THE ROYAL SOCIETY

The molecular genetics of European ancestry

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In an earlier paper we proposed, on the basis of mitochondrial control region variation, that the bulk of modern European mitochondrial DNA(mtDNA) diversity had its roots in the European Upper Palaeolithic. Refining the mtDNA phylogeny and enlarging the sample size both within Europe and the Middle East still support this interpretation and indicate three separate phases of colonization: (i) the Early Upper Palaeolithic about 50 000 BP; (ii) the Late Upper Palaeolithic 11 000–14 000 BP; and (iii) the Neolithic from 8500 BP.

Keywords: Europe; Polynesia; mtDNA; phylogeny; Palaeolithic; Neolithic

In this paper I want to refer to two regions of the world, Europe and Polynesia; Europe, because it is the main focus of our current research efforts and the topic that I was asked to address, and Polynesia because some of the lessons we learned from that, genetically speaking, much more straightforward region helped us to interpret events in the more complex European theatre.

Our work on mitochondrial variation in Polynesia, published in 1995, raised few eyebrows as its main conclusion—that Polynesia had been initially colonized from the West—confirmed the prevailing consensus built up from archaeology, linguistics and classical genetics (Sykes *et al*. 1995). Only Thor Heyerdahl, whose celebrated hypothesis that the major wave of colonization had been from the Americas, would have had cause for disappointment.

However, the following year, when we published the results of an equivalent study of Europe (Richards *et al.* 1996), whose main conclusion was that the bulk of the extant mitochondrial DNA (mtDNA) variation had its origins in the Palaeolithic, the reaction was very different. This time we were in direct conflict with the prevailing opinion that the most important influence on the modern European gene pool had been a massive influx of farmers from East of the Bosphorus during the Neolithic transition.

This is covered in more detail later, with our latest results, which have modified the original interpretation somewhat, but before that I want to say something about the nature of the controversy that our paper ignited. For instance, one distinguished architect of the prevailing view, a fellow of this Society, announced that he 'didn't believe in mitochondria'. Though one cannot expect the birth of a new theory to be painless, the reaction was disconcertingly hostile. Had we made some terrible mistake? I will argue later that we had not. Rather, I now believe, the intensity of the response had, at its roots, not just a disagreement about European prehistory but a difference of approach to questions of human population structure, which I want to explore further.

The origins of what one might call the 'classical' school can be traced to the end of the First World War when a husband and wife team, Ludwik and Hanna Hirschfeld, published a paper in the *Lancet* entitled 'Serological differences between the blood of different races—the results of research on the Macedonian front' (Hirschfeld & Hirschfeld 1919). This was a survey of the frequencies among the Allied soldiers of blood groups A and B, whose Mendelian credentials had by then been established. The Hirschfelds noticed that the blood group frequencies were quite different among groups of soldiers from different countries (figure 1). For obvious military reasons they did not have access to the figures for Germans and relied on their memories from before the war for these values. It is reassuring to note that even this very first paper in the field was not short on speculation, a trend which continues to this day. In their view, humans were divided into two biochemical races, A and B, with different origins. Although they were uncertain about the origin of race A, the high frequency of blood group B among soldiers from the subcontinent convinced them that 'we should look to India for the cradle of one part of humanity. Both to Indo-China in the East and to the West, a broad stream of Indians passed out, ever lessening in its flow, which finally penetrated Western Europe'.

I have drawn a diagram from their data (figure 2) using the same techniques as used nowadays. This is a diagram of the genetic differences between the populations. How might these be interpreted? Some relationships look perfectly reasonable. Italians and French are close, with Germans a little further away. But there are some unexpected features. For example, Russia and Madagascar share the same position on the diagram. Is this the evidence of a long-forgotten Russian invasion of Madagascar, or vice versa? Indians are on a separate branch from everyone else and 'Negroes', actually from Senegal, are almost as similar to Arabs as English are to Greeks. How are we to explain these bizarre comparisons? One reason for them is that only a single locus is being considered.

To counteract this shortcoming, Cavalli-Sforza and Edwards developed a statistical method that was able to compute the accumulated allele frequency data from several loci (Cavalli-Sforza & Edwards 1967). One

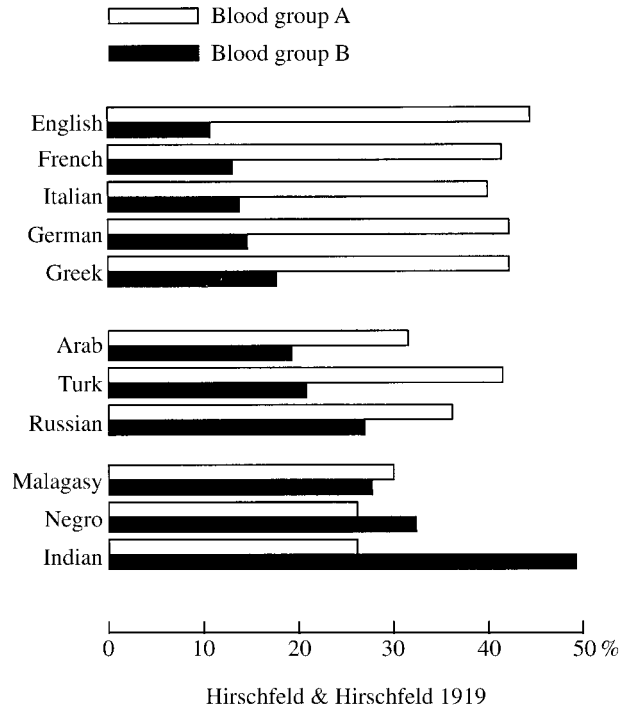

Figure 1. Frequencies of blood groups A and B from different ethnic groups. Data from Hirschfeld & Hirschfeld (1919).

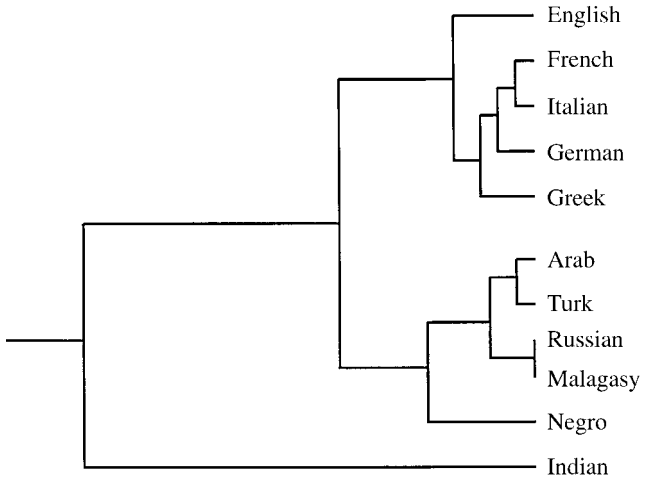

Figure 2. UPGMA diagram constructed from blood group B data from figure 1.

outcome of this approach has been the development of diagrams using tree-building methods such as I used above, but where the population relationships now look far more sensible. Figure 3 is one such for several world-wide populations. This has been a considerable achievement of the classical school, which saw its ultimate expression in the publication of *The history and geography of human genes* (Cavalli-Sforza *et al*. 1994).

But there is a snag. The diagrams, which look very much like genetic trees of the population phylogeny, are not really trees at all. They are diagrams that look like trees. They are 'phenograms'—diagrams of similarities and differences—not 'cladograms', which do attempt to reconstruct real evolutionary relationships. They only begin to work as evolutionary trees—for which they are often understandably mistaken—if human evolution were a succession of clean population splits with no subsequent interbreeding. That might work for different species but not for human populations. They are, as we know, completely interfertile and highly mobile. It is certainly an inappropriate premise in Europe, where one would have to imagine say, a proto-Anglo-Danish population that split with no subsequent biological interaction.

Wilson's paper in 1987 (Cann *et al.* 1987) on mtDNA was a landmark in more than one sense. The initial furore that greeted its appearance centred around the claim that all modern humans had a comparatively recent African origin and the skirmishes that ensued were principally fought around that issue. However, it also introduced a completely new way of treating human populations, not as effectively separate 'species', but as collections of individuals whose genes had their own histories. To illustrate what I mean let me return to Polynesia.

Our paper in 1995 showed that the mitochondrial variation, assessed by control region sequence, was divided into two clades each with a few closely related haplotypes (figure 4). There was such a big mutational distance between them that it is inconceivable that they all shared a common origin within Polynesia, which has only been inhabited for the past 2000–3000 years. Comparisons with mtDNA from potential source populations showed that the most frequent clade, accounting for 95% of sequences, came from South-east Asia, probably Taiwan, whereas the other, with a frequency of 4%, came from the highlands of New Guinea (the other 1% was a mixture of haplotypes from a variety of sources). Figure 5 highlights the position of Polynesia and New Guinea on the population diagram. They are a very long way apart. The mitochondrial result tells us that Polynesians have a mixture of mtDNA from two different sources and the historical reason for this admixture is very interesting and significant. But the population diagram misses the connection.

Let us now return to Europe. In our paper in 1996, we drew a mitochondrial phylogeny using the sequence variation contained in about 350 base pairs (bp) of the first hypervariable (HVS I) segment of the control region (figure 6). The phylogeny was drawn as a single network, which retained ambiguities due to parallel mutation. We imagined we saw six clusters in the diagram. They were not very distinct and often only separated by a single mutation. We then calculated the divergence time for each cluster and saw that most of them dated back well into the Palaeolithic. One, which we called 2A, stood out as having very clear Middle Eastern ancestry and lower diversity and we thought this cluster might reasonably be attributed to the Neolithic farmers. But the frequency of this group was only 15%, hence our conclusion that the data are best explained by a relatively small-scale Neolithic contribution and a much larger surviving Palaeolithic component. The controversy that ensued, to which I have already referred, has been widely covered, (e.g. Lewin 1997) and has led to a lively correspondence (Cavalli-Sforza & Minch 1997; Richards *et al.* 1997; Barbujani *et al.* 1998; Richards & Sykes 1998). There were four main objections.

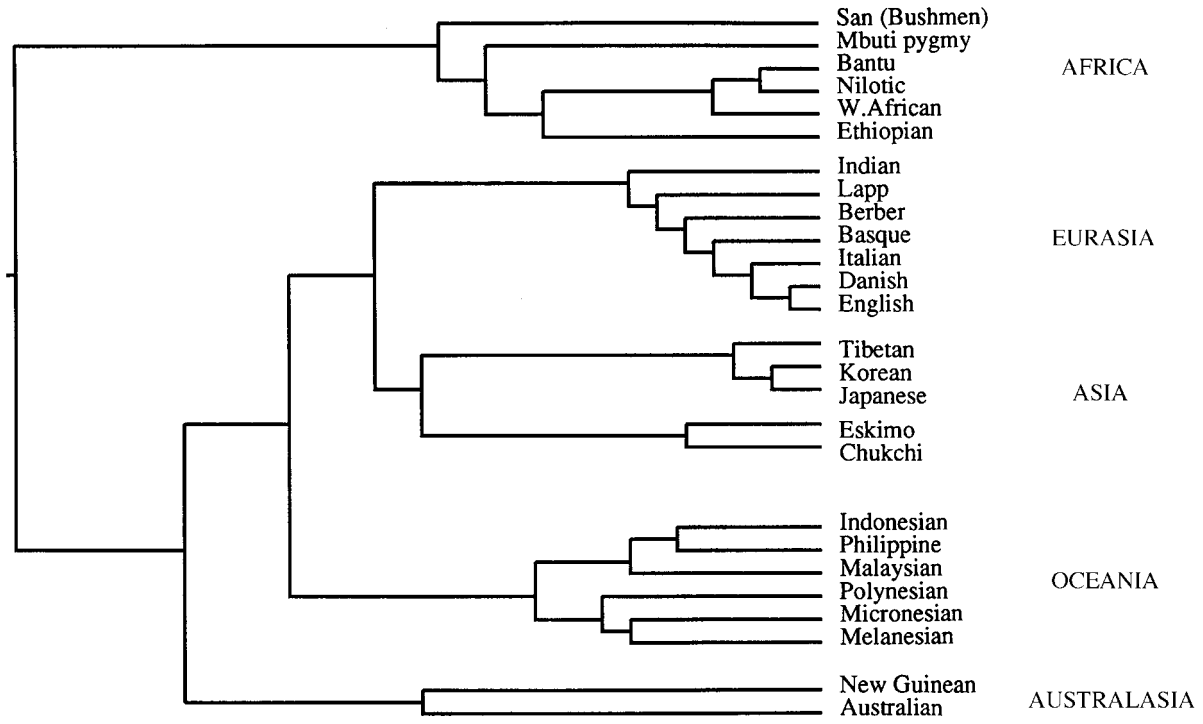

Figure 3. Genetic tree of worldwide populations (redrawn from Cavalli-Sforza *et al.* (1994)).

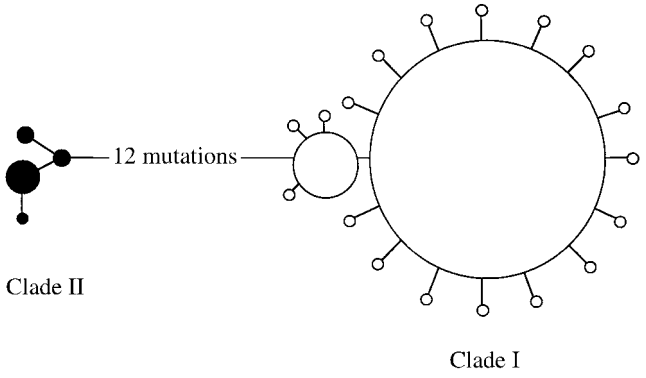

Figure 4. Mitochondrial DNA phylogeny for Polynesia. Circles are different haplotypes determined by control region sequence with areas proportional to their frequency in the sample. Distances between haplotypes reflect the number of mutations. Data from Sykes *et al.* (1995).

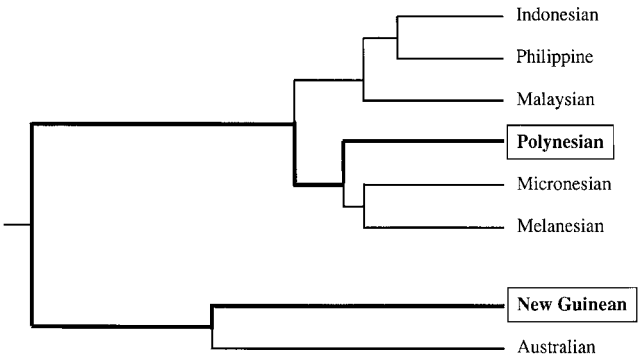

Figure 5. The positions of Polynesian and New Guinean populations on the genetic tree from figure 3.

(i) *The male and female contributions of Neolithic immigrants were different*

It is inescapable that mtDNA only has things to say about females, whereas the demic diffusion model, built on nuclear-encoded classical marker frequencies, considers an average of maternal and paternal contributions. It remains to be seen what the results of ongoing Y-chromosome surveys will reveal in Europe, but they may show considerable differences in the sexes. As an example of this, we find in Polynesia that although at least 99% of mtDNA predates European arrival, at least a third of Y chromosomes come from Europeans (Hurles *et al.* 1999).

(ii) *The phylogeny was incorrect*

As I have already mentioned, the clusters were defined by the control region sequence. They were not separated by long branches and it follows, therefore, that they had low statistical support. We have since gone outside the control region to add more characters in order to resolve the issue. Some of these are RFLP variants, others are sequence dimorphisms in coding genes which cannot be assayed by restriction enzymes. The result is a much more robust phylogeny with all the reticulations resolved and clusters much better separated (figure 7). By-and-large there is an excellent agreement between this phylogeny and our earlier effort defined by the control region alone. All the earlier clusters survive intact and can now be broken down into further subdivisions. We have abandoned our earlier eurocentric nomenclature in favour of the alphabetical notation used by Torroni *et al.* (1996). The correspondence between them is shown in table 1. The principal differences are that: (i) group 4 (now K) joins others from group 5 (now U); (ii) group 1 is broken down into H and V; and (iii) group 3 is broken down into I, W and X. All the groups can still be recognized by their

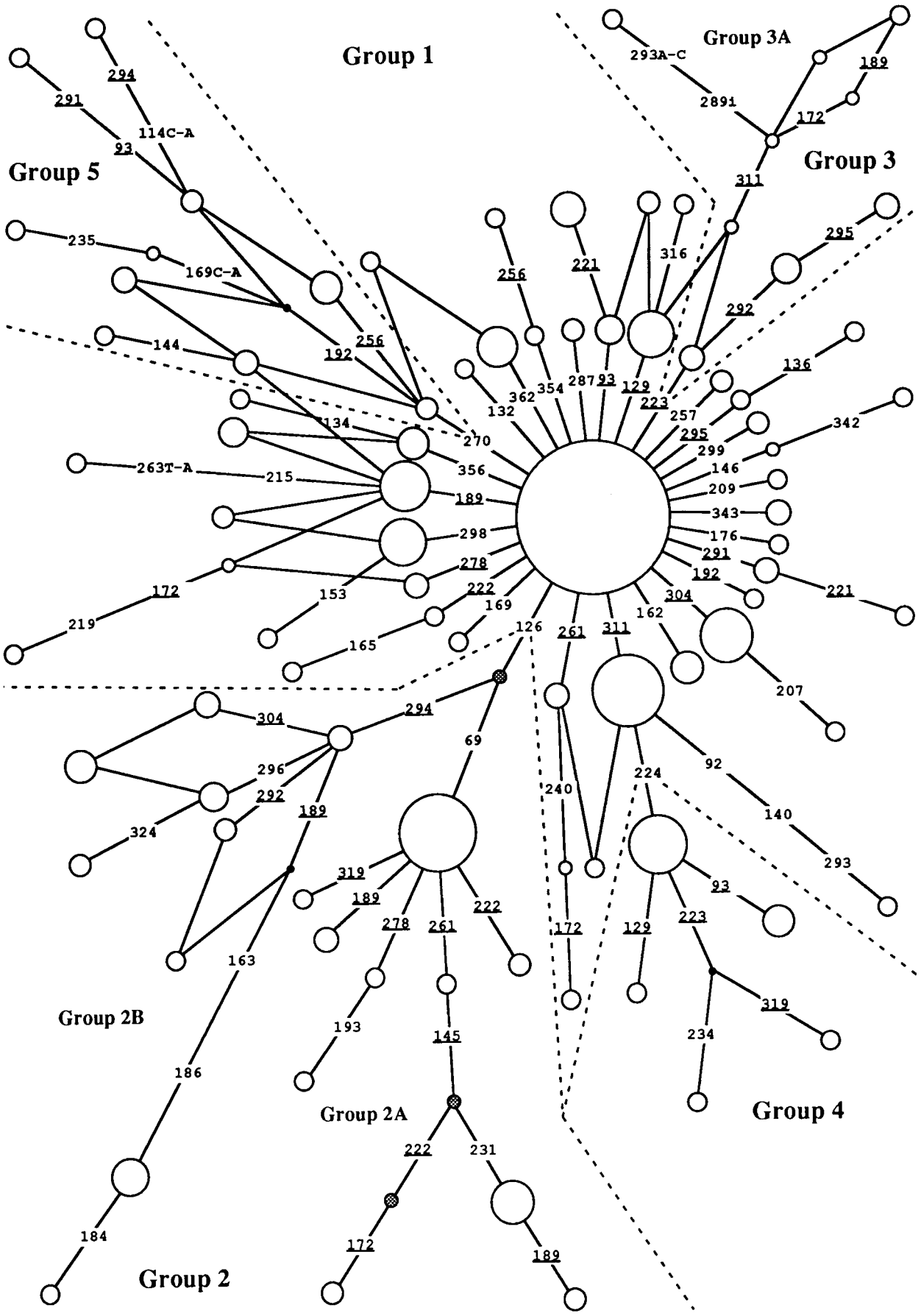

Figure 6. The 1996 mtDNA phylogeny. This is a reduced median network of the control region sequence haplotypes occurring more than once in the sample. The circles and connecting lines follow the same scheme as figure 3, but with the control region variant (−16 000) also shown. Dotted lines separate the different groups. From Richards *et al.* (1996).

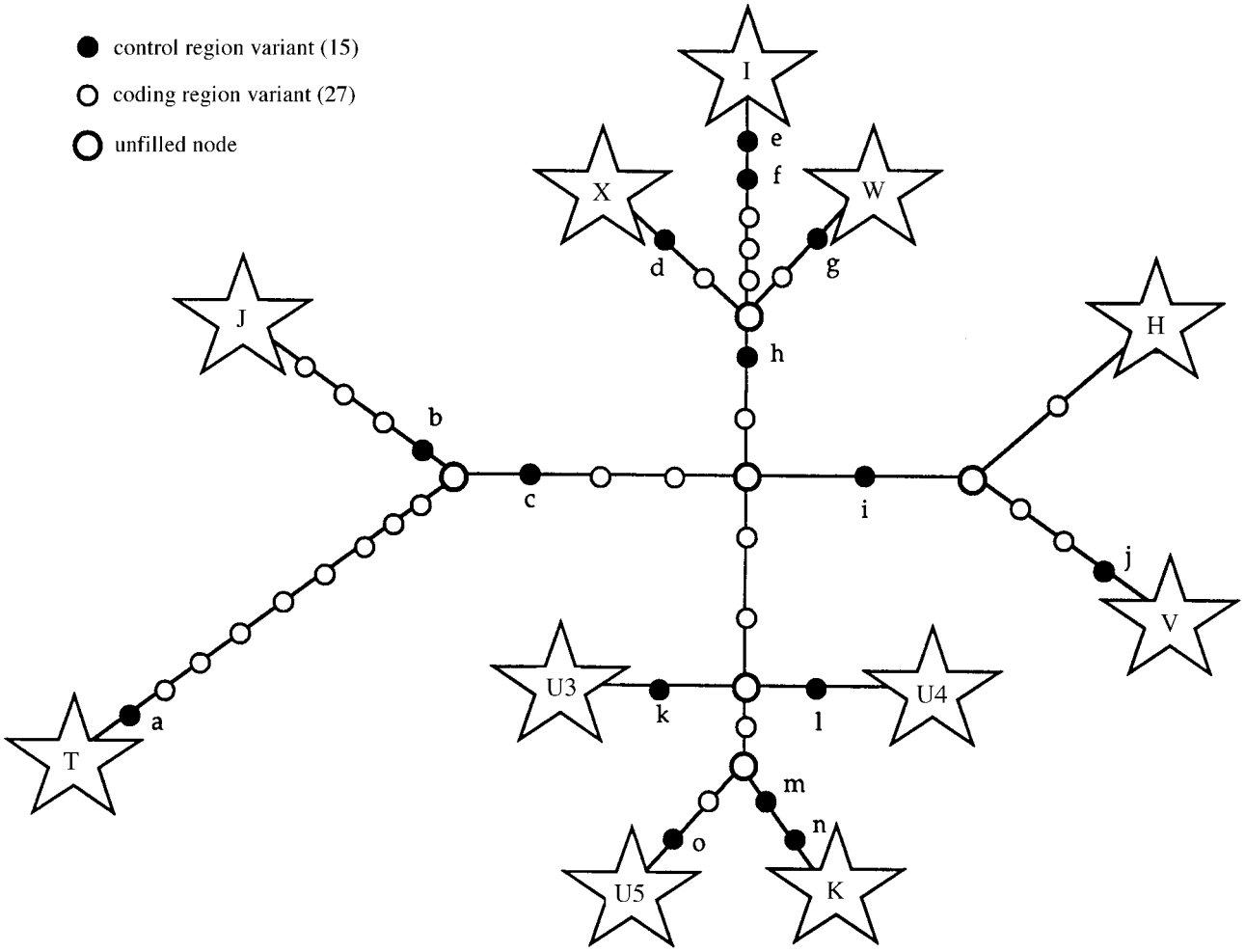

Figure 7. European haplotype clusters showing the characters that separate them. Mitochondrial control region positions are as follows: a, 16294; b, 16069; c, 16126; d, 16278; e, 16129; f, 16391; g, 16292; h, 16223; i, 00073; j, 16298; k, 16343; l, 16356; m, 16224; n, 16311; o, 16270.

Table 1. *Correspondence of numerical (1996) and alphabetical (1998) classification of European haplotype clusters*

1996 classification	1998 classification
1	H and V
2A	J
2B	T
3	I, W, X
4	K
5	U

control region sequences alone and only one site is required (bp 00073) from the second hypervariable segment of the control region (HV II) to distinguish H from the very rare ancestral U haplotype.

(iii) *The mutation rate estimate was wrong*

There has been speculation recently that the mutation rate used for estimating mtDNA divergence is too slow by almost an order of magnitude (Howell *et al.* 1996). The faster rate was arrived at by extrapolation from a few pedigrees segregating for the mitochondrial disease phenotype LHON. Some individuals within the pedigrees had more than one mitochondrial allele—a state known as heteroplasmy. Heteroplasmy is the inevitable transition state between the time a new allele arises, presumably by mutation of a single DNA molecule, and when it becomes fixed in the maternal line. Heteroplasmy can persist for several generations as the new and old alleles battle it out—not literally, the process is entirely random—until one is triumphant and the other eliminated. The mutation rate, estimated from the LHON pedigrees, was about eight times higher than that used for divergence estimates. However, the main reason for this discrepancy was that aside from the small sample size and the reporting bias (pedigrees without new alleles tending not to be written up), the new mutations were in HVS II whereas divergence date estimates use data from HVS I. Studies on HVS I heteroplasmy in our laboratory and

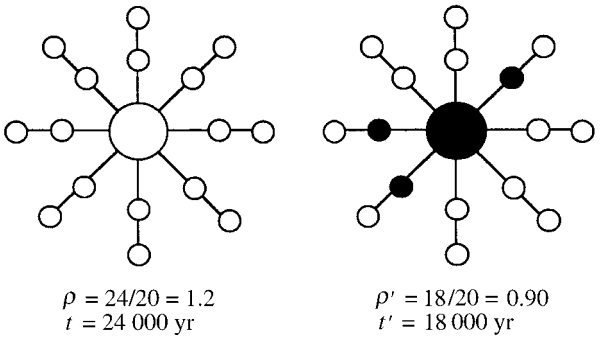

Figure 8. Calculation of ρ uncorrected and corrected for multiple founders.

elsewhere found mutation rates compatible with the rates we and others used in estimating divergence times (Bendall *et al*. 1996; Jazin *et al*. 1998). In addition, field data from Polynesia supported the usual rate where new alleles arising from the common central haplotype (figure 4) did so at a rate which aged the cluster at about 3000 years, a date compatible with the archaeological dates for first colonization (Macaulay *et al*. 1997). So it seems that the rate is about right despite the flurry of anxiety.

(iv) *Dating the clusters*

In our 1996 paper we used the pairwise differences (π) to estimate diversity within a cluster. The improved phylogeny, which identifies the cluster founder, enables us to employ the simpler and more reliable statistic, ρ, to estimate diversity (Foster *et al*. 1996). ρ is the average number of mutations that have accumulated from the cluster ancestor and it can be converted directly to a divergence date by using a mutation rate, which, for the HVS I region we sequence, is 1 per 20 000 years. By itself, this makes very little difference to the previous cluster dates and still leaves them—apart from 2A (now J)—still firmly embedded in the Palaeolithic.

However, divergence dates are not the same as arrival times. If there were already some diversity within the clusters *before* they arrived in Europe, then the arrival dates estimated without taking this into account would be too old. The way round this is to identify haplotypes within the clusters that were already in the source population. In the 1996 paper, the only Middle Eastern data available were from a small Bedouin sample with a very high frequency of cluster J, including founders of several subclusters. It was this that gave J a young divergence date in Europe. It was clearly important to substantially increase the sample size of the source population, which for Europe meant Anatolia, the Near and Middle East, or very roughly East of the Bosphorus. We now have data from several more sites in the region as well as more in Europe and have found haplotypes in most of the clusters that are found in Europe. It is straightforward to correct ρ for this pre-existing diversity by subtracting the shared founder haplotypes. In the theoretical example (figure 8) the presence of three shared haplotypes reduces the divergence date from 24 000 to 18 000 BP.

To illustrate the effect on actual clusters, figure 9 shows three examples. In U5 there are virtually no shared haplotypes between Europe and the Middle East so that

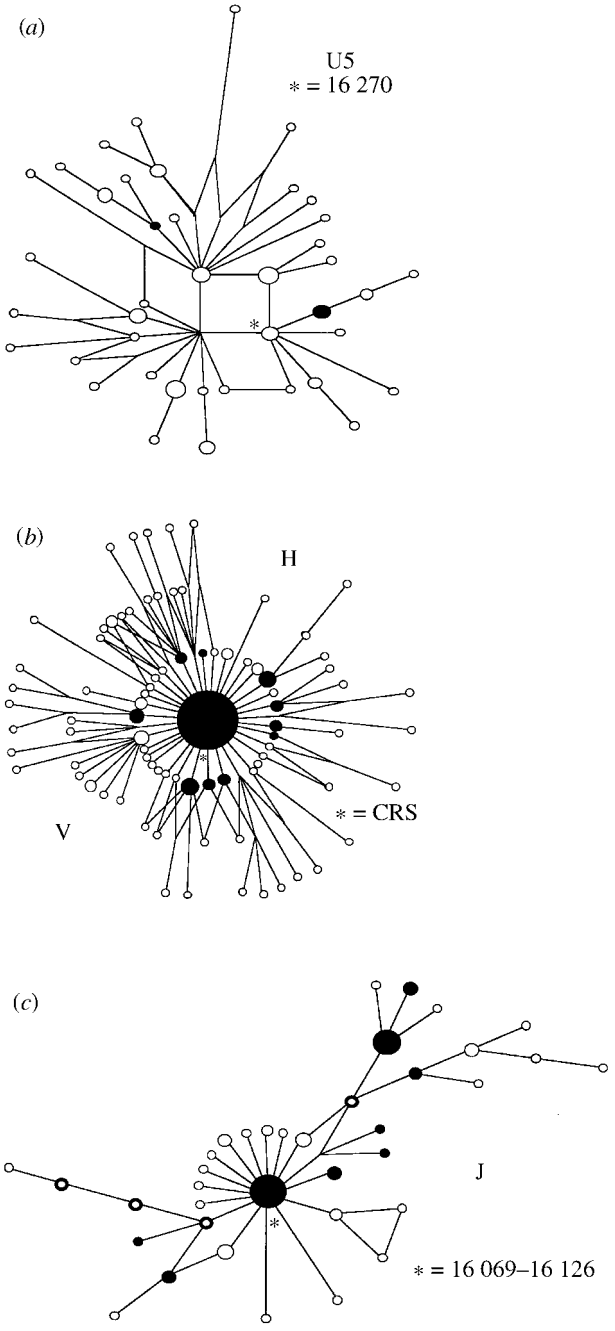

Figure 9. Three European clusters showing haplotypes shared with the potential source populations of Anatolia, Near and Middle East. Haplotypes found only on Europe are in white, shared haplotypes are in black. Nodes on the phylogeny that are present in the source populations but not Europe are shown as white with bold borders. CRS, Cambridge Reference Sequence.

date remains at about 50 000 BP. Cluster H has several shared nodes, all towards the centre, as one would expect from a relatively distant common ancestry. This brings down the date in Europe from 21 500 to 12 500 BP. Last, J has multiple shared haplotypes, already taken into account in the 1996 paper, which reduces the overall divergence date of 28 000 BP to a corrected European date of 8000 BP. Table 2 and figure 10 show the corrected and uncorrected dates for the clusters. A striking feature is the way that, apart from U5 and X, all the uncorrected Palaeolithic dates now move forward to the period

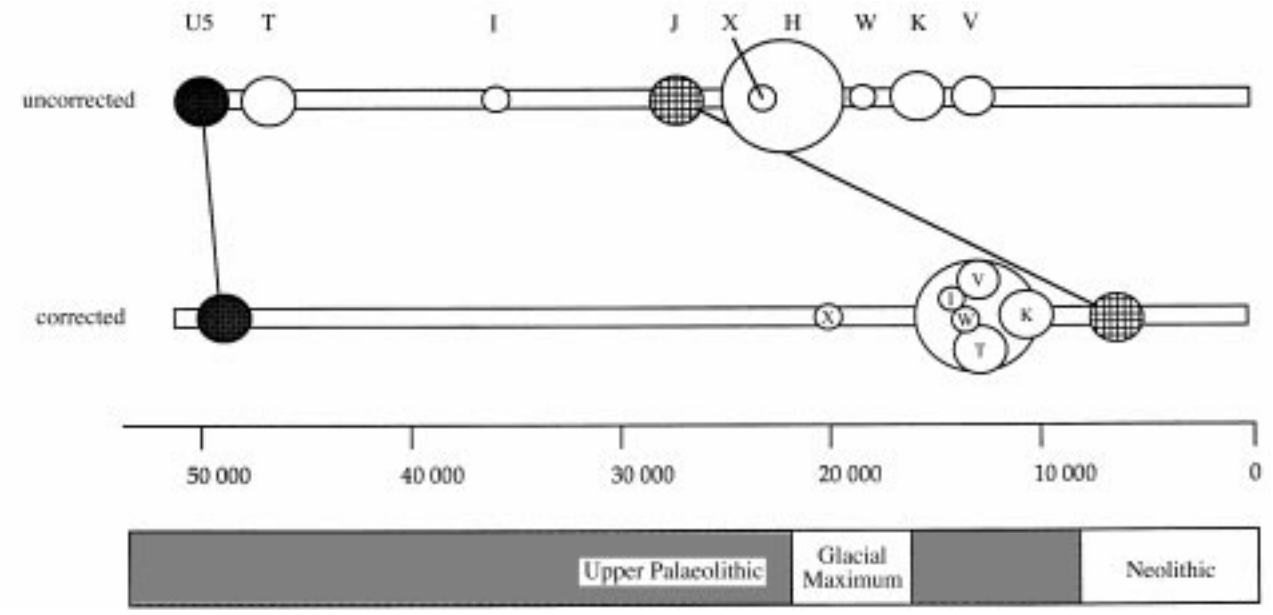

Figure 10. Uncorrected and corrected divergence times for the European clusters. Areas of circles are proportional to cluster frequencies.

Table 2. *A summary of three main waves of European colonization*

component	dates (BP)	main associated clusters	contribution to modern gene pool
Neanderthal	300 000	unclassified	0%
Early Upper Palaeolithic	50 000	U5	10%
Late Upper Palaeolithic	11 000–14 000	H, V, I, W, T, K	70%
Neolithic	8500	J (+ more of H, T, K?)	20%

11 000–14 000 BP. Once again, only J is Neolithic. X, a curious and rare group also found in native Americans, remains at 20 000 BP (but with a wide confidence interval due to small sample size).

In summary, the phylogeny and mutation rate are largely confirmed. However, correcting for pre-existing diversity does have a significant effect on the cluster dates for Europe which brings most of them into the Late Upper Palaeolithic, but not quite into the Neolithic.

Can we now offer any context for these revised results? Only U5 remains stubbornly Early Upper Palaeolithic with the extant diversity developing over 50 000 years in Europe. This is a good match to the first appearance in the European archaeological record of anatomically modern humans, including Cro-Magnon, who brought with them the Aurignacean lithic culture. They shared the continent with the Neanderthals until about 28 000 BP when the last Neanderthal disappeared from southern Spain. We have now examined over 2000 European mtDNA sequences without finding a single one that is sufficiently distinct to be credibly Neanderthal. It is now probably safe to assume that there was no interbreeding with female Neanderthals.

By 18 000–20 000 BP, Europe was firmly in the grip of the last Ice Age. There is a distinct lack of authenticated archaeological sites in North Europe between 22 000 and 14 000 BP and it is thought that the population, which would have been in group U5, moved into refugia either in south-west France and Cantabria or in the Ukraine to the east, to escape the worst of the conditions. As the climate warmed and the ice retreated there was an expansion out of the refugia across northern Europe which, by this time, supported large herds of big game. Good radiocarbon dates show the first archaeological sites at 13 000–14 000 BP in northern Europe (Housley *et al*. 1997). The majority of the Palaeolithic clusters have their European divergence dates at about this time so our interpretation would be that it was this late glacial expansion from the refugia that distributed the mitochondrial ancestors of most modern Europeans. Quantitatively, we believe it was this event, and not the Neolithic, that was the most significant in shaping the modern mitochondrial gene pool.

Finally, group J is still the only convincingly Neolithic cluster. The striking distribution of two important subclusters, J1a and J1b, roughly shadow the two major farming routes into Europe, one along the Mediterranean and Atlantic coasts and the other through the river valleys of central Europe. This is the most marked geographical distribution that we have yet detected for any cluster and we have no reason yet to revise our earlier suggestion that cluster J is a signal of the Neolithic farmers. Table 2 summarizes these interpretations.

Group J, which is, in our opinion, entirely Neolithic in Europe, makes up only 16% of the modern mtDNA

lineages. This does not necessarily mean that the Neolithic farming pioneers were composed exclusively of group J—indeed it would be very surprising if they were. There are also small subclusters of H, T and K that have young dates in Europe and we are currently examining whether these too might be Neolithic in origin. In other words, the overall Neolithic contribution to the mtDNA gene pool might edge over 20%. Cavalli-Sforza and his colleagues used the first principal component, which accounts for 28% of the variance, to argue for the overwhelming influence of the demic diffusion. He now considers this value (28%) to be an estimate of the Neolithic contribution (Cavalli-Sforza & Minch 1997). This is getting too close to our revised value to sustain a controversy on the intrinsic data for very much longer.

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Discussion

N. Bradman (*University College London, UK*). Which Near Eastern populations did you sample and what leads you to believe that they are appropriate for investigating the Neolithic contribution from the Near East to the European gene pool?

B. Sykes. We included in our analysis a total of 284 samples from Bedouin Arabs and Yemenite Jews from the Arabian peninsular, Israeli–Palestinian Arabs from Israel, Druze, Turks and Kurds from North-east Turkey. We would certainly like to increase both the number and geographical spread of this sample, particularly in Anatolia and Iraq. For obvious reasons, this last area is proving difficult to access. However, we are always on the lookout for samples from the Near East and I am very grateful for your offer to share material from Syria and Armenia. As to which populations might be the most appropriate for investigating the Neolithic contribution by identifying multiple founding lineages in the European gene pool, our preference is to look carefully at populations now inhabiting the areas from which the Neolithic transition emerged—that is Anatolia and the Fertile Crescent—while at the same time being aware of the considerable population movements in the region in historic and, presumably, prehistoric times.

C. Renfrew (*University of Cambridge, UK*). One of the most positive features of this important work is the calculation of coalescence times for the identifiably post-migration component of each haplogroup. But given that Anatolia is a key area on any account—and could I make a plea for a clear distinction to be drawn between Anatolia (i.e. Turkey) and the 'Middle East'—should not a much larger sample be sought from that area? Might not the recognition of further diversity among the different haplogroups then push group 1 and its companions past the 8500 BP threshold, and give some of them at least a Neolithic date?

B. Sykes. This is, of course, a very important question and one we have considered. Establishing haplotype matches is certainly sensitive to the sample size from the source population in Anatolia and further East—and I take your point about the geographical descriptions. To take group 1, now group H, the Europe–Anatolia matches are all toward the centre of the phylogeny and restricted to the central haplotype and its first degree derivatives (i.e. haplotypes differing by a single mutation). (See figure 9.) In order to bring the date down from 12 500 to 8500 years, we would need to find matches for almost all of these primary derivatives, leaving virtually no room for Europe-specific primary haplotypes to have arisen from the centre since the Neolithic, which is implausible. However, as I indicated towards the end, elements of group H, and other groups, might well have first entered Europe during the

Neolithic, so that the current diversity distribution is a palimpsest of more than one event. We are currently developing statistical methods to disentangle such mixtures.

M. Pluciennik (*University of Wales—Lampeter, UK*). While analyses of both contemporary and ancient genetic material are providing interesting and relevant information, I am interested in the constraints of the data and limits of the current models in relation to archaeological interpretations. We must remember that whatever sorts of modelling techniques are used to provide cladistic or phylogenetic pictures, these representations of haplotypes or lineages are still only providing implied genetic histories, with unknown or uncertain relationships to other types of histories and prehistories we may wish to write.

Speaking as a prehistorian, it must be pointed out that social and other relationships within and between 'populations' (however defined) are only partly addressed by genetic analyses, which obviously only refer to those social dynamics which have implications for gene flows and genetic histories. There is no necessary relationship between genetic, cultural, social and linguistic (pre)histories, for example. There are also problems of scale and resolution which much be addressed by prehistorians and others who need to take into account past population dynamics. At present it seems as though genetic analyses are most useful in providing a broad-brush and large-scale approach to questions such as, for example, the repopulation of northern Europe after the Late Glacial Maximum, or possible population movements and admixture in the earlier Holocene associated with the transition to farming. However, most archaeologists would not agree that in relation to the Mesolithic–Neolithic transition in Europe for example, we have a mosaic of processes which vary in nature, scale and tempo; and it is unlikely that (except in the unlikely case of huge surviving samples of ancient DNA, current genetic analytical techniques will be able to elucidate local and regional processes at the sort of resolution which is required by archaeologists in order to write informed and specific prehistories. It is likely that other and more widely applicable techniques (because of better survival), such as the collection and analysis of partly genetically controlled features such as dental and cranial morphologies from local burial populations, may allow us better resolution in terms of measuring gene flow in specific areas and communities, in conjunction with other forms of archaeological information.