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Chapter 2
Living with archaeogenetics: three decades on

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The aftermath of the Neolithic transition has the longest pedigree of any topic in archaeogenetics and is an ideal lens through which to track the growth of the discipline. Here, I retrace from a personal perspective the history of archaeogenetic accounts of the European Neolithic, including some of the missteps and stumbles along the way. In particular, I emphasize the neglect of the uniparental markers, especially mitochondrial DNA, in much recent work. I argue that incorporating such analyses can move on the narratives written using aDNA from sweeping, broad-brush narratives to more nuanced discussion of the detailed processes involved in colonisation and integration. As a case study, I take a closer look at the mitochondrial and Y-chromosome evidence from Neolithic Britain and Ireland, illustrating the complexity of the picture emerging for both the Neolithic transition and the arrival of Beaker-using people, at the beginning and end of the period.

In the spring of 1990, I replied to an advert in the *New Scientist* for a postdoctoral position working with archaeological DNA (or 'ancient DNA', aDNA). I knew little about archaeology but had become jaded by microbial genetics during my doctoral work in Manchester and was very keen to move closer to the humanities. I began work at the University of Oxford's Institute of Molecular Medicine in August, tasked with solving the mystery of the Anglo-Saxon settlement of Britain by Robert Hedges and Bryan Sykes, with whom Erika Hagelberg had just published the first DNA supposedly amplified from archaeological bone samples in *Nature* (Hagelberg *et al*. 1989). Whether it really had been was a moot point. It was the early days of the polymerase chain rection (PCR, amplifying short fragments of DNA for sequencing) and Bryan had built — and, characteristically, then marketed — his own water-bath-based PCR machines. But within a few months, I was bogged down with the seemingly intractable problems of PCR contamination — of extraneous DNA being preferentially amplified over any traces surviving in the sample. It began to seem that aDNA research might have been born prematurely.

Early days

At the time, the most influential archaeogeneticists, although we tended to call ourselves molecular anthropologists at the time, were Allan Wilson in Berkeley and Luca Cavalli-Sforza, the godfather of human population genetics, in Stanford. They were both working with contemporary data, with research focused on modern human origins and the Neolithic transition in Europe, respectively. I found the 'classical-marker' approach of Cavalli (Ammerman and Cavalli-Sforza 1984) uninspiring, but the phylogeographic analyses of mitochondrial DNA (mtDNA) by Wilson and his colleagues fresh and exciting. It was only three years since the commotion generated by the Berkeley group's big *Nature* paper, published on New Year's Day, 1987 and backing the out-of-Africa model (Cann *et al*. 1987).

As well as phylogeography and mtDNA analysis, Wilson's lab had also pioneered both PCR itself and the recovery of DNA from what always seemed to be called 'ancient remains.' (Despite, or perhaps because of, the release of *Jurassic Park* in 1993, there was a widespread avoidance of over-hyped talk of 'fossil DNA'.) Although Svante Pääbo's 1985 *Nature* cover article on Egyptian mummies (Pääbo 1985) failed to stand the test of time, like most early work with humans as well as claims about dinosaurs, Russ Higuchi's work with the extinct nineteenth-century quagga, published the year before, also in *Nature* (Higuchi *et al*. 1984), showed the potential, since it was unlikely that there was any quagga (or closely-related zebra) DNA lurking in the Berkeley lab waiting to contaminate the PCRs there.

So, I was extremely enthusiastic about Bryan Sykes' proposal that we take our lead from Berkeley and work simultaneously on *both* archaeological samples and modern mtDNA sequences. At the same time, it was Cavalli's research area that we were especially interested in. Since I was soon reading Colin Renfrew's books on the European Neolithic and Indo-European languages, I was very keen to apply Wilson's approach to Europe.

Robert had been asked to carbon-date the Tyrolean Iceman, and showed that he was older than had been expected by the archaeologists. He was dated to the Late Neolithic, around 5200 years ago. But Robert had been given more bone than the accelerator needed, and of course Bryan pushed for us to have a go at his DNA too. By now we had quite a lot of experience and had been fortunate to be able to prepare samples in a different part of Oxford (the Research Lab in Keble Road) and set up PCRs in a different building again, at the John Radcliffe Hospital, next to the Institute of Molecular Medicine.

The project's technician, Kate Smalley, and I carried out independent extractions and PCR sequencing of his mtDNA control-region with (for once) a clear result, which we contributed to a 1994 publication in *Science*, by Oliva Handt and Svante Pääbo in Munich — the official group assigned to the DNA analysis (Handt *et al*. 1994). Despite months of patient PCR cloning work, they had been struggling with the sample they had received, which seems to have been less generous than the one given to Robert, and, in the end, we sent them some of ours to confirm the result. We promoted it as the first case of an aDNA sequence authenticated by replication in two different laboratories.

We also managed to convincingly sequence some 4000-year-old Archaic Indian samples from Newfoundland. But after four years' hard slog, that was pretty much our only success in terms of aDNA at the time. Despite our seemingly modest targeting of only 300 or so base pairs of mtDNA, the Anglo-Saxons had pointedly refused to provide us with any useful data (Richards *et al*. 1993; 1995). The problems with contamination seemed overwhelming and we started to think that they might be insurmountable. It seemed that the bubble might have burst. In 1995, I moved to working full-time on contemporary human mitochondrial variation. We heard that Svante had decided to abandon working with human aDNA at around the same time (Pääbo 2014).

Our single major success of the 1990s, the Iceman sequence, was only 350 base-pairs (bp) long. This was a dozen or so years before 'next-generation DNA sequencing' (NGS) took off. NGS revolutionised

not only genomics in general, but aDNA work in particular, because it meant we could work with extremely short fragments, and that we could recognise damage signatures, making the confident authentication of archaeological sequences finally a reality. By then I was at the University of Leeds where I experienced the revolution first-hand. Luca Ermini, a visiting student from the lab of Franco Rollo, one of the pioneers of extracting aDNA from plant remains at the University of Camerino (Ermini *et al*. 2008). The 3.2 billion bp of his whole genome came only four years later (Keller *et al*. 2012). While his mtDNA lineage was virtually extinct in the present day, the rest of his genome turned out to look like that of a Sardinian. There was a perfectly simple explanation, but it was years before we realised what it was.

Finding farmer founders

We did not completely abandon aDNA in the 1990s. But we did focus most of our attention on modern mtDNA patterns. I had been lucky enough to be contacted early on by an enthusiastic young German chemist (and Anglophile) Peter Forster and, through him, to have met the unorthodox graph theorist Hans-Jürgen Bandelt in Hamburg who, in a way, became my scientific 'guru'. With the help of their insights and expertise, we learnt to analyse the lineages graphically with networks, rather than with the parsimony-tree approach for which Allan Wilson's group had been severely lambasted. And they also developed a very simple molecular-clock dating approach, termed 'ρ dating', that could be used hand in hand with the networks, a method that, despite mathematically rather illiterate comments in some quarters, stands up perfectly well today (Macaulay *et al*. 2019). Peter also laid the groundwork for what we came to call founder analysis – a heuristic approach to dating migrations. In essence, this is simply subtracting the source variation — that is, the mutational variation that arose before arriving in a particular sink population — from the molecular age estimates in a particular sink population. In this way, we can convert an overall coalescence age — based on the total variation in a sink population — to a migration time, by dating the founder lineages that arrived when the population formed (Forster *et al*. 1996; Saillard *et al*. 2000; Macaulay and Richards 2013).

In a way, this was also what the Berkeley group had been doing when they estimated the age of the non-African lineages to date the out-of-Africa migration. It was also the approach of someone with an equal claim to Wilson to have pioneered human mitochondrial analysis, working initially on Native Americans and later also on Europeans: Antonio Torroni, in Rome (Torroni *et al*. 1993; 1996), who became another close colleague. Although sometimes misunderstood by more conservative population geneticists, this approach has been a keystone of our phylogeographic analyses of contemporary uniparental marker variation ever since.

It was more complicated for Europe, where the lineages were more entangled with those of the assumed Near Eastern source, than for America. Even so, our innovations were essentially small tweaks to the phylogeographic approach of the earlier work — in particular, to help head off some of the storm of criticism that had assailed the Berkeley group from all sides in the early 1990s. Founder analysis wasn't quite the chronological dimension we'd like to have got from aDNA, but it gave us a handle on approaching archaeological questions with modern variation.

Using this approach, we tried to evaluate the scale of the Neolithic dispersal into Europe and the extent to which the local Mesolithic populations had contributed to the ancestry of Europeans. We

did this rather heuristically in 1996, and more formally and with a much larger dataset in 2000, by which time Hans had thrown himself into the task of tightening up the analysis, and we were now working closely with Vincent Macaulay, a Bayesian refugee from physics (Richards *et al*. 1996; 2000).

Unfortunately, what I thought we had achieved seemed to get obscured by the smoke created by our intruding into what turned out to be an area of major contention. When Peter and I identified a particular set of lineages (within what later became known as haplogroup J) with a distinct pattern in Europe and clear Near Eastern ancestry, my immediate response was: *We've found the farmers!* But the implication was that a good three-quarters of modern European maternal ancestry was pre-Neolithic. Bryan's response, therefore, which was undoubtedly what generated the headlines (and a *New Scientist* cover, seven years after that advert for my job), was: *Cavalli got it wrong*. Thus, we ended up in a miniature version of the kind of storm suffered by the Berkeley group over human origins.

Frustratingly, we were frequently regarded as supporting the cultural diffusion of farming across Europe, when in fact we were proposing a pioneer-dispersal model, involving leapfrog colonisation of Near Eastern migrants, with later assimilation of Mesolithic hunter-gatherer groups into the farmer-islands. It was certainly a view that emphasised the contribution of the indigenous inhabitants of Europe, along the lines of Marek Zvelebil's view from archaeology (Zvelebil 1986; 1995; 2000; 2001a; 2001b) but also of dispersal and colonisation (Rowley-Conwy 2011), and not just from the Balkans or south-east Europe (Zvelebil 2001a) but also from the Near East. Most of us thought of ourselves as refining Cavalli's 'demic diffusion' view, rather than overturning it, although it is fair to say that, like Marek, who referred to the image of 'Panzer divisions' (Lewin 1997), we were not too enthusiastic about the idea of a 'wave of advance'.

Ancient DNA strikes back

I am not sure this was very wrong, as far as it went, but by comparing Europe *en bloc* with the Near East *en bloc*, we underestimated the demographic impact of those pioneers in central and western Europe. When the first ancient mtDNA from Mesolithic central Europeans began to appear in 2009, most carried haplogroups U4 and U5, with earlier Palaeolithic Europeans also including other branches of haplogroup U — mainly U8b and U2e (Bramanti *et al*. 2009). Haplogroup U branched off from other lineages around 50,000 years ago, and we had proposed it being carried by the earliest Upper Palaeolithic populations. But we also saw haplogroups H and V, T2 and K (which is actually a part of U8; by no means all of haplogroup U was indigenous to Palaeolithic Europeans) and later on even parts of J, as arriving — or, at any rate, spreading across most of Europe — with the Late Glacial (Soares *et al*. 2010).

Now, we not only have data from pre-Neolithic and Neolithic human remains, but much of the data are not from short mtDNA sequences but whole mitochondrial genomes (or 'mitogenomes') (Brandt *et al*. 2014; Posth *et al*. 2016). And as a result, we now know that whilst many of these lineages are indeed seen in eastern and southern Europe before the Neolithic, they are in quite a small minority there — the U4 and U5 lineages mostly predominate — and, crucially, they were already present in Anatolia in the Early Neolithic.

Moreover, aDNA from hundreds of Early Neolithic Europeans, coming especially from Wolfgang Haak at the Max Planck Institute in Jena, David Reich in Harvard, and their colleagues, showed that the 'Neolithic mitochondrial package' included more than just haplogroups J, T1, U3 and a few sub-clusters of H and W that we had proposed in 2000 (Brandt *et al*. 2013; Haak *et al*. 2005; 2010). The main Early Neolithic lineages in central Europe were J1c, T2b, T2c, T2e, K1a, some V and H, a few assimilated U5 lineages (but less than 5%) and, most surprisingly, N1a1a. In the south, the situation was even more varied. We had J2b, K1b and X2b lineages as well, some T1a, more (and more diverse) haplogroup H (although still nothing like the high frequencies at which we see it today), and a larger and more diverse selection of assimilated Mesolithic haplogroup U lineages. There were fewer N1a1a lineages, but they were still there, and we could trace their ancestry right back into the western Anatolian Neolithic.

N1a1a is vanishingly infrequent in modern Europeans, and in fact the frequency of the other lineages in the LBK (*Linearbandkeramik*) was also drastically different from in present-day central Europeans. The conclusion had to be that the pattern for Europe had not been fixed in the Early Neolithic but had been overwritten later on. This invalidated a crucial assumption of Cavalli's, that the first, and therefore most important, principal component of European genome-wide variation was due to the Neolithic expansion from the south-east into the Mesolithic population of Europe. It was an assumption that we had made ourselves when archaeologists often pointed out to us that subsequent population movements might have smothered the Neolithic pattern.

It was this assumption that led us to overlook statements about the Late Neolithic Corded Ware like this one from Andrew Sherratt: '...one of the largest and most revolutionary transformation(s) of European prehistory' (Sherratt 1994, 193). Or rather, we imagined it was largely a social and cultural revolution, based on the formation of new contact networks, rather than a demographic one as well (Soares *et al*. 2010). This was why the conclusions from the genome-wide work from the Max Planck/Harvard and Copenhagen labs respectively, published back-to-back in *Nature* in 2015 (Allentoft *et al*. 2015; Haak *et al*. 2015), seemed so ground-breaking from our point of view.

They showed that genetic patterns changed enormously in Europe in the third millennium cal BC, due to dispersals from the Pontic-Caspian steppe. They did this mainly using genome-wide and Y-chromosome data, although it had been prefigured by an earlier study of Corded Ware and Bronze Age mtDNA that pointed to the introduction of new maternal lineages too (Brandt *et al*. 2013). One with an extraordinarily wide distribution and shallow time depth, for example, is T1a, a rare lineage which we had attributed to dispersal earlier in the Neolithic (Pala *et al*. 2012). T1a did indeed spread to a limited extent along the Mediterranean with the Early Neolithic, but it was distributed much more widely across Europe and Asia, from Eastern Europe via the Caucasus, in the Late Neolithic/Early Bronze Age. Its distribution matches that of a new genome-wide component, with its source ultimately in Iran, that spread across the Caucasus on to the steppe and then both west and east. It reached almost every part of Europe, bar Sardinia. This was why the Iceman, who lived before this development, resembled present-day Sardinians, who somehow isolated themselves from this continent-wide transformation.

We know now that there was assimilation of hunter-gatherers in Europe after around 6000 years ago, throughout the Middle Neolithic and into the Late Neolithic, especially on the fringes, such as

the western Mediterranean, the regions adjacent to the North Sea, and east-central Europe, but also in the interstices in central Europe (Bollongino *et al*. 2013). This had been expected on archaeological grounds (Sherratt 2004; Zvelebil and Dolukhanov 1991), although the case had been overstated for western Europe (Zvelebil 2001a). But there are two ironies when trying to look back on this from present-day variation.

First, some of the groups with the most assimilation succumbed to the newcomers from the east and much of that variation was lost forever, although it survives in north-east Europe more than elsewhere (Mathieson *et al*. 2018; Saag *et al*. 2017; Saag *et al*. 2021). But the second concerns the newcomers themselves. Pastoralism on the western steppes emerged from intermarriage between local steppe hunter-gatherer elites and Neolithic groups (primarily women) dispersing from Mesopotamia and Iran via the Caucasus (Wang *et al*. 2019). This meant that not only was a fresh set of Near Eastern Neolithic lineages introduced into Europe (on the female side), but a fresh set of Mesolithic European hunter-gatherer lineages were introduced (on the male side), alongside, of course, the mixed heritage in the rest of the genome.

Complicating things even further, when the Corded Ware-using groups formed in eastern Europe, they did so by incorporating yet *another* substantial ancestry component — that of the local Neolithic of eastern Europe (again, evidently mainly women) — who were, in turn, themselves largely descendants of the early pioneer farmers of east-central Europe (Papac *et al*. 2021; Saag *et al*. 2021). But overall, the upshot was that, when we look back from the present at lineages across Europe from the end of the Neolithic, the hunter-gatherer ancestry we see is not primarily due to assimilation of western and central European Mesolithic groups. Much of it derives from the eastern European Mesolithic.

Having said this, in a final twist, it looks as if the eastern European Late Mesolithic *itself* was the result of a merging of local hunter-gatherers with others who had expanded from western and central Europe in the postglacial. This can be seen in the appearance of U5b2 lineages in the east, alongside the more local U5a and U4. Moreover, there seem to have been local turnovers and replacements of populations throughout the Mesolithic and Neolithic in northern and eastern Europe. In retrospect, the assumption we shared with Cavalli that we might be able to recover the main episodes solely from today's genetic patterns seems overly ambitious. At the same time, in the light of these nuances, the new popular narratives framed around 'mass migrations' seem crude and simplistic.

Complications in south-east Europe

Even given these subtleties, we were left with some nagging doubts. Some researchers have been quite dismissive of both mtDNA and phylogeographic analyses over the years, but from our perspective there had not been any knock-out criticisms. The founder analyses that we have performed over the years continued to suggest that around three-quarters of the present-day mitochondrial lineages arrived before the Neolithic in Europe. How then could we explain these results? Were they really wrong?

Although our early analyses, based only on short mtDNA sequences, lacked the clear resolution that we can see with complete mitogenomes, this does not seem to have skewed the results very much

— we see the same pattern with the latter. Again, we have worked very hard on the mitochondrial molecular clock in the intervening years, and we feel quite confident about the mutation rate we are using, which is also quite well supported by completely independent studies, some based on aDNA calibration points (Soares *et al*. 2009; Fu *et al*. 2013; Pala *et al*. 2014).
Moreover, the results should not be skewed by subsequent movements within Europe. Nor should they be adversely affected by subsequent movements into Europe from the Near East – in fact, such movements are what it is expressly designed to detect. And if there had been heavy back-migration from Europe to the Near East — from sink to source — since the Neolithic, that should reduce the estimates, not increase them (Richards *et al*. 2000).

One very real possibility is that the modern Near East just does not represent the source adequately, but the aDNA data that we have do not really support that view. There has been a huge amount of mixing between the two distinct source pools of the Near East — the western and eastern limbs of the Fertile Crescent — and some Iron Age and medieval arrivals from Central and East Asia, but not much more migration from Europe than we had already allowed for in the 1990s. For example, we still see N1a1a in Anatolia today, despite its dwindling presence in Europe since the Early Neolithic. So why do we continue to obtain this result, if it has been discredited by aDNA studies? There is a nagging feeling that the results might still be telling us something meaningful after all.

Pedro Soares tested this using data from haplogroups J and T, generated during a PhD project co-supervised by Luisa Pereira (Pereira *et al*. 2017). Previous work by Maria Pala had suggested that these haplogroups might not have dispersed entirely from the Near East in the Neolithic, but that some lineages may already have reached south-east Europe from the Levantine glacial refuge after the Last Glacial Maximum (Pala *et al*. 2012). This was backed by aDNA evidence for haplogroup J2b1 dating to around 10,000 years ago, in Mesolithic Sardinia (Modi *et al*. 2017).

So, we separated the mitogenome lineages from central and eastern Mediterranean Europe from those in Iberia and central/northern Europe when we carried out the founder analysis. When we did this, we found that two-thirds of those in Mediterranean Europe dated to the Late Glacial, and only one-third to the Neolithic. But when we dated those in Iberia and central/northern Europe, including Mediterranean Europe with the Near East as the source, the situation was reversed — most of the lineages dated to the Neolithic. Pedro's group have since found a similar pattern for other lineages — most notably, including some from haplogroup H.

The simplest explanation for this pattern seems to be that the Neolithic Near East was not the sole source for Neolithic Europe but that some lineages had already expanded into the eastern Mediterranean in the Late Glacial and were assimilated by the later Neolithic pioneers moving across the Aegean from Anatolia, 9000 years ago. Perhaps this is also hinted at by the presence of lineages belonging to the supposed 'Neolithic mitochondrial package' in the Iron Gates Mesolithic, including various haplogroup K and H lineages, and indeed J2b1, as also seen in the Sardinian Mesolithic (Mathieson *et al*. 2018; Modi *et al*. 2017).

There are further complexities when we look at the patterns of uniparental markers across Europe. Although the genome-wide picture has suggested to many something like Jared Diamond's portrayal of early farmers steamrolling across the continent (Diamond 1997), the Y-chromosome data is much

more equivocal. The male lineages most clearly associated with Neolithic dispersal from the Near East are G2a2-L1259, along with the much less frequent H2d-ABR039, H2m-SK1192, E1b1-P2, T1a1-L162, and perhaps J2a-M410. Yet these lineages form less than three-quarters of continental Early Neolithic male lineages, in the most recent Harvard database, although they do comprise all of those amongst the LBK heartland in Germany and Austria. What is more, in south-east Europe, and the Mediterranean as far as Iberia, they are down to less than half. Numerous male lineages from the Mesolithic persisted into the Neolithic in Europe: C1a2-V20 and R1a1-M459 in southeast Europe, R1b-M343 in Mediterranean Europe and, most strikingly, I2a1-L460 across the continent. The British Neolithic carries only I2a1-L460 male lineages, with no G2a2-L1259 whatsoever.

This is not the heavy assimilation we see later during the Middle Neolithic in the genome-wide patterns. These male lineages look to have been assimilated very early, some in south-east Europe, some in the south-west, and possibly some in the north-west. There is little evidence of early assimilation in central Europe, fitting nicely with the archaeological picture of a major, rapid demic expansion there (Price *et al*. 2001). But either we are seeing a significant sex bias, or the male lineages are corroborating our suspicions regarding the female lineages, with a high level of early assimilation in south-east and Mediterranean Europe.

The Neolithic of Britain and Ireland: the view from the uniparental markers

This brings us finally to the situation in Britain and Ireland, which is different again. For such a tiny corner of the world, trying to tease out the pattern of settlement using contemporary variation is a fairly hopeless task, although numerous efforts were made, and a few broad conclusions, such as the influence of Norwegian Vikings on the Northern Isles, were possible (Wilson *et al*. 2001; Leslie *et al*. 2015). The impact of aDNA work on our understanding has therefore been profound.

The genome-wide aDNA data of the past few years have confirmed that Britain and Ireland were resettled both in the Early Neolithic and the Chalcolithic (Cassidy *et al*. 2016; Olalde *et al*. 2018; Brace *et al*. 2019), thus supporting a form of pioneer colonisation, appearing first in south-east England from northern France and dispersing throughout Britain and Ireland (Whittle *et al*. 2011; cf. Sheridan 2010; Rowley-Conwy 2011). And we have finally been able to revisit the issue of the Anglo-Saxon settlement, which, again, we see had a major, lasting impact on the British gene pool (Gretzinger *et al*. 2022).

But, of course, there is much more to it than that, just as Booth *et al*. (2021) have argued in elegant detail for the Beaker period. Archaeogeneticists have a distressing tendency to write each paper as though they have solved one of the perennial questions of archaeology, or to posit new, and often spurious, questions that they know they can answer (or have already answered but not yet published), whilst ignoring gaps that seem obvious to everyone else. In practice, notwithstanding the enormous and genuine progress of the last few years, no archaeological 'problem' of any interest is ever quite resolved by the appliance of science, as, for example, Hofmann (2015) has spelled out in the case of the LBK. The problem is not helped when some geneticists do not engage sufficiently with archaeological (or linguistic and other) expertise, and work with simplistic, discredited or outdated models (Pluciennik 1998; Vander Linden 2016; Fernández-Domínguez 2018; Furholt 2018; 2019; Bandelt *et al*. 2002) — although, to be fair, efforts are being made to address this (Eisenmann *et al*. 2018) — or ignore the political implications of their work (Hofmann *et al*. 2021).

In the case of Neolithic Britain and Ireland, there has been little attention yet devoted by archaeogeneticists to the scale of colonisation, the number of colonisation episodes, or the routes taken, in contrast to the intensive work by archaeologists (e.g. Sheridan 2007; Whittle *et al*. 2011; Cummings 2017; Shennan 2018). And, having worked with uniparental markers for thirty years, my close colleagues and I are frequently surprised at the extent to which they (especially the mtDNA) have been neglected since the dawning of the NGS age, just at the time when there is a torrent of new and highly informative data from the avalanche of ancient whole-genome studies (Bandelt 2018). In fact, of course, the phylogeographic approach becomes far more powerful when aDNA is available in large volumes. The uniparental markers can help us to pinpoint the fine details (let alone difference in behaviour between the sexes) that may otherwise be overlooked with the all-encompassing but blunt approach of the whole genome (Richards and Macaulay 2013). It is worth briefly taking a closer look at the British-Irish case to see what we might learn if we paid more attention to the uniparental systems.

Male 'forager' lineages

There are a quite lot of data now for the British and Irish Mesolithic and Neolithic (there are no pre-Mesolithic data as yet): 92 males with whole-genome profiles on the Harvard database (Cassidy *et al*. 2016; 2020; Olalde *et al*. 2018; Brace *et al*. 2019; Sanchez-Quinto *et al*. 2019; Dulias *et al*. 2022). Of course, most of these are Neolithic; only five are Mesolithic (there are a further three Mesolithic females), of which one is typed to only poor resolution, as is also true for three of the Neolithic samples. We should also bear in mind that Y-chromosome haplotypes and their place in the phylogeny for aDNA are estimates; they are always based on scoring fragmentary data, with many gaps, and may (for example) be positioned deeper in the tree than they should be, due to missing data towards the tips. Finally, Y-chromosome nomenclature is a huge challenge for almost all of us, because of the tradition that the subclades in the tree be renamed wholesale almost every year by ISOGG, the organisation recognised as setting the standard. Since the names of lineages routinely switch in confusing ways, to accommodate the sprouting of new branches caused by the addition of new data, it is important to clarify the terminal single nucleotide polymorphism (SNP) defining whatever haplogroup we are talking about, cumbersome as it may seem.

The Neolithic male lineages in Britain and Ireland include a diverse array of mainly I2a1b-M438 and I2a1a-P37 lineages (in a similar 2:1 ration in both regions), exclusively I2a1-L460 in Britain, but with two Irish individuals belonging to haplogroup H2-P96. These are lineages with a source in the Near East, possibly the distinctive eastern Fertile Crescent Neolithic population, and thought to have dispersed into northwest Europe via the Mediterranean route (Rohrlach *et al*. 2021). All the British and remaining Irish Neolithic male lineages belong to haplogroup I2a1-L460, with large numbers of closely related haplotypes within the two subclades, I2a1a-P37 and I2a1b-M436. Overall, the more common lineages are shared between Britain and Ireland, suggesting that there was likely a common pool, and that the unshared lineages are just due to sampling.

The five male Mesolithic individuals from England, Wales, and Ireland all belong to haplogroup I2-M436. Of the four that are well typed, all belong to one of the two subclades of I2a1-L460: three I2a1b-M436 and one I2a1a-P37. There is a single individual carrying I2a1a2-M423 in Ireland, one with I2a1b1-M223 in Wales, and two with I2a1b2a-L38: one in Ireland and the other in England, at

the famous Cheddar Gorge in Somerset. These are clearly very closely related to those seen in the Neolithic, and several of them are shared with Neolithic individuals. As a result, Brace *et al*. (2019) suggested 'stability' on the male lineage from Mesolithic into Neolithic, in contrast to their argument for almost complete Neolithic replacement of the mtDNA and autosomes.

However, these lineages are also shared with both other Mesolithic and other Neolithic groups in western and northern Europe, so we cannot assume that the sharing of a local lineage implies local ancestry and assimilation. In fact, many Mesolithic Y-chromosome lineages are both ancient and extremely widely dispersed, so these could have arrived from almost anywhere in continental Europe. For example, the major western Neolithic lineage, I2a1a2-M423, dates to 14,200 years (YFull: https://www.yfull.com/tree/; Adamov et al. 2015) and is seen in the Mesolithic of Ireland, Luxembourg, and Sweden. It is very frequent in an arc across the Neolithic of Atlantic Europe, in Iberia, France, Ireland, Britain (in fact, predominating in the Neolithic of Orkney, where it persists into the Bronze Age), and Scandinavia, and virtually absent elsewhere (Dulias *et al*. 2022).

So, although the most parsimonious explanation might at first sight seem to be local assimilation in Ireland or Sweden, given the high frequency and diversity of these lineages in Iberia and France the explanation is probably more complex. They comprise more than a third of I2a1 lineages in Neolithic France and Iberia and more than half of those in France alone (Brunel *et al*. 2020; Rivollat *et al*. 2020; Seguin-Orlando *et al*. 2021). I2a1 itself comprises almost two-thirds of lineages in France and Iberia but only around 15% in central Europe, where I2a1a2 is almost absent.

I2a1a was involved in the Late Glacial Magdalenian expansions across Europe, dispersing as far as the Serbian Iron Gates and Mesolithic Ukraine, but with I2a1a2 present in both France and Spain in the Early Neolithic. I2a1b is seen earliest in the Mesolithic of Italy, although it appears rapidly across Europe, again from Britain and France to the Iron Gates and Ukraine, so it perhaps may also have been caught up in the Late Glacial dispersals, although it is curiously absent from (well-sampled) Iberia before 4000 cal BC. Thus, even though both are present in Mesolithic Britain, I2a1a and I2a1b might well have been assimilated from Mesolithic enclaves on the Mediterranean, such as that suggested in northern Italy by Broodbank (2013, 150) and then dispersed both into north-west Europe along the Rhône and Loire rivers (the Chasséen) and around the Mediterranean coast to Iberia (Shennan 2018), perhaps with further episodes of assimilation of related lineages *en route*.

Female 'farmer' lineages

This is not to say that there was no assimilation within Britain and Ireland, so that the Mesolithic hunter-gatherers were completely lost. Brace *et al*. (2019) themselves pointed to minor levels of continuity into the Neolithic in Scotland, and we have identified at least one potentially local Mesolithic mitochondrial lineage that has survived into the present day (Dulias *et al*. 2022). Interestingly, if we examine the British and Irish Mesolithic mitochondrial lineages, we see a rather different pattern.

There are six distinct lineages amongst the seven well-typed Mesolithic individuals, of which, curiously, three belong to the Eastern European U5a2, with the remainder belonging to the West European U5b1 and U5b2. (A caveat to what follows is that we are looking at the level of subclade

resolution here; these 'lineages' are far from being identical at the individual sequence haplotype level.)

What is especially intriguing is that, because the U5a2 lineages are on the edge of their range, they do not match with other western, central or Mediterranean European individuals either in the Mesolithic or Neolithic, but two of the three do match with Neolithic individuals from Britain (and one subclade seen in Mesolithic Ireland, U5a2d, persists into present-day England). Indeed, the same seems to be true for one of the U5b1 lineages (at least, it is seen in the English Chalcolithic), and the U5b2a lineage also lacks matches in western European lineages that postdate the Upper Palaeolithic. With the caveat noted above, that these observations should be confirmed by a more detailed phylogenetic analysis of the lineages (which, as for the Y chromosome, is challenging with aDNA because of the poor quality of the data), this makes assimilation the most likely explanation for all of these lineages: that is, more than half of the known local Mesolithic maternal lineages.

The basal U5a2 lineage, on the other hand, lacks matching lineages anywhere, and the other U5b1 lineage is seen in Mesolithic individuals in northern Italy, as well as numerous Iberian and French Neolithic individuals, supporting the suggestion above that there was assimilation of Mesolithic people by Neolithic immigrants along the Mediterranean before they dispersed north-west.

Still, these likely assimilated hunter-gatherer lineages only amount to around 2% of maternal lineages in the Neolithic of Britain and Ireland overall. Even if we sum all of the U5 lineages in Neolithic Britain and Ireland, they only amount to 13% of the lineages, and the majority of these were most likely assimilated on the continent. So, overall, it does seem that the uniparental markers support the conclusions from the genome-wide evidence that rather few traces of the local Mesolithic people survived into the Neolithic. This is concordant with the view of some (by no means all) archaeologists that the insular Mesolithic population was thin on the ground and perhaps dwindling already well before the arrival of the newcomers (Tolan-Smith 2008; Mallory 2017), in contrast to the intensification that was taking place around the coasts of Atlantic Europe and at the Iron Gates, but similarly to inland continental Europe (Rowley-Conwy 2011).

On the other hand, the detailed analysis of mtDNAs raises the possibility that perhaps most of the local population were indeed assimilated by the newcomers (Whittle *et al*. 2011), but that there were relatively very few of them to assimilate, or that the new arrivals spread more rapidly. The precision with which this implies we can tease out both the survival of those lineages, and the sources of those that arrived subsequently, suggests a fruitful avenue for future research that investigates the fine processes involved, evaluating the extent and nature of colonisation and integration or assimilation in different times and places, rather than sweeping summaries concerning replacement of one population by another.

We can take a similar approach to the next major 'replacement' in Britain: the arrival of Beaker-using people just after 4500 years ago. Again, genome-wide and Y-chromosome studies have pointed to a replacement of 90–95% (Olalde *et al*. 2018) but once more — and to a greater extent than with the Mesolithic-Neolithic transition — a detailed look at the mitochondrial lineages suggests a greater degree of continuity, and a sex bias undetected by genome-wide approaches. Whilst less than 6% of the male Neolithic lineages survived into Beaker, Chalcolithic and Bronze Age Britain, around 20% of

the mitochondrial lineages persisted, suggesting greater assimilation of female than male lineages (Dulias *et al*. 2022), consistent with the much more complex and nuanced process inferred by Booth *et al*. (2021). Moreover, the process was, not surprisingly, far from monolithic, depending on social configurations at the local level. For example, in Orkney, we found that the situation was reversed, with the autosomal and female lineages being largely replaced, whilst the Neolithic male lineages persisted until at least the Middle Bronze Age (Dulias *et al*. 2022).

Conclusion: the end of the beginning?

All of this is a far cry from Cavalli-Sforza's early work on the wave of advance in Neolithic Europe. Even so, is it fair to describe his work as being 'wrong', as does David Reich in his popular account of the NGS revolution (Reich 2018)? Was Cavalli really wrong and has aDNA now finally got it right? Has there really been a huge paradigm shift in archaeogenetics?

Thanks to NGS, aDNA has undeniably come of age. At Huddersfield, we now have a thriving aDNA Facility, led by Ceiridwen Edwards, and have run a successful Leverhulme Trust doctoral programme that generated hundreds of ancient genomes. I have been astonished at what she and they have been able to achieve in the last few years.

Still, without wishing to minimise the technological advances, which are genuinely awe-inspiring to someone who was attempting to study aDNA in the 'dark ages' of the 1990s, it is hard to say that we are really now working with a completely new set of ideas. Instead, the turn from contemporary variation towards aDNA that the technology has made feasible a more serious engagement with archaeology for many genetic researchers which, rather than some great transformation, has led to more subtle approaches to the interpretation of historical genetic data. It seems more reasonable to say that Cavalli was partly right and that hopefully we are a bit more right today, but despite all the insights of the past few years, we still have a long way to go.

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