

The Archaeogenetics of Europe

Review

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A new timescale has recently been established for human mitochondrial DNA (mtDNA) lineages, making mtDNA at present the most informative genetic marker system for studying European prehistory. Here, we review the new chronology and compare mtDNA with Y-chromosome patterns, in order to summarize what we have learnt from archaeogenetics concerning five episodes over the past 50,000 years which significantly contributed to the settlement history of Europe: the pioneer colonisation of the Upper Palaeolithic, the Late Glacial re-colonisation of the continent from southern refugia after the Last Glacial Maximum, the postglacial re-colonization of deserted areas after the Younger Dryas cold snap, the arrival of Near Easterners with an incipient Neolithic package, and the small-scale migrations along continent-wide economic exchange networks beginning with the Copper Age. The available data from uniparental genetic systems have already transformed our view of the prehistory of Europe, but our knowledge of these processes remains limited. Nevertheless, their legacy remains as sedimentary layers in the gene pool of modern Europeans, and our understanding of them will improve substantially when more mtDNAs are completely sequenced, the Y chromosome more thoroughly analysed, and haplotype blocks of the autosomal genome become amenable to phylogeographic studies.

Introduction

Around 1.1 million years or so ago [1] members of the genus *Homo* first set foot in Europe. Most of the events that took place in Europe since are beyond the reach of archaeogenetics — the application of genetic techniques to the study of the human past. For a start, nothing from before around 45 thousand years ago (kya) survives, at least in the signatures of the non-recombining genetic marker systems, the maternally inherited mitochondrial DNA (mtDNA) and the paternally inherited Y chromosome. The genetic past is thus very much our past, as archaeogenetics relies primarily on the variation in present-day populations, such that only the ancestral lineages of living subjects are available for inferences. Lineages that became extinct in the past are usually hidden, and there is thus a progressive reduction of information the further back in time we go. Both uniparental

genetic systems, furthermore, suggest complete replacement of archaic hominin lineages by those of anatomically modern humans. Anatomically modern humans and Neanderthals are thought to have co-existed in Europe from around 45 kya until c. 30 kya and perhaps even more recently [2,3] — but if interbreeding took place, as occasionally suggested on the basis of fossil evidence [4], its genetic consequences have since been lost, at least from these marker systems [5,6]. Ancient mtDNA studies have shown us a few glimpses of Neanderthal variation, diverging from modern humans around 550 kya [7–9], although the subsequent Neanderthal genome project has attracted some controversy [10]. Even if we focus on the last 50,000 years or so, it may seem that archaeogenetics can capture little of the dynamics of the growth and development of human communities. Yet, if we take the ‘long view’, advocated by the historian Fernand Braudel [11], and start to focus on the long-term dynamics rather than the ‘crests of foam’ of individual events, then dispersal, colonization and settlement patterns take on a new significance, and archaeogenetics can begin to find its role. Although genetics may capture little of the detail of the development of human communities — the province of historians and archaeologists — it is well suited to identifying dispersal, colonization and settlement patterns. Moreover, focusing on surviving lineages, we are not misled by transient episodes that may be mistaken for the establishment of settlement by archaeologists or palaeoanthropologists.

Geographically, Europe is a western promontory of Asia, surrounded by water on three sides [12]. The oscillations of the Gulf Stream have led to rapid climate fluctuations that likely have had major effects on the spread and extinction of archaic human populations, including the Neanderthals [13]. For modern humans, however, and especially during the warmth and stability of the last 11,500 years (the Holocene), the peninsula has facilitated maritime mobility around the resource-rich littoral zone, leading to dense exchange networks as well as to population growth across the diverse societies that have sprung up amidst its varied and tightly packed ecological zones [12].

Europe is itself not really a continent, geographically speaking; and indeed, Europeans share their basic pattern of mtDNA variation — in other words, the range of major basal clades, or ‘haplogroups’ — with people in Southwest Asia, and to some extent also in Central Asia, as well as — with a substantial reduction in diversity — in North Africa. This is partly true also for the Y chromosome, but with some complications. The mtDNA may be rather more representative of Braudel’s *longue durée* [11] than the Y chromosome, which sometimes seems alarmingly susceptible to founder events [14].

Taking the long view, we can divide the prehistory of modern humans in Europe into five major establishing episodes: first, the pioneer colonisation of the Upper Palaeolithic — itself an aspect of the dispersal of modern humans out of Africa; second, the Late Glacial re-colonisation of much of the continent from southern refugia after the Last Glacial Maximum (LGM); third, the postglacial re-colonization by Mesolithic groups of deserted areas after the end of the Younger Dryas (marking the end of the Pleistocene and

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Box 1

Archaeological industries of Europe and the Near East.

Lower Palaeolithic (c. 2,600–300 kya): *Homo habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*. Simple stone tool technologies: the earliest techniques, e.g. the Oldowan of Africa, were concerned with the production of small flakes, choppers and chopping tools. The Acheulean (from c. 1.5 Mya) is characterised by bifacial stone tools such as handaxes, but some sites with exceptional preservation have yielded wooden artefacts, e.g. spears.

Middle Palaeolithic (c. 300–30 kya): *H. neanderthalensis* and early *H. sapiens*. Technology was geared to the preparation of stone nodules to produce cores, which were used to produce flakes under controlled conditions, e.g. Levallois technology. The Mousterian industries of the Middle Palaeolithic are characterised by triangular stone points, whose margins have been carefully chipped ('Mousterian point'). The flakes were also turned into a wide variety of other tool forms; a few Middle Palaeolithic sites have yielded wooden spears.

Upper Palaeolithic (c. 50–11.5 kya): mainly *H. sapiens*. Characterised especially by blade technology, including smaller bladelets. Bone, antler and ivory working also very common, as is art and symbolic activity. 'Initial Upper Palaeolithic' industries are varied in their tool-types: many in the Levant and on the Russian plain show strong evidence of the use of bladelets, beads and pendants. 'Transitional' Upper Palaeolithic industries, e.g. *Châtelperronian* (France), combine Upper and Middle Palaeolithic attributes, and are widely assumed to have been made by Neanderthals. The *Aurignacian* (c. 45–30 kya), extending across Europe and into the Near East, is characterised by antler projectile heads, a generalised array of stone tool types, and bladelets. The *Gravettian* (c. 33–20 kya) was also spread across Europe, and is defined by stone projectiles and distinct bladelets. It fragments, retreats and simplifies towards the Last Glacial Maximum (LGM), replaced by regionally-specific industries, e.g. the *Solutrean* (c. 24–18 kya) in western Europe — characterised by finely-made bifacially-worked stone points (no bladelets) and copious evidence of art — and the *Epigravettian* (c. 20–10 kya), in Italy and perhaps also in central/eastern Europe, which developed traditions characteristic of the Gravettian. The Late Glacial *Magdalenian* (c. 17–12 kya) created a huge array of stone and bone tool types, including bone/antler harpoons and bladelet tools, and vast quantities of art and symbolism. It is primarily concentrated in mid-latitude western Europe, but is linked with the post-LGM population expansion, reaching northern England and southern Poland.

At the end of the Pleistocene, a series of more localised industries sprang up, as population densities increased and Europe became more wooded, before suffering over a millennium of climatic deterioration in the Younger Dryas.

Mesolithic (c. 11.5–5.3 kya): *H. sapiens*. Bladelet tools are very common, and many assemblages seem to have been geared to the exploitation of aquatic and woodland resources. It ended at different times in different places, eventually giving way to the Neolithic, but lasting longest in northern parts of Scandinavia (e.g. Ertebølle culture of the western Baltic).

Neolithic (c. 10–4 kya): Initially characterised by settled occupations, growing of crops, and later augmented by husbandry of some animal species and the use of ceramic pottery, this was the cultural 'package' that spread from the Levant/Fertile Crescent through Anatolia and into Europe. Stone technology still played an important role, particularly in the production of weaponry.

Neolithic/Copper Age (c. 6.3–4.3 kya): The climate at the beginning of this period turned cooler and drier, triggering changes in economy and society; emerging exchange networks connected metallurgy centres with peripheral areas.

Bronze Age (c. 4.3–2.7 kya): Spread into Europe from the east, characterised by bronze utensils and weaponry, though stone technology still used. Exchange networks further extended, promoting the spread of culture and probably also the major language families known today.

the beginning of the Holocene); fourth, fresh dispersals of Near Easterners with an incipient Neolithic package; and fifth, small-scale migrations along continent-wide economic exchange networks from the Copper Age onward. While all of these remain highly controversial, each has left a legacy that remains like a sedimentary layer in the gene pool of modern Europeans. After initial analyses of mtDNA control-region sequences and Y-chromosome biallelic and microsatellite markers [15–17], complete mtDNA sequences [18] and recent Y-chromosome analyses will form the focus of this review.

The phylogeographic approach combines three elements: a phylogenetic tree, the geographic distribution of lineages on the tree, and the time depth of lineages, especially those that are restricted to a particular area. The timescale is provided by converting the diversity of lineages to age estimates by means of a molecular clock. Although the problem of poor time estimates remains for the Y chromosome, for the mtDNA there has recently been some progress [9]. Precision has been addressed by using data from the entire mtDNA — in the past, estimates were obtained either from just the short, fast-evolving control region or, more recently, from the more informative coding region. However, there has also been concern that purifying selection on the coding

region has led to over-estimates of time depths for recent ages. We now have a time-dependent clock that corrects for this effect, leading to a new mitochondrial time scale for modern human evolution. We here apply this new chronology to the prehistory of Europe.

First Settlement of Europe by Modern Humans

Although there is disagreement as to how modern human behaviour should be defined, symbolic behaviour and long-distance exchange networks seem to be crucial [19], and it is increasingly agreed that it emerged in sub-Saharan Africa over a long period and was established there by around 100 kya [20–22]. Anatomically modern humans, apparently with shell-bead ornamentation [23], appeared briefly in the Near East c. 130–75 kya only to be replaced by Neanderthals by c. 75–45 kya, so they presumably became extinct or retreated back into Africa as the climate deteriorated [24]. Initial Upper Palaeolithic toolkits, characterised primarily by high proportions of blades, appear in the Levant 50 kya and in Europe from 41–45 kya [25,26], although definitive anatomically modern human fossils are not found until 41 kya, at Peștera cu Oase in Romania [27]. Zilhão and colleagues [28] argue for an arrival c. 42 kya; Bar Yosef [29] argues for c. 45 kya, on the basis of the Initial Upper

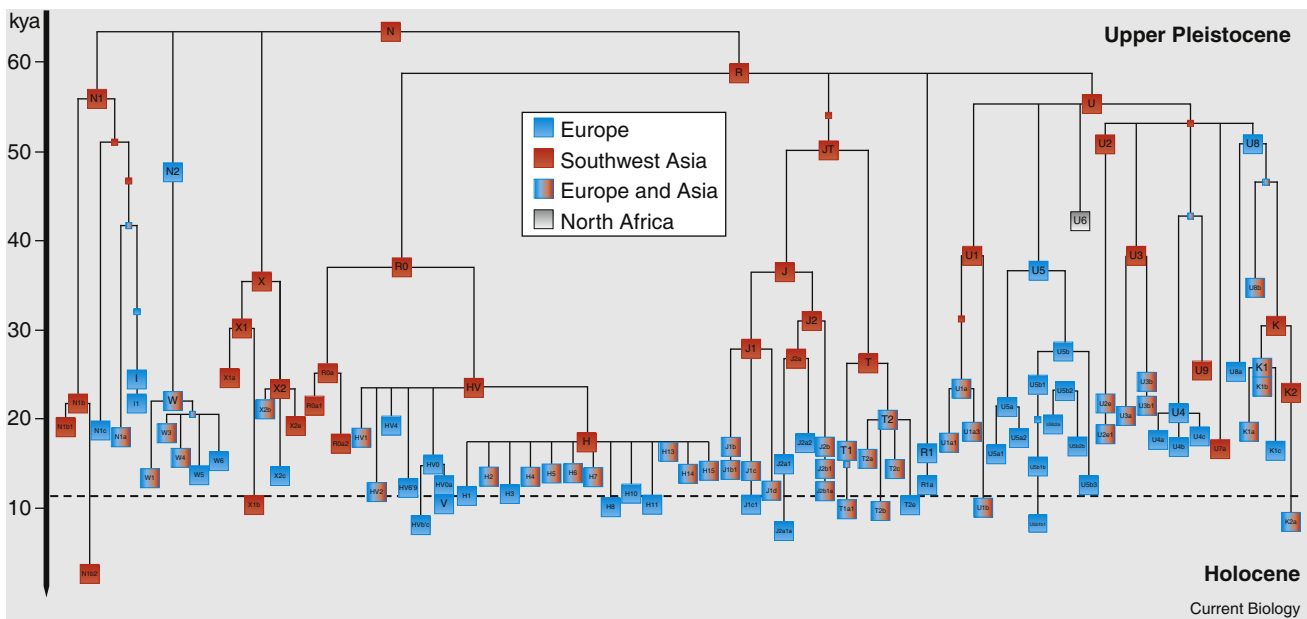


Figure 1. Phylogenetic tree of human mitochondrial DNA haplogroups commonly observed in Europeans, southwest Asians and North Africans. The timescale is based on maximum likelihood (ML) estimates and a time-dependent complete mtDNA genome clock [9]. Haplogroups are colour-coded according to their region of origin (with minor gene flow ignored), although caution is needed given the large sample sizes needed for reliable phylogeographic inferences. Haplogroup nomenclature and an updated dataset can be found at <http://www.phylotree.org> [136].

Palaeolithic material at Bacho Kiro in Bulgaria. Radiocarbon dates at this time depth are, however, unreliable [30].

The genetic evidence has added a further dimension to the story. According to the new mtDNA clock, the settlement of Eurasia was indeed initiated by a single rapid burst, around 60–70 kya, rather than 45–50 kya, and appears to have taken place along the tropical ‘southern coastal route’ from the Horn of Africa via Arabia and South Asia to Southeast Asia and Australasia [31–34]. The settlement of the continental interior took place later, as the coast-dwelling populations began to move up the major rivers. Arrival in the Near East and Europe did not take place until 50 kya, in line with the archaeological evidence. Most likely, the route from the jumping-off point on the southern route (the Arabian Gulf, say) into the Levant was blocked by desert until the climatic amelioration of c. 50 kya [35]. There seem to have been dispersals from the Near East both north-west into Europe and south-west into North Africa, marked by different sub-branches of haplogroup U: U5 in Europe and U6 (together with M1) in North Africa [36,37]. Fossil anatomically modern human remains on the Nile at Nazlet Khater in Egypt, c. 42,000 years old [27], might be attributed to a migration out of Africa via the ‘northern route’, but mtDNA evidence suggests that no such pathway left any descendants in the modern gene pool. Alternatively, it may represent rather the dispersal of Initial Upper Palaeolithic people from the Levant into North Africa [36].

It is unclear from the archaeological and fossil record whether the widespread Upper Palaeolithic industry known as the Aurignacian signals the arrival of anatomically modern humans in Europe. Alternatively, they may have arrived with other Early Upper Palaeolithic industries (Box 1), some of which may rather have been associated with Neanderthals, and were acculturated to the Aurignacian later on [29,38]. The earliest Initial Upper Palaeolithic signal in Europe, the Bachokirian of Bulgaria, which probably dates to 45 kya,

may have been the predecessor of the Aurignacian more generally, which is not found in the Near East until much later. Initial Upper Palaeolithic acculturation of Neanderthals is also still debated, and although the suggestion that the Initial Upper Palaeolithic Châtelperronian of south-west France represents Neanderthal acculturation [39] has been criticised [29,40], it is nevertheless acknowledged that late Neanderthal Mousterian industries probably borrowed blades from the Initial Upper Palaeolithic in their final stages.

The most ancient mtDNA lineages in Europe belong to haplogroup U5 and U8, which appear to have originated within Europe from the root of haplogroup U (Figure 1). U8 appears to have an age of c. 50,000 years in Europe, although its sub-clade K appears in the Near East around 30 kya (Table 1). U5’s presently estimated age of c. 37,000 years may be an underestimate due to dramatic post-LGM expansions of its major sub-branches and is too imprecise to be informative. Indeed, the arrival could have taken place at any time between the current age of the U5 root and that of the ancestral haplogroup U node (c. 56 kya). Effectively, given various approaches to dating and their associated 95% ranges, the age of colonisation based on mtDNA can only be narrowed to 30–55 kya (Table 1). The Y-chromosomal haplogroup I, which, like the mtDNA U5, is largely restricted to Europe, is an obvious candidate for a signal of Initial or Early Upper Palaeolithic male ancestry [41], especially as it is now known to be a sister clade to the Near Eastern haplogroup J [42,43] (Figure 2), as U is with the other main west Eurasian mtDNA basal clades, R0 and JT, but its age is far from clear.

Human population sizes remained low for the next 30,000 years or so, with various mtDNA lineages, such as haplogroup I, arriving from the east [44]. Some may have arrived with the Gravettian toolkit that emerged in central and eastern Europe from around 33 kya, or some might, like U/U5, date back to the first settlement, but their arrival times are very uncertain at present.

Table 1. Age estimates with 95% confidence intervals for mtDNA haplogroups referred to in the text.

Clade	ML complete sequence ^a	ρ estimates			
		Complete sequence ^a	Synonymous ^b	Synonymous transitions ^c	Coding region ^d
U	55.8 (48.5; 63.3)	50.7 (40.9; 60.9)	52.7 (37.8; 67.6)	50.4 (36.0; 64.9)	54.4 (41.9; 66.9)
U8	51.3 (44.0; 58.8)	49.1 (30.4; 68.8)	52.9 (22.2; 83.5)	50.5 (20.8; 80.2)	55.3 (31.2; 79.5)
K	31.6 (24.2; 39.2)	25.1 (16.9; 36.3)	22.0 (15.4; 28.6)	20.5 (14.1; 26.9)	28.3 (17.0; 39.6)
K2a	8.8 (5.4; 12.3)	6.8 (3.7; 9.9)	7.5 (3.1; 11.8)	7.2 (3.0; 11.4)	6.2 (3.5; 8.9)
U5	36.9 (27.5; 46.6)	31.3 (21.4; 41.5)	31.7 (13.0; 50.4)	30.3 (12.2; 48.5)	29.7 (17.9; 41.4)
U5b1 (+16189)	20.4 (14.9; 26.1)	17.4 (9.9; 25.2)	25.6 (6.3; 44.9)	24.6 (5.9; 43.3)	19.6 (8.2; 31.0)
U5b1b1	8.3 (4.4; 12.3)	9.0 (4.8; 13.3)	6.1 (0.7; 11.5)	5.9 (0.7; 11.4)	7.3 (3.6; 11.1)
U5b3	13.0 (9.7; 16.3)	13.2 (8.2; 18.2)	9.0 (5.5; 12.3)	8.1 (4.9; 11.3)	10.2 (6.2; 14.2)
U4	20.8 (15.8; 26.0)	17.8 (12.3; 23.4)	12.7 (7.9; 17.5)	12.2 (7.6; 16.8)	20.4 (13.1; 27.8)
I	24.7 (19.0; 30.5)	25.1 (16.9; 33.6)	22.0 (15.4; 28.6)	20.5 (14.2; 26.9)	28.3 (17.0; 39.6)
H	17.5 (15.6; 19.4)	15.7 (13.3; 18.0)	16.2 (12.9; 19.5)	15.2(12.1; 18.4)	18.1 (14.6; 21.6)
H1	11.1 (9.3; 12.8)	10.8 (8.8; 12.8)	9.5 (7.2; 11.7)	8.8 (6.7; 11.0)	11.0 (9.1; 12.9)
H3	11.5 (8.9; 12.9)	10.8 (8.5; 13.2)	9.5 (6.3; 12.6)	8.8 (5.8; 11.7)	11.1 (8.4; 13.8)
H5	13.9 (10.7; 17.1)	12.4 (7.3; 17.7)	15.1 (3.0; 27.2)	14.6 (2.9; 26.4)	16.1 (7.7; 24.6)
V	11.0 (8.5; 13.5)	10.2 (7.9; 12.5)	10.7 (7.6; 13.8)	10.1 (7.1; 13.1)	13.2 (9.7; 16.7)
J2a1a	7.7 (1.7; 13.9)	7.9 (2.7; 13.3)	5.3 (0; 13.4)	5.1 (0; 13.0)	9.8 (1.8; 16.6)

Age estimates are given in thousands of years and were estimated from a complete mtDNA genome database of 956 West Eurasian samples for ML and 1898 for ρ .

^a Using the time-dependent clock of Soares *et al.* [9], with ML and ρ .

^b Using the synonymous clock of Soares *et al.* [9].

^c Using the synonymous clock of Kivisild *et al.* [142] rescaled by Perego *et al.* [143].

^d Using the coding-region clock of Mishmar *et al.* [144] rescaled by Perego *et al.* [143].

Late Glacial and Postglacial Re-Occupation of Europe

The next major change occurred in the wake of the LGM, 25–19.5 kya. During this time, human populations became increasingly concentrated in refugial areas in south-west Europe, along the Mediterranean, in the Balkans and the Levant, and on the east European plain [45–47]. It is not clear to what extent this involved extinction or migration, or both. In addition, there were probably cryptic refugia in the tundra zone that may have served as stages for leap-frog migration from one part of the continent to another [48].

Several lines of evidence have indicated that the major signal in the modern European mtDNA pool is the re-expansion and resettlement of central and northern Europe in the wake of the major warming phase after 15 kya. The majority of control-region lineages date roughly to this period in the founder analysis of European mtDNAs, and haplogroup V, H1, H3, H5 and U5b1 (Figure 1; Table 1) all appear to have originated in south-west Europe and to have expanded after the Ice Age, with several possible dispersal routes back into western, central and northern Europe [18,49–56]. There seems likely to have been both an Atlantic route into Norway and a central European route into eastern Fennoscandia [51]. The discovery of links (especially within haplogroups V and U5b1b1) between Saami in northern Europe and Berbers in North Africa, at opposite extremes of this expansion, provides a particularly striking illustration of the power of the phylogeographic approach [54], and has exposed the weakness of alternative approaches to genetic data [57].

Nevertheless, the details of the expansion process have remained a little cloudy. Archaeologically, there is a strong signal of both range and size expansion from around 15 kya as the Magdalenian industry spread from the south-west into western, central and northern Europe. The picture is complicated, however, by the fact the Magdalenian does not seem to have any antecedents in the previous Solutrean, the industry of the LGM in the western refugia. Rather, it seems to have emerged from the Badegoulian, which arose in eastern Europe at the LGM and appears to

have then spread into the western refugia [47], perhaps via the aforementioned cryptic refugia. This seems to tie in with the genetic evidence because, similarly, the lineages that evidently expanded from western refugia also appear to have their antecedents in the east. Haplogroup H, the most frequent mtDNA haplogroup in Europe at 45% in modern Europeans on average, seems likely to have arisen in the Near East c. 18 kya. Its founder age in Europe is currently estimated at c. 15,000 years ago, suggesting an entry after the LGM. Because of the more recent founder effect, however, both values may underestimate the true time depth. Similarly, haplogroup V — a sister clade of H (Figure 1) — which also re-expanded from the south-west after the LGM, has an ancestry within Europe, but likely arose ultimately from HV lineages evolving further to the east [49].

However, fresh analyses (Table 1) of the present database of almost 2000 complete mtDNAs from European lineages suggest postglacial rather than Late Glacial expansion times for most of the lineages spreading from south-west Europe (Figure 1). Although H5 (13.9 ky) and U5b3 (13.0 ky) [58] seem to date to the Late Glacial, haplogroups V, H1 and H3 all date to 11–11.5 kya — the end of the Younger Dryas glacial relapse, after which temperatures stabilised at levels similar to today.

It is striking that at present — with the minor exception of the rare haplogroup U5b3, which most likely expanded from the glacial refuge in the Italian Peninsula [58] — the mtDNA evidence points to resettlement of much of western and central Europe only from the Franco-Cantabrian/Iberian refugia. It has been argued that several lineages that are most prominent in eastern Europe, in particular within U4, may be the result of expansions from an eastern refuge, perhaps in the Ukraine [59]. The earlier coalescence times (immediately after the LGM) of these lineages tend to support this notion. Broadly, though, eastern European mtDNAs do not differ dramatically from those of western and central Europeans, although with a small increase in lineages from

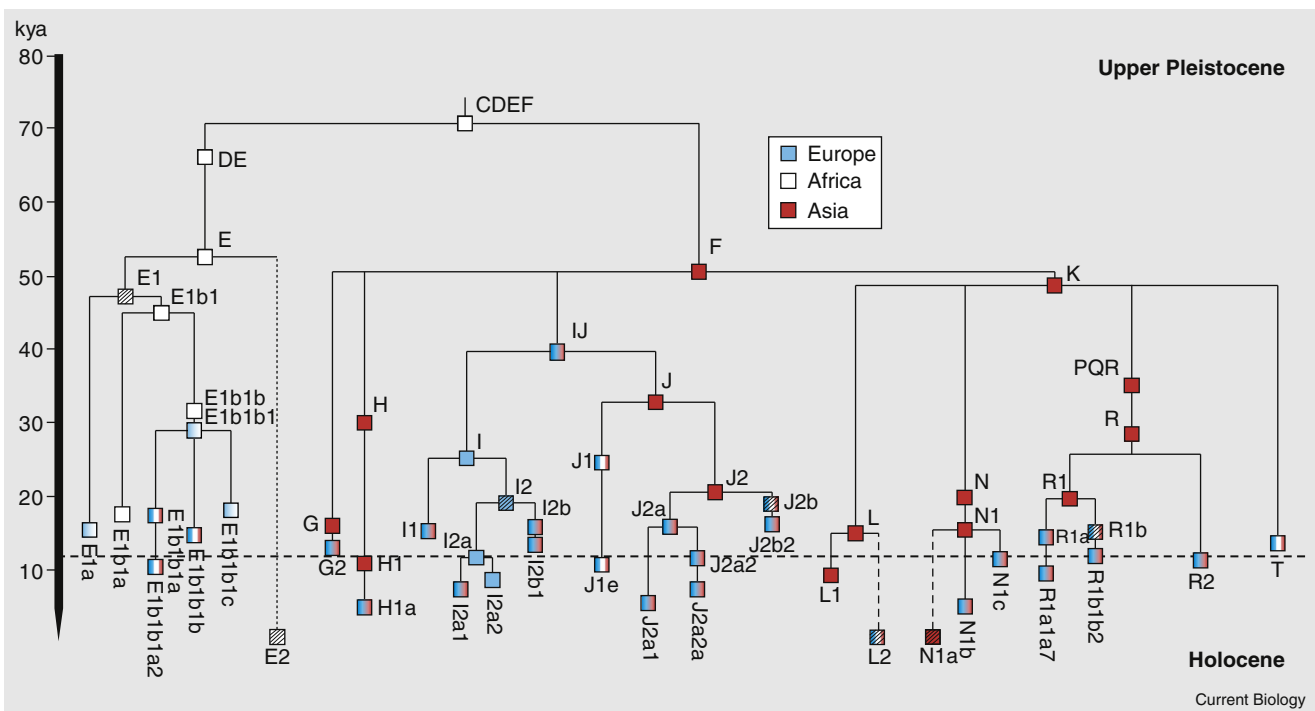


Figure 2. Phylogenetic tree of human Y-chromosome haplogroups observed in Europe. Some haplogroups are shared with Asians, Africans, or both. Nomenclature according to [42] and [137]. Although time estimates depend strongly on the method used and the assumptions made, an indicative timescale is provided, based on previous estimates [41,43,69,96,97,138–141]. The time location of the striped nodes as well as of the nodes at the end of dashed lines is arbitrary due to lack of information.

the Caucasus, Near East and Central Asia [60,61], unlike for the Y chromosome. Y-chromosome distributions may indeed point to other refugia, albeit tentatively at present. Again, Y-chromosome haplogroups implicated in Late Glacial or postglacial expansions form the majority of lineages in the continent today. Several sub-clades of haplogroup I have been suggested to have expanded from the Franco-Iberian (I1 and I2b1) and Balkan (I2a1) refugia, respectively [41,62]. The subclade of I2a, I2a2, is the dominant Y-chromosome lineage in Sardinia [41], which was first settled c. 15 kya [63]. Its age, distribution and postulated source (southern France) strikingly match those of the Sardinian-specific female counterpart (mtDNA haplogroup U5b3a1) [58].

More surprising is the status of Y-chromosome haplogroup R1, which, unlike mtDNA haplogroup I, is not indigenous to West Eurasia but appears to have originated in South Asia, possibly in the early settlements associated with the southern route dispersal [64]. This appears better substantiated than the alternative suggestion of a Central Asian origin [65]. Two major subclades of R1 appear in Europe: R1b in the west and R1a in the north-east. It has been suggested that R1b mirrors mtDNA haplogroup H and the forerunner of V in arriving from the east shortly after the LGM. Then, with the Late Glacial, its main subclade R1b1b2 expanded into western and central Europe [66–68], with a possible expansion at the same time from Anatolia [69]. R1a might then represent an expansion from an eastern refuge, perhaps in the Ukraine, although it might also have been the result of more recent dispersals [62,66,70–72].

The Mesolithic in Europe marked a new way of life: due to a much warmer climate, Europe became densely forested,

megafauna perished and a new mode of subsistence took hold. Hunting preference shifted from reindeer and mammoth to red deer and pigs, and gathering as well as fishing became more important. Over time, coastal communities in particular became more sedentary and underwent considerable population growth, but in the woodlands of central Europe Mesolithic communities appear to have remained less dense and more mobile, although with some suggestions of incipient agriculture or horticulture [73,74]. Nevertheless, for Europe, the Mesolithic and its antecedents appear to have left by far the largest mark on present-day mtDNA and Y-chromosome variation [18,44,66,75].

The Advance of the Neolithic

As the Mesolithic developed in Europe, Holocene populations in the Near East responded to their changed circumstances rather differently. The Natufian people — who could be regarded as the Mesolithic people of the Near East [76] — had already become more sedentary during the Late Glacial, with an increasing reliance on the harvesting of wild grain and, some would argue, by 12 kya were beginning to adopt cereal agriculture, a process that is increasingly recognised to have been gradual and geographically dispersed [77]. Others suggest that cultivation first appeared in the Pre-Pottery Neolithic A that followed the Natufian. The first domestic plants are unequivocally attested in the early Pre-Pottery Neolithic B from 10.5 kya, with the first domestic animals documented later [78]. There has been disagreement as to whether the Neolithic is best thought of as a necessary economic response to a crisis of sedentism generated by the Younger Dryas [79], a response to population pressures, or as a change of religious and symbolic

culture. Cauvin [80] points out that the chronology would seem to support the latter, but other factors may have been important [76,81]. There has also been debate on whether the changes began in Anatolia, the Levant or the more northern part of the Fertile Crescent. Whilst genetics seems unlikely to be able to address the former issue, it might shed light on the latter. For example, the two main lineages of Y-chromosome haplogroup J in the Near East might correlate with the development of agriculture in the wetter northern zone (J2) and pastoralism in the drier south (J1) [82]. However, some of the earliest intensive exploitation of cereals, cultivation and domestication evidence is found in this relatively arid southern area [78]. In any case, J2 is thought to be the most important Y-chromosome marker for the spread of farming into southeast Europe [66,83].

Genetics has been much more extensively used to tackle one of the most long-standing debates in archaeology: how agriculture came to Europe. The 'wave of advance' model argues that the clines in many genetic markers from southeast to northwest Europe reflect a large-scale expansion of Near Eastern farmers to Europe. However, many archaeologists hypothesised either indigenous development of agriculture in Europe or adoption of plants, animals and related technologies from the Near East with only limited and geographically restricted human migration [84–87].

Founder analysis of mtDNAs in Europe, which essentially subtracts ancestral Near Eastern source diversity from lineages in Europe in order to estimate arrival times, suggested that less than 15% of European lineages were contributed from the Near Eastern Neolithic component, with the vast majority dating back to Late Glacial/postglacial times. This suggested small groups of Near Eastern people settling Europe and wide-scale adoption of agricultural technology by indigenous Mesolithic populations [44,88–90]. An initial Y-chromosome analysis (without any founder analysis) reached a similar conclusion, with a figure of 22%, comprising largely haplogroups J and E1b1b1 [66], but this figure was gradually eroded as it became clear that many of these lineages arrived from the Near East, or from North Africa, at times other than the Neolithic [91], as was the case for mtDNA [92–94]. Subsequently, fine-grained studies of the Y chromosome have indeed resolved lineages dispersing from both the Near East and North Africa, providing a much more complex picture. The scale of immigration proposed has been further lessened and a number of distinct episodes, including migration from Northeast Africa [95–98] and expansion of acculturated indigenous hunter-gatherers in the Balkans, or even younger expansions, have been proposed [43,96]. Studies of western European mtDNA and Y-chromosome variation supported this picture, with a largely Mesolithic ancestry not only for the Basques — traditionally regarded as isolated from any Neolithic 'wave of advance' as they speak a non-Indo-European language [99,100] — but throughout Iberia, the British Isles and Scandinavia [67,68,74,101,102]. These regions may still have received Neolithic immigrants, but of autochthonous European rather than Near Eastern ancestry. Though not directly contradicting classical analyses [99], these results imply a lower level of Near Eastern immigration. Some analyses based on simple admixture models suggested much higher levels of immigration, especially into south-western Europe [103–106]. However, these models departed from untenable *ad hoc* hypotheses (effectively assuming a pre-Neolithic genetic homogeneity across Europe), and accounted neither

for back-migration from Europe into the Near East (known to be high from the mtDNA results, as well as from archaeological and literary evidence) nor for subsequent post-Neolithic immigration, lumping all similarities between Europe and the Near East as Neolithic [75].

The low Near Eastern genetic input during the early Neolithic does not imply that there were no large-scale dispersals within Europe acting to spread the Neolithic [107]. There was a pause of several hundred years in the Balkans after the arrival of the Neolithic from Anatolia, before the very rapid spread of the *Linienbandkeramik* farming culture across the North European Plain, leading to a major population increase [108]. Possibly, people who adopted the Neolithic package in south-western Europe then dispersed into central Europe. Strontium isotope analysis has suggested a combination of immigration and contact [109], but the different scenarios can only be tested by much more detailed analysis of genetic patterns within Europe itself.

Analyses of ancient mtDNA from *Linienbandkeramik* sites in central Europe suggest that these populations — which indeed did not show clear evidence of Near Eastern ancestry — did not survive or did not get fully integrated into succeeding populations, a conclusion supported by a drastic population decline inferred from site density and the atypical exploitation system of the *Linienbandkeramik* which was not passed on to its successors [108,110,111]. It seems that the pioneer farming communities of central Europe, however they emerged, left few descendants beyond the Neolithic. In this regard, the fate of the Neolithic pioneers who spread along the rivers of central Europe may be mirrored by that of domestic pigs: modern domestic pigs have a local European ancestry, suggesting indigenous domestication, but analysis of Neolithic remains has shown that domestic pigs were initially imported from the Near East. The mtDNA lineages from these animals subsequently died out, to be replaced by indigenous wild boar lineages that were incorporated into the domestic gene pool [112]. Even more recently, ancient DNA work on Late Palaeolithic and Mesolithic human specimens has been taken to imply large-scale Neolithic replacement in northern and eastern Europe [113], but the data may rather suggest, similar to our re-dating of H and V lineages above, that Mesolithic dispersals from the south and west arrived rather late in northern and eastern Europe. Discontinuity is clearly an important feature of the prehistoric mitochondrial record of Europe, as these authors suggest, but there are major problems with sample size and population substructure (let alone contamination) when analysing DNA from prehistoric human remains.

Although many human Neolithic pioneers may also have been replaced by autochthonous Mesolithic groups [110], better adapted to an unstable ecosystem but subsequently 'domesticated' by Neolithic practices themselves, it is likely that some distinctive Near Eastern Neolithic component to central European mtDNAs exists — for example, some J lineages [114] — but their conclusive identification requires a further improvement in the phylogenetic resolution of haplogroup J. Some J lineages may have arrived earlier than the Neolithic, so that the levels of Neolithic immigration might still be over-estimated, as has also been suggested for the Y chromosome [43,115]. Possible candidates for Neolithic immigration from the mitochondrial genome dataset so far amassed would, however, include J2a1a and K2a, both dating to 8–9 kya within Europe (Table 1). In any case, it

seems clear from the mtDNA control-region and Y-chromosome results that, first, the Neolithic most likely dispersed into Europe by human migration, accompanied by a spread of domestic plants and animals beyond the migrants; second, the immigration from the Near East was minor, and there was substantial adoption of farming by indigenous groups in many parts of Europe; third, internal European migrations from the Eneolithic (Copper Age) onward may have later considerably reshaped the genetic landscape.

The question of the spread of the Neolithic became intertwined with that of the dispersal of the Indo-European languages, as a result of Renfrew's proposal that the Proto-Indo-European language spread from Anatolia with early farming [100,116]. This hypothesis has become less plausible in the light of the mtDNA and Y-chromosome evidence as well as archaeological and linguistic criticisms [117,118]. Although computational analyses of lexical data have been cited in its support [119], historical linguists find such analyses unpersuasive because of the unreliability of word-lists (especially due to borrowing) and because the approach ignores the strong likelihood of convergence and underestimates the rate of language change [120]. The implied reinstatement of glottochronology — dating language splits — has also failed to win backing from linguists [121], and there has been widespread scepticism as to whether archaeology and linguistics can be combined so readily [122]. Paraphrasing Kohl [123], conflating language, culture and genetics is the “cardinal sin” of molecular anthropology. If any consensus remains, it is probably that if there is any single explanation to be found for the spread of Indo-European, it is more likely to lie with the next major change to reshape Europe in the wake of a continent-wide system collapse. Possibly incurred by climatic changes c. 6 kya, this culminated in Sherratt's “secondary products revolution” of the 3rd millennium BC, when a number of agricultural innovations, including wool, the plough, the horse and wheeled vehicles, were introduced and spread within Europe [118,124–127]. This is, however, a time window little explored by archaeogeneticists to date.

Conclusions

Although archaeogenetics has hitherto been graced with few well-defined methodologies, it has been used to test hypotheses and draw inferences in a number of ways. At the more formal extreme, hypothesis-testing procedures based on evolutionary and population-genetics theory suffer from the well-known chasm between the rejection of a null hypothesis and the inference of specific demographic scenarios [128]. We would argue rather for a transdisciplinary approach in which hypotheses are evaluated within the framework of models supplied by archaeology, palaeoanthropology and palaeoclimatology [129]. Founder analysis [44] is an attempt to formalise such an approach to identifying colonisation events.

Although it may seem that the contribution of archaeogenetics to understanding European prehistory has so far been rather small, it has probably led the way to a major reappraisal of the longer-term processes. Archaeogenetics led, for example, to the proposal of a single southern coastal route for the anatomically modern human settlement of Eurasia, and first indicated the major role of the LGM in shaping the demographic history of Europe and therefore the critical role of climate change in European demographic history. Furthermore, in the last ten years or so, archaeogenetics

has been applied to many problems at the regional scale. Although the achievements may often have been exaggerated, issues such as the origin of the Etruscans [93], the Viking settlements in the British Isles [67,130], the Jewish Diaspora [131,132], the Arab slave trade [133] and the trans-Atlantic slave trade [134,135] have all been tackled. We hope that more finely-grained studies will be possible in the future, especially as more of the Y chromosome becomes routinely analysed, and once haplotype blocks of the autosomal genome become amenable to phylogeographic analysis. But to date it is probably the deeper processes of the *longue durée* that have been illuminated most clearly by the new approach.

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