archaeologists had thought this might indicate a different migration from that which brings farming to most of western Europe. The DNA shows that they were indeed different, they exhibit a more Iranian- than Levantine-farmer ancestry; the rest of European farmers indicate a mainly Levantine source, spreading up via Anatolia from ~ 8.8 kya.

Over the next couple of thousand years, farmers as far apart as Spain, Germany and Hungary still show more than 90% of their DNA coinciding with that of the Levantine farming peoples. This retention of the dominant influence of the source population for several millennia suggests that there was little mixing with Hunter-Gatherer populations at this time.

Farming takes several thousand years to reach the far north of Europe and, although the Hunter-gather populations there appear to adopt some domesticated animals and later some crops, they still retain many aspects of Hunter-Gatherer life and culture for a substantial period. Around 6.3 kya we get the appearance of the Funnel Beaker ceramic culture associated with the erection of substantial Megalithic collective tombs in northern Europe. Colin Renfrew had suggested that the latter were marking a delineation of the Mesolithic Hunter-Gatherers from the Neolithic farmers coming up from the south. It is possible that the apparent pause in the conversion/mixing of northern Hunter-Gatherers with farmers might be a technological one in that the heavier soils presented the southern farmers with the need for further developments before farming could make much headway.



Funnel Beaker Pottery

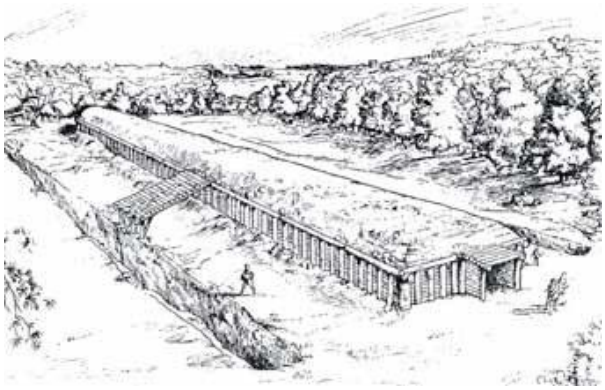
A Model of Funnel Beaker Tomb

Figure 10 Funnel Beaker Culture

The DNA of people in Funnel Beaker burials has indeed now shown a greater element of Hunter-Gatherer in the DNA mix compared to results further south. Over the next two thousand years we see a general increase of Hunter-Gatherer ancestry in Neolithic sites with up to around 20% of DNA stemming from Hunter-Gatherers – so it appears that these populations do eventually substantially mix, albeit after a considerable period of time remaining apart (conjugally at least). We may now view the resulting mid-Neolithic cultures as resulting from inputs from both farmer and H-G culture.

It seems that from then on, until about 4.5 kya (2500 BCE), the population of western Europe largely stabilises. The DNA of the Levantine farmers predominates in the majority of the population, but with a not insignificant mix of indigenous Hunter-Gatherer ancestry. Given the population densities of farmers naturally tends to be significantly higher than that Hunter-Gatherers, it seems to me that this is compatible with what is ultimately a reasonably amicable blending of the two populations.

By the mid-Neolithic this population blend is creating the tools and monuments we know well:-



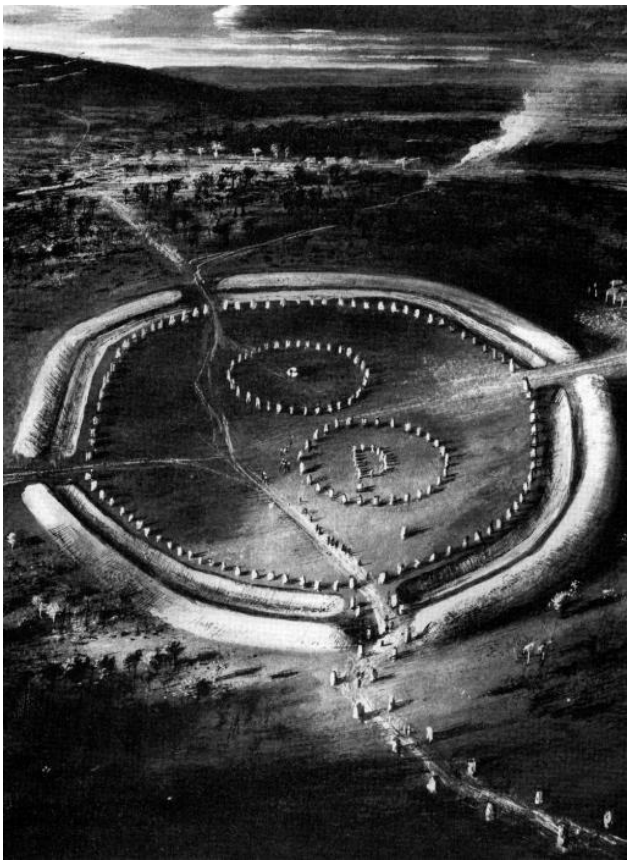


Figure 11 Neolithic Tools, Artefacts & Structures
(Artist reconstructions of Fussells Lodge Longbarrow, & the Avebury Avenue, Henge and Stone Circles)

In summary, as the western branch of the farmers spread across Europe, at first they tended to remain separate but later began to mix with the Hunter-Gatherer populations so that by the late Neolithic we have people with up to something like 20% Hunter-Gatherer DNA. Some very northern parts of Europe, including the British Isles, kept a sort of arms-length attitude to this technology for some thousand or more years, maintaining a *Mesolithic* style of life. The great megalithic structures of the north may have started as statements of this difference, but carried on when they finally adopt the farming technology. In Britain this switch occurs some 1500 years after farming first appeared in the Seine valley, but once it starts it spreads throughout the island within a few generations.

The descendants of the Levant farmers also spread down into east Africa where their genetic legacy is greatest in present day Ethiopia. Those of the Iranian farmers spread east into the Indus valley and also into the Steppe lands north and east of the Black and Caspian seas. This eastern arm, composed of descendents of probably the first people to domesticate the goat, were able to create herding economies in areas less favourable for the large scale cultivation of the newly domesticated crops, although the latter are still part of the agricultural scene.

In each case, this great technological revolution produces a blending and hence, to some extent, a homogenising of DNA – a feature we are seeing in the world at the present time as a result of our current technological revolutions.

Back in the 1950's Marija Gimbutas, a Neolithic & Bronze Age expert, described how, as these Neolithic farming societies matured, major ritual sites involving large groups become much more evident, {though we now know that Hunter-Gathers had undertook large inter-band ritual activity from at least 12 kya, such as at Gobekli Tepe in Anatolia, and so many large megalithic sites may have begun as Hunter-Gatherer initiatives}. She claimed that though there was more stratification of the society than in H-G bands, there was still a very communal attitude, as exemplified in their burial practices, with no weapons present. She argued that the archaeology suggested a central role was played by women in these farming societies, and violence was nothing like as endemic as it would become when the Bronze Age got underway. Indeed Gimbutas saw such a contrast with what appeared to be the male warrior-dominated society of the Bronze Age that she argued for a substantial replacement of peoples by an incoming migrant group.

She went further and identified this Group with a people coming from the Eurasian Steppes; a people she called *the Kurgans*, from the name long given in those regions to the large individual mounds over pit-graves, that first appeared around this time - a major shift from the communal grave practices of the Neolithic. She also claimed that it was their arrival, not that of the farmers, that spread the Proto- Indo-European language (PIE) through Europe in the West, and to north India in the East. For many decades this aspect of her analysis was dismissed by most archaeologists.