



GENETICS, ARCHAEOLOGY AND CULTURE

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Received: 10/04/2014

Accepted: 28/05/2014

ABSTRACT

This article explores historical and contemporary approaches to the use of genetic and archaeological evidence in the interpretation of European Prehistory. It begins by reviewing the early work of anthropologists, which was ambitious in scientific scope and effort, but doomed in interpretation by the framework of colonial expansion and racial hierarchy within which it arose. It briefly considers the emergence of serology and genetic studies, and the gradual displacement of the racial paradigm following the Second World War. *The Neolithic transition and the genetics of populations in Europe* model of Ammerman and Cavalli-Sforza is used to generate a fuller discussion of the dimensions involved in combining archaeological and genetic evidence, and alternative mechanisms are explored. The potential for ancient DNA to contribute to this and other debates is raised, and the prospects offered by more recent scientific developments in human genetics are considered. Genetic studies—modern and ancient—have become established as having the potential to support archaeological investigations with considerable breadth and time-depth. The paper aims to offer a nuanced consideration of a number of issues arising from this discussion and concludes that genes, environment, language and archaeology are individually and together legitimate and pressing subjects of enquiry for the scholar of the past.

KEYWORDS: prehistory, genetics, ancient DNA, anthropology, Europe

1. INTRODUCTION

In this article, research in human genetics is explored with regard to its implications for archaeological inquiry. The article begins with a brief historical review of attempts made since the nineteenth century to use anthropometric measurements to derive models of the origins of Europeans and—from the mid-twentieth century—the incorporation of blood group protein distributions into these models. The article then focuses on an early and significant attempt to unite biological evidence of this kind with archaeological evidence: the demic diffusion model of Ammerman and Cavalli-Sforza for the spread of agriculture in Europe during the Neolithic.

This model is used in a qualitative demonstration that there is much greater plasticity with which genetic and archaeological evidence can be interpreted, and to explore some of the parameters that might be taken into account. To support the contention, alternative mechanisms are rehearsed and debated in further detail using genetic and archaeological evidence, including the application of ancient DNA to questions of European prehistory.

Finally, the breadth of archaeological inquiry that may be becoming amenable to analysis is considered.

2. GENETICS, ARCHAEOLOGY AND THE PREHISTORIC SETTLEMENT OF EUROPE

2.1 *The biological study of origins*

An illustration of early empirical studies of biological variation in Europe is offered by the work of John Beddoe (1826-1911). Beddoe published sixty scholarly papers in physical anthropology, which underpinned a century of anthropometric research (Gray 1911), including that of William Ripley who wrote *The Races of Europe: A Sociological Study* (1899). Beddoe was a “pioneer of making exact observations on the physical characteristics of living men”. He collected over one hundred thousand personal observations regarding pigmentation of the

hair and eyes (Ripley 1899, p. 108). According to Ripley’s (1899, p. 63) estimate, over 11 million individual anthropological observations had been made by the late nineteenth century. There is little doubt that these authors understood the implications of measurement as articulated at the time by Lord Kelvin:

“I often say that when you can measure what you are speaking about, and express it in numbers, you know something about it; but when you cannot measure it, when you cannot express it in numbers, your knowledge is of a meager and unsatisfactory kind: it may be the beginning of knowledge, but you have scarcely, in your thoughts, advanced to the stage of *science*, whatever the matter may be”. (Thompson 1883)

Although founded on claims to scientific precision in measurement, Beddoe’s and Ripley’s interpretations reflected the nineteenth century obsession with average types. Their contemporary Adolphe Quételet (1796-1874) had observed that variation in many demographic phenomena—be they biological, social or criminological—could be represented by mean or average values that were relatively stable. Quételet proposed that a hypothetical ‘average man’ could be used to understand both variation and the relationships between phenomena:

L’homme que je considère ici est, dans la société, l’analogie du centre de gravité dans les corps; il est la moyenne autour de laquelle oscillent les éléments sociaux (Quetelet 1835, p. 21).

Like Quételet, the observations Beddoe (1885) and Ripley (1899) collected tended to be expressed as mean values for a group. Illustrations supposed to typify the appearances of people of different British regions, for example, appear in both Beddoe’s and Ripley’s work. Furthermore, these studies emerged at a time of colonial expansion, industrial development and religious proselytization. Prevailing beliefs not only fostered, but demanded explanations of diversity based on racial taxono-

mies, which justified the subjugation of the dispossessed.

Darwin's theory of evolution by means of natural selection (1859) became widely known and was frequently used to support this paradigm. Darwin's own views remain the subject of controversy and debate. In his correspondence, Darwin evidently accepted the existence of race and saw the predominance of White and Anglo-Saxon races as quite natural. It is not, however, self-evident that he believed in the fixity of racial types and racial progress or, for example, wished to endorse the evils of slavery:

"I was told before leaving England, that after living in Slave countries: all my opinions would be altered; the only alteration I am aware of is forming a much higher estimate of the Negro's character. It is impossible to see a Negro and not feel kindly towards him" (Darwin 1833).

The possibility of an alternative to racial taxonomies for the description of human biological variation only began to emerge following Landsteiner's discovery of the ABO blood group system (Landsteiner 1900) and with scientific challenges to racial fixity such of those of Boas, who questioned the heritability of skull shape (Boas 1912). Nevertheless, racial models continued to be adopted. Ripley's *The Races of Europe* was substantially revised by Carleton Coon (1939), but in the aftermath of the Second World War racial typology was morally discredited and more plausible scientific alternatives gradually began to gain credibility (Marks 1995).

As a consequence of war came the need for blood transfusions for injured servicemen. In the search for compatible donors, geographic patterns in the distribution of ABO blood groups became apparent, which begged explanation. With regard to the British Isles, these explanations still tended to rely, if not on racial explanations, then on tribal ones (Evison 2000). Elevated blood group frequencies in the modern population of British regions were associated with corresponding areas of raised frequencies in adjacent countries. In partic-

ular, the Viking Era migrations were evoked to associate regional blood group frequencies in Britain and Ireland with those of Norway, Denmark and Iceland. While migration-as-explanation was falling out of favour with contemporary archaeological belief (see Chapman and Hamerow 1997), population geneticists continued to turn to mainstream archaeologists for migration-based explanations of the patterns found in their data. Even in the instance of Viking Era migrations, when movements of people are quite well corroborated by historical, archaeological and linguistic evidence, it was not always possible to clearly reconcile them.

As scientific understanding of serology progressed, many new blood proteins became available for investigation and gradually the genes underlying them could be analysed directly at the level of the DNA itself. The accumulation of further markers, however, did not facilitate more easy resolution and explanation of the distribution patterns observed: they revealed only further complexity—and sophisticated quantitative analyses became necessary to distil out the statistical factors underlying them. This work culminated in the influential study of Ammerman and Cavalli-Sforza, who proposed a model—relying on both genetic and archaeological evidence—to suggest that the spread of agriculture from South East to North West Europe during the Neolithic was a process that incorporated a gradual, but substantial transmission of genetic markers.

2.2 *Synthesizing genetics and archaeology: the demic diffusion model*

In *The Neolithic transition and the genetics of populations in Europe*, Ammerman and Cavalli-Sforza (1984) presented a comprehensive account of the results of a twelve year collaboration based on the belief that "a bridge can be established between subjects as seemingly diverse as archaeology and genetics" (1984: 133). Building on earlier work (Ammerman and Cavalli-Sforza 1971, 1973, 1979), the authors put forward

the 'wave of advance' model as an explanation for the spread of early farming in Europe, invoking 'demic diffusion' where the spread of agriculture "is due to the movement of farmers themselves" (Ammerman and Cavalli-Sforza 1984: 6). Demic diffusion is based upon an assumption of increased population growth in farming communities, implying a shift from a low hunter-gatherer population to a high farmer population (1984: 63-67, 135)—and a substantially greater genetic contribution from the latter group.

Ammerman and Cavalli-Sforza (1984: 63-82) fundamentally relied on a correspondence between the pattern of the earliest archaeological evidence of farming and the pattern of distribution of major gene frequencies in Europe—both develop along a southeast to northwest gradient—to provide empirical support for their hypothesis. The analogous example of the spread of agriculture in sub-Saharan Africa (1984: 139)—a historically attested 'wave of advance' supported by genetic and linguistic evidence—lends further plausibility to the model. Demic diffusion is a "processes operating essentially at the local level" (1984: xiv) and it is culture which drives demographic—and hence gene frequency—changes: "cultural events in the remote past played a major role in shaping the genetic structure of human populations in this part of the world" (1984: xv).

Ammerman and Cavalli-Sforza stipulate that the 'wave of advance' model is not a colonisation model (1984: 61), in that it recognises the importance of local events and that it is culturally—not biologically—'deterministic'. Therefore, rather than debate these abstract considerations, I would like to examine some criticisms of the 'wave of advance' model made on empirical archaeological and genetic grounds. Zvelebil, in particular, criticised the model extensively on archaeological, ethnographic and—with the spread of farmers having become associated with that of Indo-European languages (Renfrew 1987)—linguistic grounds (Zvelebil 1986, 1989;

Zvelebil and Rowley-Conwy 1986, Zvelebil and Zvelebil 1988, Zvelebil 1998).

The strength of the 'wave of advance' model in explaining the observed correspondence between the maps of gene frequencies and earliest agricultural sites is that the Mesolithic-Neolithic transition appears to be the only period in European prehistory when the mixing populations could be presumed to be sufficiently different in size and genetic profile to bring it about. Zvelebil vehemently disputed any significant difference in the magnitude of agriculturalist and forager-farmer populations (1998: 412-3), and argued for continuity in settlement sites and stylistic aspects of material culture (*cf.* Ammerman and Cavalli-Sforza 1984: 39, 47). But whilst the archaeological evidence—in some parts of Europe—may not unequivocally support the arguments of Cavalli-Sforza *et al.* it cannot be said to refute them. The prehistoric archaeological record simply does not offer the resolution to allow the competing numerical models to be distinguished, and old sites and symbols may be adopted by new people—often quite deliberately. Equally, a lack of 'goodness of fit' between the contours of the archaeological and genetic maps associated with the spread of agriculture does not appear to be a substantial flaw—the 'wave of advance' model is inevitably coarse grained.

None of the criticisms seem to undermine the crux of the demic diffusion model by offering a convincing alternative explanation for the southeast to northwest genetic gradient in Europe, although Zvelebil (1998: 415) preferred a Neolithic 'star-burst' to a 'wave' as being more in keeping with archaeological and ethnographic evidence.

2.3 A Palaeolithic alternative

It is doubtful whether more recent historically identifiable migrant populations were sufficiently large and genetically distinctive to bring about such a major trans-European pattern long after relatively large agricultural communities had become established (*cf.* Renfrew 1998: 418). Further-

more, early studies of maternally inherited mitochondrial DNA variation in Europe have led to the realisation that much of the pattern of genetic diversity in Europe may be much older than the Neolithic and the influence of the spread of agriculture may be small (Richards *et al.* 1996; Sykes 1998, 1999). Richards *et al.* specifically suggested that the southeast to northwest gradient may reflect Upper Palaeolithic colonisations (1996: 197). More detailed consideration of archaeological and palaeoecological evidence indicates that demic diffusion accompanying the spread of agriculture may hardly need to be invoked at all in southern Scandinavia (Zvelebil 1986, Rowley-Conwy 1985) and, in Iberia, Jackes, Lubell and Meiklejohn reached similar conclusions further supported by evidence from physical anthropology and population genetics (Jackes *et al.* 1997a, b; *cf.* Zilhão 1998).

If the southeast to northwest gradient dates back to the Upper Palaeolithic or earlier then an alternative to the 'wave of advance' model must be found which incorporates demographic events of comparable magnitude to the spread of agriculture, but occurring long prior to the Neolithic. Two requirements of such a model can be identified: i.) relative genetic distinctiveness must arise between regions of Europe by the Upper Palaeolithic and ii.) admixture between communities in the regions must lead to the southeast to northwest gradient being in place prior to the late Upper Palaeolithic. There are two possible mechanisms by which relative genetic distinctiveness could have developed in Europe by the end of the Upper Palaeolithic. Geographical differences in patterns of natural selection due to disease and resistance to disease—or other environmental effects—could have led to such an outcome. Although many of the wide range of genetic markers that have been the subject of investigation in European populations are related to immunity, it would be difficult to identify a series of disease episodes following the same geographical pattern, but affecting a different gene or set of genes each

time. Although zoonoses accompanying pastoralism or epidemics associated with increasing settlement density might provide explanations, such scenarios barely apply to the Palaeolithic.

The second mechanism which might have generated relative genetic diversity in Palaeolithic Europe is isolation, leading to genetic diversification between populations via founder effects and genetic drift. It is important to remember, however, that human communities hardly ever exist in isolation. The overwhelming message of population genetics—and one often overlooked—is *admixture*. Population geneticists may be able to strip away recent admixture in the hope of finding the genetic profile of an earlier population, but in making interpretations it is often forgotten that admixture is also primordial and that genetic markers cannot as a rule be rooted in ethno-historic groups.

As Terrell *et al.* (1997) have argued, genetic isolation can rarely be assumed even in communities in the world's most remote geographical regions—in fact, social conventions which promote outside marriage are most well-developed in remote communities, terrestrial or maritime—as Cavalli-Sforza acknowledged (Cavalli-Sforza and Cavalli-Sforza 1995). Given the age of most genetic variation and the degree of admixture evident in all modern human populations, it is safe to assume that such social mechanisms existed amongst the sparse communities of Palaeolithic Europe. Nevertheless, at the height of the last glacial maximum, there was an unusual potential for a significant degree of genetic isolation to have developed between the communities inhabiting different regions of Europe.

Prior to the final Pleistocene glaciation Upper Palaeolithic communities are clearly visible in the archaeological record throughout the central latitudes of Europe, extending from Cantabria and South West France to the Central Russian Plain (Gamble and Soffer 1990, Soffer 1987). Gamble (1982, *cf.* Soffer 1987: 335-9) has argued that a degree of commonality in certain aspects of material culture—in particular, Venus

figurines – could be interpreted as an indicator of cultural and social communication across Europe at *circa* 25,000–23,000 BP, and Gravettian technology is typical of lithic inventories found throughout the continent, although regional complexity is evident (Gamble and Soffer 1990).

Both settlement and material culture patterns exhibit marked changes following the onset of the final glaciation. In the south of France, occupation continued throughout the final glaciation, but settlement density probably diminished (Rigaud and Simek 1990: 83, Jochim 1987). In northern Spain, the number of sites is maintained in the region of Cantabria, but dwindles elsewhere (Straus 1990: 93), and continuity of occupation is also evident in parts of Portugal (Zilhão 1990: 117). A large part of Eurasia from the Russian plain eastward may also have been occupied (Velichko and Kurenkova 1990: 259). Most significantly, archaeological and radiocarbon evidence (Soffer 1990: 228–52) indicate the existence of substantial refugia populations adjacent to the Don and elsewhere in the Russian Plain following temporally and regionally variable patterns. Soffer (1987: 343) suggests that these settlements may have been the result of movements from Moravia to the East – and also to Lower Austria – as climatic conditions deteriorated.

There is also archaeological evidence of continued habitation in regions to the south and east during the height of the late Pleistocene glaciations. For Italy, Mussi (1990: 133) argues for a gradual increase in population size from 20,000 to 16,000 BP. Occupation during the Late Glacial Maximum is also evident in Greece at sites such as Theopetra (Kyparissi-Apostolika 1990, 1999) and Frankthi (Perlés 1987) caves, and the Klisoura Gorge (Koumouzelis *et al.* 1996). A number of other Upper Palaeolithic sites have also been identified in Greece, although Upper Palaeolithic utilisation of them may not have commenced until after *circa* 20,000 BP (Runnels 1995; Koumouzelis *et al.* 1996: 146, 149) or, in the case of Klithi, after 16,000 BP (Bailey and Gamble 1990:

158). Some further settlement in the former Yugoslavia at 17,000 to 20,000 BP may be evident on the basis of radiocarbon determinations (Bailey and Gamble 1990: 152). Whilst clearly significant, the extent of settlement in Italy and Greece during the Late Glacial Maximum is difficult to establish. It should be recalled that isolated archaeological sites or finds of skeletal remains are very likely to represent the use of large ‘catchment’ territories by whole communities. It is probable that other Upper Palaeolithic landscapes in the region are now submerged, especially in the northern Adriatic (Bailey and Gamble 1990: 151, 165). A temperate dry steppe environment prevailed in Italy, Greece and along the Mediterranean coast of Anatolia through to the Levant, where further Late Upper Palaeolithic settlement – the Kebaran – is evident from *circa* 19,000 BP (Bar-Yosef 1987: 233, 1990: 63–9).

It is clear that communities survived in the refugia of the Ukraine and Central Russian Plain, Franco-Cantabria, and Italy and Greece between 21–13 Kyr BP, although the size and significance of the latter populations is only gradually being recognised.

What was the extent of communication between these refugia populations at the height of the late Pleistocene glacial maximum (occurring at around 18 Kyr BP)? Although a corridor existed between the British Isles and Scandinavian ice sheet to the north and the Alpine glaciers to the south, extensive permafrost and extreme periglacial conditions prevailed in large areas of central and eastern Europe even extending to polar or arctic desert (Jochim 1987: 321; Soffer 1987: 333). Following a comprehensive accelerator mass spectrometry (AMS) dating survey, Housley *et al.* (1997) inferred that much of northern Europe was uninhabited at the height of the Last Glacial Maximum. This concurs with more broadly based interpretations of the archaeological evidence. The Paris Basin appears to have been unoccupied at this time (Schmider 1990: 51), and the western and eastern parts of the North West European Plain were

probably isolated from one another (Otte 1990: 60). A "minimal human presence" is postulated for Germany between 20,000 and 15,000 BP which, even then, decreases at the Last Glacial Maximum (Weniger 1990: 173).

There are a small number of radiocarbon determinations which may indicate that complete depopulation in North and North Central Europe did not occur. In Germany, however, the material from Aschenstein ($18,820 \pm 180$ BP) is—as Weniger (1990: 171) notes—regarded as "badly documented and without any typological significance" and the date from Hohler Fels IIa ($17,100 \pm 150$ BP) is seen as possibly suspect by both Housley *et al.* (1997: 28) and Weniger (1990: 173). Post glacial-maximum dates have been determined or proposed for Hallines in northern France, Kanne and Orp in Belgium, Sweikhuizen in the Netherlands and Vaucelles in the Belgian Ardennes (Otte 1990: 61). Housley *et al.* (1997: 42) regard the date of $16,000 \pm 300$ BP from Hallines in the Paris Basin as anomalous and in any case argue for these late dates—relative to the Late Glacial Maximum—as representing an early wave of settlement after abandonment.

Remaining radiocarbon date estimations at or about the Last Glacial Maximum have been determined for Rosenberg and Grubgraben in Austria (Montet-White 1990) and Stránská Skalá IV ($18,220 \pm 120$ BP) in Moravia (Svoboda 1990: 198). A small number of sites in the Carpathian Basin (Slovakia and Hungary) have also been estimated to date to between 18,000 and 16,000 BP (Svoboda 1990: 201, Kozłowski 1990: 220), with dates of $18,700 \pm 190$ and $17,050 \pm 350$ BP having been determined for Arka in Hungary (Kozłowski 1990: 220). Radiocarbon dating evidence from the Rhineland (Street and Terberger 1999) also suggests continuing occupation at *c.* 19,000–17,000 BP. Nevertheless, the overwhelming picture for North and North Central Europe during the Last Glacial Maximum is one of abandonment.

The degree of contact between Italy and Greece and adjacent territories at the height

of the Last Glacial Maximum is more difficult to assess. The Alpine glaciers to the north of Italy and the Dinaric Alps, Pindus and Rhodope mountain ranges to the north of Greece would have formed a substantial topographic barrier, but communication to the East via the Mediterranean or Black Sea coasts may have been quite straightforward. Contact between Italy and Western Europe appears to have diminished at this time, but—conversely—closer relationships between material from Italy and Greece are evident (Mussi 1990: 140).

Thus, it is possible to identify two and—possibly—three clusters of Pleistocene refugia communities in Europe—centred on South West France and Cantabria, Ukraine and Central Russian Plain and Greece and Italy—which may have been isolated during the height of the final Pleistocene glacial maximum.

Here discussion is restricted to the genetic consequences of the period of separation and renewed contact between these clusters of communities. There is little doubt that a long period of absolute or effective separation would have led to genetic drift and increasing distinctiveness in gene frequencies, even if they had been relatively homogeneous to begin with. Any contact with communities at the European periphery—in the Near East, western Asia or North Africa, for example—may have accelerated such a process. Archaeological evidence demonstrates that human communities were active in each of these areas at the height of the Last Glacial Maximum (Close and Wendorf 1990; Bar-Yosef 1987, 1990; Soffer 1990). Founder effects due to a population bottleneck occurring during the prehistoric settlement of Polynesia (Hagelberg and Clegg 1993) was generated over a short time period and was—at least in Central Polynesia—perhaps propagated despite a degree of continued contact. Simulation models of Ammerman and Cavalli-Sforza (1984: 120–1) indicated that variation in gene frequencies between adjacent hunter-gatherer groups of the order of magnitude required to prime the southeast to northwest genetic gradient would arise after

about 3,000 years, roughly corresponding to the last Pleniglacial. Complete isolation of Palaeolithic refugia populations would not have been required to bring about genetic drift—'isolation by distance' (Sokal *et al.* 1989: 290) would have been sufficient.

Following on from the suggestion of Richards *et al.* (1996; Sykes 1998, 1999), an alternative to the transition to agriculture model implies that genetic drift occurring during the Late Pleistocene was followed by genetic admixture developing after the glacial maximum and into the Holocene, leading to the gradual breakdown of any discrete boundaries which may have arisen, and to the development of the south-east to northwest gradient that we see today.

A close genetic affinity with populations in the Levant is evident in contemporary populations of South East Europe, and communication between Italy and Greece and the Levant at or prior to the Upper Palaeolithic is therefore implied in this model. Communities in the South East Mediterranean may have been more populous, leading to the higher number of genes correlating with the southeast to northwest direction of the gradient than *vice versa* (Cavalli-Sforza *et al.* 1994). The southeast to northwest gradient may be seen as the result of three vectors corresponding to admixture of the East Mediterranean, South West France and Cantabria, and Ukraine and Central Russian Plain population clusters, channelled by topography and, in the case of the north-south component, potentially enhanced by climatically related environmental effects.

Topographic barriers are frequently recognised as offering barriers to gene flow (Barbujani and Sokal 1990) and coastal routes as offering routes of transmission. Sometimes overlooked are major communication and migration routes between regions. These would include major river estuaries—such as those of the Thames and the Wash in England (Falsetti and Sokal 1993), which closely face continental Europe—as well as the major plains, which

themselves form reservoirs of population during periods of demographic expansion, and may—like 'Doggerland' (Coles 1998) or the North Adriatic (Bailey and Gamble 1990: 151, 165)—have become inundated following postglacial rises in sea level.

While other principal components of Cavalli-Sforza *et al.* could be accounted for via a combination of topographic, climatic and demographic forces, the weakness of post-hoc accommodative arguments must be recognised (Clark 1998: 407). A pattern of resettlement may be provisionally inferred from the archaeological evidence, but the spread of genes and material culture may not be congruent with it. From the Late Glacial Maximum onward, material cultural traditions in Europe are more regionally distinct, with the Solutrean and Magdalenian emerging West of the Alps and the Epigravettian to the south and east (Otte 1990: 65). Sicily and the mountains of central Italy appear to have been reoccupied soon after 16,000 BP (Mussi 1990: 133), presumably from adjacent local populations. Early Holocene assemblages from Moravia exhibit late Gravettian and Magdalenian traditions (Svoboda 1990: 202) and it is debated whether the appearance of Magdalenian material in central Europe represents demic diffusion from the West or cultural transformation of local Gravettian groups (Otte 1990: 61)—even after the last European glaciation it is not possible to automatically equate intrusion of culture with movement of people. The Carpathian Basin also indicates significant reoccupation by groups using Epigravettian lithic material (Kozłowski 1990: 222-3).

It may be difficult to distinguish demographic events of the Pleistocene from those of the early Holocene on genetic grounds. The situation in Greece—and in the Balkans and Anatolia—is opaque. There may be a hiatus of occupation during the earlier part of the Upper Palaeolithic (Runnels 1995). The significance of the Mesolithic in Greece, and the influence of migration and settlement at the outset of the Neolithic, remains widely contested (Willis

and Bennett 1994, Edwards *et al.* 1994, van Andel and Runnels 1995). Both Frankthi (Perlès 1990) and Theopetra (Kyparissi-Apostolika 1990, 1999) caves were clearly utilised during this period, however. Whilst the demographic changes associated with Holocene settlement of the eastern Mediterranean from the Near East and the spread of farming—and subsequent events—may have further contributed to the southeast to northwest gradient, they may not have been its primary cause (*cf.* Zvelebil 1998: 414, Renfrew 1998: 418). Similarly and importantly, cyclic genetic drift and admixture processes may have taken place in earlier cold glacial periods in the European Pleistocene affecting other ancestral populations, resulting in a complex accumulated pattern of admixture, as an early analysis of mitochondrial DNA variation in Europe seemed to indicate (Richards *et al.* 1998). The concept of a 'Pleistocene pump' affecting Eurasian and African flora and fauna—including humans—has been postulated for some time, following observations of ancient climatic correlations between East Africa and Europe (van Zinderen-Bakker 1962). Finally, in a sparsely populated post-glacial phase, Mesolithic populations may also have been subject to a degree of isolation (Jacobs 1992). Barbu-jani and Bertorelle (2001) have discussed the potential for European population pre-history to have been the subject of repeated founder effects.

The Pleistocene drift or drifts and Holocene admixture scenario postulated here on the basis of genetic and archaeological evidence could potentially be falsified, if any of the following could be demonstrated i.) if it can be established that the southeast-northwest genetic gradient does not pre-date the Mesolithic, ii.) if the existence of significant refugia populations in Italy and Greece during the Last Glacial Maximum cannot be established, iii.) if effective isolation of refugia populations at the height of the Palaeolithic can be disproved, iv.) if significant communication between Greece and the Near East during the late Middle or Upper Palaeolithic cannot be estab-

lished, or v.) if discontinuities in the occupation of Greece following the Upper Palaeolithic cannot be reconciled with an early southeast to northwest genetic gradient (if an incongruous pattern of reoccupation following a Mesolithic hiatus was to be established, for example).

The early genetic evidence indicating a Palaeolithic origin for much of the underlying gene frequency variation in Europe was based on the analysis of mitochondrial DNA (Sykes 1998, 1999). Unlike mitochondrial DNA variation—which can partially be calibrated against the archaeological and palaeontological records—there has been little prospect of dating classical genetic marker distributions in Europe, and of dating the principal component synthetic maps derived from them (e.g. Cavalli-Sforza *et al.* 1994: 287-96). Hence—for example—the doubt expressed by Cavalli-Sforza *et al.* (1994: 293) regarding whether a pattern on their third principal component map should be attributed to Kurgan or Sythian settlement—archaeological horizons occurring several millennia apart. Although appearance may suggest otherwise, geneticists cannot readily date features on single gene or principal component maps, in reality they have sought to find correspondence between features on the maps and archaeological horizons.

If the antiquity of genetic variation in Europe is accepted—on the basis of the mitochondrial DNA evidence—then there is no evident reason why the first principal component of Cavalli-Sforza *et al.* 1994: 292) and the classical genetic markers which correlate may not be of similar age. Studies restricted to the analysis of Human Leukocyte Antigen (HLA) complex support the existence of the southeast to northwest genetic gradient in Europe (Piazza and Lonjou 1997), but—although the authors state that the most immediate interpretation is that it traces “the HLA dissected image of the Neolithic spread of farmers to Europe” (Piazza and Lonjou 1997: 383-4)—there is at present no implicit reason why this pattern could not be attributed to the Palaeolithic as well.

A potential means by which assumptions relying on modern gene distributions could be verified is by direct ancient DNA analysis of human skeletal material of Neolithic, Mesolithic and even Palaeolithic date. Early ancient DNA results suggested that the analysis of such rare and precious specimens is not without promise (Krings *et al.* 1997, Béraud-Colomb *et al.* 1995). Ancient HLA (see above) analysis of a Palaeolithic specimen from Theopetra Cave in Greece yielded DRB1*03, DRB1*11, DQB1*02 and DQB1*03 variants (Evison *et al.* 1999). Haplotype DRB1*11-DQB1*03 from the Theopetra skeleton conformed strongly with southeast to northwest genetic gradient in HLA alleles (Charron 1997; 738, 749) and is therefore a haplotype whose *prevalence* in Greece should have post-dated the life of this individual by at least 7000 years, according to the 'wave of advance' model. Haplotype DRB1*03-DQB1*02 from the same skeleton exhibits a negative association with the same pattern (Charron 1997; 738, 749) and—on the basis of the 'wave of advance' model—could be presumed to have been a common haplotype in Palaeolithic Europe. Whilst the HLA type recovered from the Theopetra skeleton is consistent with the outcome of predicted admixture between Neolithic and Palaeolithic refugia populations, it is clearly impossible to draw any conclusions on the basis of this single case. Contamination is commonly recognised as a major problem in ancient DNA analysis. Nevertheless, research has continued to progress (e.g. Lambert and Millar 2006) and the reliability of analysis of specimens of Palaeolithic age—including the *Homo sapiens neanderthalensis* genome (Green *et al.* 2006)—is convincing. Interestingly, the ancient DNA analysis of the 'Denisovians' may support the concept of Palaeolithic drift and admixture events (Reich *et al.* 2010).

2.4 Contemporary genetic studies

In a recent and exciting development, ancient DNA analysis has been applied to the investigation of appearance traits in

archaeological populations in Europe (Wilde *et al.* 2014)—in particular to the genes relating to pigmentation. These authors find evidence for natural and sexual selection for reduced skin pigmentation in Europe over a period of 5000 years—related in part to diet, sunlight and vitamin D synthesis—offering substantiation of North-South gradients found in some alleles of modern populations. The authors propose that a move from a vitamin D rich hunter-gatherer diet to a more vitamin D impoverished diet during the transition to agriculture led to natural selection for reduced pigmentation in the skin favouring more efficient vitamin D production—especially at increasing latitudes. These findings accompany, for instance, evidence from modern populations of copy number variants associated with the starch-reducing enzyme amylase being carried at higher numbers in populations where cereal diets are more ancient (Novembre *et al.* 2007). The persistence of the lactase gene important in adult milk consumption has also been found to have been the subject of strong selection pressure over about 7,000 yr (Tishkoff *et al.* 2007).

Some Y-chromosome evidence suggests that agriculture was substantially a process of cultural diffusion in southeast Europe (Battaglia *et al.* 2009) and survival of Palaeolithic Y-chromosome markers are reported for the Cretan highlands (Martinez *et al.* 2007). Relative influences of topography on gene distributions—and by implication on the cultural processes that drove them—are discussed with regard to the Atlantic 'Façade' coastal routes of Europe (McEvoy *et al.* 2004) and to a counter-clockwise route for expansion of paternally-inherited Y-chromosome markers into Eastern Europe from southern Siberia about 12-14 Kyr BP (Rootsi *et al.* 2007). Conversely, the identification of maternally-inherited mitochondrial DNA markers in Slavs is interpreted as evidence for west-east migration from the Franco-Cantabrian refugia (Malyarchuk *et al.* 2008). More recent arrival of Anatolian lineages is post-

ulated for Tuscany (Brisighelli et al. 2009). In a wide-ranging study of modern and archaeological specimens using both Y-chromosome and mtDNA markers, Haak et al. (2010) identified shared affinities of early farmer populations with contemporary Near Eastern and Anatolian populations.

2.5 *Genetics and culture*

The refugia populations postulated for the Late Glacial Maximum are abstractions whose ethnic composition will not be a direct reflection of gene frequencies or—necessarily—of material culture symbolism recovered from the archaeological record. Transmission of cultural traits—Epigravettian, Magdalenian—could potentially reflect demic diffusion, cultural transmission or cultural assimilation, or a combination of the three. Although migration-based explanations fell out of fashion in archaeology as genetic evidence became more readily available, contemporary genetic studies continue to associate distributions of material culture horizons with migration. The Y-chromosome evidence of Battaglia et al. (2009) was used to imply a population expansion that paralleled the range of Neolithic Impressed Ware; Haak et al. (2010) associated genetic markers with the distribution of the Linearbandkeramik (LBK) archaeological horizon, and Brotherton et al. (2013) associate mitochondrial DNA distributions with the Bell-Beaker culture.

Richerson and Boyd (2008) boldly maintain that migration remains an engine for social change.

By contrast, population admixture—a further abstraction—is sometimes likely to reflect a variety of social processes including those relating to identity, and evidence for social and economic restructuring may be evident in the archaeological record (Mussi 1990: 140-2, Bailey and Gamble 1990: 157-64). In examining the Y-chromosome evidence for the Anglo-Saxon migrations to Britain, Thomas et al. (2008) adopt in part a traditional approach to in-

terpretation of gene distributions. They take a significant and divergent step, however, in attempting to incorporate the effect of cultural status in marriage patterns in their model. There is some evidence that marriage patterns may affect gene distributions in modern populations (Bannerjee 1985, Roberts and Kahlon 1972). Although population geneticists claim to detect signals of ancient settlement, the modern population of Europe shows evidence of considerable shared ancestry or *admixture*, although regional variation in the extent to which this ancestry is shared does occur (Ralph and Coop 2013).

Ancient DNA analysis has been applied to biological sex and kinship studies in funerary archaeology at sites of varying ages from an early stage (Shinoda and Kunisada 1994, Gerstenberger et al. 1999, Keyser-Tracqui et al. 2003). Ancient DNA analysis (Thomas et al. 2008, Haak et al. 2010) of paternally-inherited Y-chromosome markers and maternally-inherited mitochondrial DNA may further permit different trends in male and female lineages to be identified at a scale beyond a local burial context.

Examination of the different factors that affect the distribution of genes and material culture and the implications for beliefs, intentionality and the intended and unintended consequences of social action raise immensely complex questions, and several authors have attempted to address relationships between culture, the genome and genetic variation on a large scale (Chiaroni et al. 2009, Laland et al. 2010). Novembre and Di Rienzo (2009) address climatic, environmental and historic dimensions of special patterns in human genetic variation. Collard and co-workers have examined factors affecting cultural evolution, including population size (Collard et al. 2013a, 2013b), while Storer et al. (2007) explored 'landscape genetics'.

2.6 *Some comments on ethical and 'race' issues*

Given the unfortunate early history of biological studies of European origins, de-

velopments that permit the analysis of skin pigmentation (Sulem et al. 2007, Wilde et al. 2014) and even face shape (Liu et al. 2012) in ancient and contemporary populations may be worthy of some scrutiny—it may eventually be possible to associate archaeological skeletal morphology directly with modern or ancient genetic analysis.

Most archaeologists recognise that interpretations of the past are tied to current political agendas—as has been the case in Greece (Hamilakis and Yalouri 1996, Karakasidou 1997). Manipulation of interpretations of human biological variation have been well documented (e.g. Kohn 1995, Gould 1981). Studies of IQ measurements associated with ethnic groups have been used to serve discriminatory ideologies (Tucker 1994) and debatable interpretations of evidence from ancient skeletal remains—such as Kennewick Man—have been used to fuel political debates (Marks 1998). It is not surprising that archaeologists have expressed concern regarding the interpretation of genetic variation (Mirza and Dugworth 1996, Pluciennik 1996, cf. Hedges 1996, Evison 1996), especially given the preoccupation of population geneticists with ethno-historic migrations as explanations for the patterns in their genetic data and their tendency to equate genes, language and culture (Cavalli-Sforza et al. 1988)—preoccupations that have been encouraged by archaeologists (Renfrew 1987). In *History and Geography of Human Genes*, Cavalli-Sforza and co-workers (1994) presented a compendious analysis of blood protein distributions on all continents. Again, patterns evident in the analysis of single genes disappeared as variation in markers are analysed cumulatively. This observation is hardly what would be expected if primordial racial types could be readily revealed in gene distributions. Nevertheless, interpretation of the cumulative patterns observed again tended to rely on migration-based explanations. Sometimes these migrations are well-attested historically, sometimes they are supported by traditional interpretations of the arc-

haeological record and sometimes they are folkloric. The idea of a co-evolutionary law for culture, genes and language is not tenable, however (Moore 1994, Terrell and Stewart 1996, Terrell et al. 1997)—although there appears to be no reason why co-transmission cannot occur in many circumstances. The modern patterns of these dimensions of society must presumably be the consequence of historical events and therefore the legitimate subject of scientific, archaeological and historical enquiry. The explanatory value of migration in archaeology may be controversial (Chapman and Hamerow 1997), but the value of literal interpretations deriving from an ‘indigenist’ stance might also be questioned. “This position, in which cultural change is cast as a self-contained affair, is probably no more tenable in its extreme form than the one it attempts to replace” (Ammerman and Cavalli-Sforza 1984: xiv). Surely the notion of a community largely impervious to the social and technological developments of its neighbours, and not receiving from or contributing to the body of their populations, is as implausible archaeologically as many a ‘migrationist’ scenario, and relies equally on the equation of peoples, language and culture—in a temporal dimension. Again, to threaten such myths in society can be costly (Karakasidou 1997: xi-xxiii). It is ironic that the demographic isolation implicit in indigenism in its extreme forms would lead to the existence of biological races which, to re-iterate, do not occur in humans.

Population geneticists are clear on a number of important issues. There is no scientific evidence to indicate the existence of biological races in the human species (e.g. Cavalli-Sforza et al. 1994: 19-20)—races are social constructs. Nevertheless, a small amount of genetic variation does exist and, in Europe, both genetic heterogeneity and spatial patterning are evident. Relatively early in the era of new genetics, Sokal et al. (1989: 289) noted the patterns observed are too complex to be explained away as the result of a small number of trans-

continental migrations, and geographical and environmental factors clearly have considerable influence (Barbujani and Sokal 1990, Sokal *et al.* 1989: 290)—one of which may be the relationship between latitude and exposure to ultraviolet light in sunlight, and skin pigmentation and a nutritional requirement for vitamin D (see also Wilde *et al.* 2014, above). Admixture remains the predominant feature of the genetics of European populations (Ralph and Coop 2013).

The criticism of genetics in archaeology, or its perhaps sophomoric dimension, appears to have dissipated since the mid-1990s, suggesting this phenomenon too was a product of its time.

CONCLUSION

Study of the origin of the inhabitants of Europe began in an age where our understanding of biological evolution, heredity and the concept of genes and the genetic control of the structure and metabolic pathways of the body were essentially unknown. Scholars measured what they could see or sense—the shape of the body and of the skeleton, the spoken languages and apparent differences in culture between the people of different regions. In the absence of a proper understanding of

differences between biology and culture, they were frequently conflated. As scientific knowledge advanced and democratic society progressed, ideas of racial fixity and taxonomy were abandoned. Studies of variation in humans moved to blood group serology and then to the analysis of genetic polymorphisms. Rather than clarifying racial taxonomies, variation in these traits proved inexplicable in terms of primordial populations and race and racial hierarchy became redundant concepts in human biology. The scientific precision enabled by the direct analysis of human DNA sequences in modern and ancient samples has revealed immense complexity and a high degree of admixture in the European gene pool. Nevertheless, many trends in Palaeolithic, prehistoric, historic and more recent populations can be detected, which can be associated with archaeological contexts and horizons on local, regional and continental scales. Like archaeological, linguistic and environmental evidence, these demand explanation by scholars of the past. Like each of these, the nature of its formation, perpetuation, modification and survival is immensely complex and affected by particular influences, some of which may be shared with the others and some of which may not.

ACKNOWLEDGEMENT

I would like to acknowledge the kind interest and companionship of Marek Zvelebil during my postgraduate studies in the Department of Archaeology and Prehistory, University of Sheffield.

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