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INSTITUTE OF ARCHAEOLOGY AND ETHNOLOGY
POLISH ACADEMY OF SCIENCES

MAN – MILLENNIA – ENVIRONMENT

STUDIES IN HONOUR
OF ROMUALD SCHILD

EDITED BY
Zofia Sulgostowska and Andrzej Jacek Tomaszewski

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CATRIONA PICKARD, BEN PICKARD AND CLIVE BONSALE

REASSESSING THE MITOCHONDRIAL DNA EVIDENCE FOR MIGRATION AT THE MESOLITHIC-NEOLITHIC TRANSITION

INTRODUCTION

The key human migrations that are considered to have shaped the genetic makeup of Europe are the initial Upper Paleolithic colonization, a subsequent retreat to southern refugia during the Last Glacial maximum, and the post-glacial ('Mesolithic') northward re-expansion from these refugia (*e.g.* Torroni *et al.* 1998, 2000, 2001; Reidla *et al.* 2003; Achilli *et al.* 2004; Forster 2004; Pereira *et al.* 2005). While the existence of these events is well established, the genetic impact of the subsequent spread of farming across Europe has been hotly debated.

Two main theories are currently proposed to explain the appearance of agriculture in Europe: migration and acculturation (*e.g.* Zvebil, Dolukhanov 1991; Price *et al.* 2001). Analysis of the mitochondrial DNA (mtDNA) and nuclear DNA of modern populations and ancient humans are the current methods of choice to determine the relative contributions of the two processes (*e.g.* De Benedetto *et al.* 2000; Dupanloup *et al.* 2004). This has not been a straightforward task as the DNA approach has ignited interpretational conflicts arising from the varied statistical methodologies applied to extract meaningful data from the genetic palimpsest of ancient and modern mutations that have arisen since our ancestors left the African continent. The history and current state of this debate has been reviewed extensively (Chikhi *et al.* 1998a, b; Simoni *et al.* 2000a, b; Barbujani, Bertorelle 2001; Forster *et al.* 2002; Forster, Matsamura 2005).

Two recent studies (Chandler *et al.* 2005; Haak *et al.* 2005) have highlighted several unresolved archaeological and genetic issues arising from the interpretation of ancient DNA samples, and proposed migrations at the Mesolithic-Neolithic transition. In this article, we discuss the findings of these two studies. A hitherto unconsidered implication for such research is the potential effect of environment on the frequency of particular allelotypes in a population. In particular, it is postulated here that natural selection may have played a role in the distribution of mtDNA haplo-

groups throughout Europe, adding a further layer of complexity to the analysis of the ancient migrations and movements of peoples.

EXAMINING ANCIENT DNA IN THE CONTEXT OF THE MESOLITHIC-NEOLITHIC TRANSITION

The transition in Portugal

Consideration of the mechanism behind the adoption of agriculture in Portugal has resulted in two opposing camps – those favouring demic diffusion in the form of maritime colonization of areas left uninhabited by hunter-gatherers (*e.g.* Arnaud 1982; Zilhão 1993, 2001) and those proposing gradual, indigenous adoption of the 'Neolithic package' through long-distance exchange mechanisms (Geddes 1983; Estevez 1988).

Zilhão, a leading proponent of the migration theory, based his argument on the fact that the earliest ¹⁴C ages for (Cardial) Neolithic sites in northwest Italy, southern France and Iberia are very similar, suggesting a near-synchronous appearance of agriculture throughout the west Mediterranean region *c.* 5400 cal BC (Zilhão 2001). From the radiocarbon evidence Zilhão calculated that Neolithic agriculture spread along the Mediterranean littoral at an average rate of at least 10 km/year, which he suggested was too rapid to be explained by acculturation, or by a land-based colonization involving a steadily advancing frontier as predicted by the 'wave-of-advance model' of Ammerman and Cavalli-Sforza (1973). Instead, he argued for colonization by small, sea-faring groups who established Neolithic enclave settlements ('leapfrog migration'). This hypothesis is based on very few ¹⁴C dates for northern Italy and southern France. It also overlooks the possibility that many Early Neolithic sites in those regions have been lost owing to rising sea-levels in the mid-Holocene, which may have influenced the pattern of the radiocarbon dates since many coastal sites older than 5400 cal BC are likely to have been destroyed or submerged during the transgression.

MtDNA obtained from Mesolithic and Neolithic individuals in Portugal has been interpreted by Chandler *et al.* (2005) as supporting demic diffusion and the model of maritime pioneer colonization (*cf.* Zilhão 2001). The first Neolithic farmers in Portugal are stated to be genetically distinct from the indigenous Mesolithic population based on genetic distances determined by statistical analyses (“mean pairwise distances... converted to two dimensional plots using multidimensional scaling (MDS) in SPSS” (Chandler *et al.* 2005: 784). Their conclusion is that the “Mesolithic and Neolithic inhabitants of Portugal are different genetic populations” (Chandler *et al.* 2005: 785). This key interpretation results from the authors’ application of a multidimensional scaling approach to the haplotypes. However, this approach and the related Principal Components Analysis (PCA) have been the object of some criticism (*e.g.* Clark 1998). At the resolution of haplogroup analysis the results seem far less clear-cut, with an apparently close genetic relationship between Mesolithic and Neolithic mtDNA samples (and the modern Iberian samples). It could be argued that these conflicting results stem from the small sample size (particularly for the Mesolithic population: $n = 9$) which may have exaggerated the genetic differences between the two populations.

Of chief concern is the apparent, high, within-group, genetic diversity exhibited, especially by the Mesolithic samples (*cf.* Chandler *et al.* 2005: Fig. 6) – supposedly a small population with a homogeneous and stable origin. It becomes difficult to draw firm conclusions on relatedness between Mesolithic and Neolithic peoples when the full extent of the Mesolithic genetic diversity has not been determined. It is quite possible that the haplotypes of the Neolithic DNA samples are represented in an unsampled subset of the Mesolithic population. Moreover, it would appear from the data presented that the Mesolithic and Neolithic sites sampled are quite widely separated in time and/or space, which may account for some or all of the genetic distance observed between the two populations.

In addition, the absence of the J and T haplogroups from both the Mesolithic and Neolithic DNA samples is intriguing. These haplogroups are the key indicators of Neolithic migration from the Near East into central Europe (Richards *et al.* 1998) and exist in most modern European populations including those from the Mediterranean and Iberia. This suggests that regardless of the actual mechanism of the Mesolithic-Neolithic transition in Portugal, it did not involve the direct or indirect immigration of Near Eastern peoples. Intriguingly, these haplogroups have been identified in central European Early Neolithic populations that were roughly contemporary with those in Portugal (Haak *et al.* 2005). If, like the central European pioneer farmers, the ‘Neolithic colonizers’ of Portugal

had originated in the east Mediterranean just a few centuries earlier, then one would expect haplogroups J and T still to be present in their mtDNA. Thus, it is difficult to see how the data presented by Chandler *et al.* (2005) support the hypothesis proposed by Zilhão (2001) of a rapid movement of Neolithic farmers along the Mediterranean littoral from Italy to Portugal, or indeed how they preclude an acculturation model for the introduction of agriculture to Portugal.

The transition in central Europe

Haak *et al.* (2005) also describe the isolation and amplification of mtDNA from ancient samples for the purpose of distinguishing the modes of agricultural spread. In this case, the DNA samples derive from Neolithic skeletons found in LBK or AVK contexts at 16 sites in present-day Germany, Hungary and Austria. Of the 24 individuals who yielded good-quality mtDNA information, 18 possessed haplogroups H, V, T, K, J, and U3 which, although consistent with Near Eastern origins (particularly J and T), did not provide information of sufficient clarity for the authors to claim that it supported either of the principal models of Neolithic agriculture spread. However, the remaining 6 mtDNA samples (25% of the samples analyzed) were identified as belonging to the N1a haplogroup, a surprising finding given that this haplogroup is found at only trace levels in current populations. Closer examination of the N1a haplotypes indicated that they are identical to N1a types that are currently found in Europe and central Asia. While this haplogroup does not make a substantial contribution to resolving the precise geographical origins of genetic influx into Europe, the authors maintain that it supports the view that there was a small initial influx of people into central Europe bringing agricultural practices with them, but the primary mechanism by which agriculture spread across the region was acculturation. They argue that this is evidenced by the fact that the maternal genetic contribution made by the ‘immigrants’ has been substantially diluted since the Neolithic.

In arriving at this conclusion, Haak *et al.* reject two other possible explanations of their data. The possibility that the much lower frequency of N1a in modern populations is due to ‘genetic drift’ (random change in gene frequencies) over the past 7500 years was rejected on the basis of computer simulation studies, while the possibility that N1a has been largely eliminated by later migrations was also discounted because of a lack of archaeological evidence for such migrations.

A response by Ammerman *et al.* (2006) casts doubt on the generality of Haak *et al.*’s interpretation and aspects of their methodology. They cite the limited number of samples analyzed, their restricted geographical origin, the failure to account for ancient marriage

customs (mtDNA is only inherited through the maternal line) and the broad chronological spread (*c.* 700 years) of the samples, as chief causes for concern.

In addition to the observations made by Ammerman *et al.* (2006), other explanations of Haak *et al.*'s (2005) findings merit consideration:

1. The N1a haplogroup reduced the survivability of its carriers through natural selection pressure leading to its decline since the Early Neolithic. However, present-day distributions of the N1a haplogroup appear uniform, if at a low overall level, which suggests that small-scale environmental pressures are not involved.
2. The observed frequency of N1a haplogroup carriers among the Early Neolithic population is greater than their actual frequency within the population, as the result of an 'ascertainment bias'. In other words, the skeletons analyzed are a biased sample of the Early Neolithic population. Such a situation could arise if a section of the immigrant population left a much stronger imprint on the archaeological record than other sections of that population through, for example, particular burial practices which increased the likelihood of their skeletons being discovered or found in a state of preservation more amenable to successful mtDNA extraction and amplification.
3. There were no immigrant farmers and the N1a haplogroup was already present in the indigenous population. Currently, there is insufficient evidence to rule out the presence of the N1a haplogroup in the indigenous Mesolithic population – a point also made by Ammerman *et al.* (2006). This hypothesis would explain the presence of N1a carriers among the Early Neolithic population, but it would not explain the subsequent decline in the frequency of the N1a haplogroup.

NATURAL SELECTION: A MIMIC OF MIGRATION?

Beyond the technical difficulties of working with ancient DNA and the problems of melding archaeological evidence with genetic data, there exists the issue, frequently overlooked, of the functional biology of the mitochondrion. The properties of this organelle may be important for genetic studies of ancient populations.

Mitochondrial DNA is subject to the same processes of Darwinian natural selection as nuclear DNA. In fact the DNA replication error-checking mechanisms within the mitochondrion are 10–100 times less proficient than within the nucleus. Hence, spontaneous mutations, the substrate for selection in response to environmental change, are far more numerous within mitochondrial DNA. Despite the fact that only 37 of the

hundreds of proteins required for correct mitochondrial function are encoded by the mitochondrial genome itself, there still remains the scope for changes in these genes to alter the reproductive fitness of their human hosts. In terms of the analysis of hypervariable regions of the mitochondrial genome, it is important to appreciate that, unlike nuclear DNA, there is no meiotic recombination to confuse linkage. In other words, the mitochondrial genome haplogroup in which an advantageous mutation occurs will be carried along as a passenger on the evolutionary ride and its altered frequency will reflect the degree of the advantage.

Could this phenomenon have muddied the genetic waters at the time of the Neolithic transition across Europe? The key property required for this to be a significant issue is a driving force of sufficient effect to alter reproductive fitness, *i.e.* to act as the natural selector at this time. Gamble *et al.* (2004) studied mitochondrial genetics in the context of human adaptation to colder, more northerly climates. In such conditions, to aid survival, mitochondria can convert a greater percentage of nutrient input directly into heat (mitochondrial 'uncoupling'), rather than cellular energy production. Certain mutational changes in the mitochondrial genome can promote this heat energy production survival strategy and these are predominant in the mtDNA of northern peoples as reflected in the distribution of particular haplogroups. Archaeologically, this is an adaptation that would have given an advantage to groups reclaiming land from retreating glaciers at the end of the Last Ice Age (or, perhaps, enabling their survival in the Iberian or Mediterranean refugia). In this way, it is possible to see how biologically-driven mitochondrial changes would have skewed the distribution of particular haplogroups across Europe.

Does this process have any counterpart during the period when Neolithic agriculture was spreading across Europe? Holocene climate is now known to have been highly variable. Though not as severe as those of the Pleistocene, some climatic oscillations of the Holocene were of sufficient magnitude to have affected human societies, and climate change has been cited by several authors as the trigger for human migrations or rapid changes in subsistence regime (*e.g.* Bonsall *et al.* 2002a, b; Weninger *et al.* 2005). A succession of cold events is recorded during the Holocene, those *c.* 6200 cal BC, 2700 cal BC and AD1500–1850 (the 'Little Ice Age') being especially severe, associated with reductions in average annual temperatures across temperate Europe of up to 3°C. Historical records show that climatic cooling during the Little Ice Age had a profound effect on agriculture and health in many parts of Europe, leading to famine, social unrest and emigration. Genetically, climate change during the Holocene is unlikely to have been such a selecting force as it was during the Pleistocene, but Holocene

cooling events may have had some impact on haplogroup frequencies.

Some workers (*e.g.* Pereira *et al.* 2005) have suggested that certain mtDNA subgroups result in sperm with altered motility and fertility. Haplogroups associated with increased fertility might confer a selective advantage and thus become more prevalent in a population. However, this mechanism would not be restricted to the Neolithic transition.

One environmental change specific to the transition was the emergence of an alternative source of dietary energy with the adoption of agriculture as the primary mode of subsistence (*cf.* Bonsall *et al.* 1997, 2007). The consequences of the shift from a protein/fat-based (Mesolithic) diet to a carbohydrate-rich (Neolithic) diet has been the subject of much discussion, principally in the context of its legacy in modern humans as a possible cause of the prevalence of diseases such as type II diabetes, gastro-intestinal problems and cancers (Cordain *et al.* 2005). What is clear is that for this to be of archaeological relevance, the harmful effects of this dietary switch should be manifest *before* the age of reproduction. This is because natural selection can only occur when a mutation has an effect on reproductive fitness. Certainly, this seems unlikely in modern, Western populations as the disorders implicated tend to be disorders of middle age (when individuals are, evolutionarily-speaking, less important). However, there are reasons to suppose that this harmful selection might have been magnified at the onset of the Neolithic. Health studies of Asian immigrants in Western countries in the latter half of the 20th century provide some evidence for this. The change in diet from Asian to Western was accompanied by an increase in disease. Early-onset type II diabetes and, interestingly, progestational diabetes (leading to increased foetal and maternal mortality) are observed at far higher frequency in these acculturating groups compared to the indigenous populations. Independently, mitochondrial dysfunction (or, rather, overburdening) has been implicated as one factor in type II diabetes aetiology. While equating a switch from Asian to Western diet with a switch from Mesolithic to Neolithic diet is risky, it does emphasize the potential health implications resulting from a fundamental change in subsistence strategy. It may be the case that descendants of the European Neolithic (most modern Western populations) underwent such a diet-related health 'crisis' at that time and that natural selection has, in part, altered the genetic components of energy metabolism in compensation (some of which may have involved mtDNA), thus conferring some degree of protection. This resulting genetic acclimatization has perhaps led to an underestimation of the initial impact of dietary change at the Meso-Neolithic transition.

To propose dietary change as an evolutionary selection mechanism altering the population frequencies of certain haplogroups requires that mitochondrially-encoded gene-products are in some way affected by, or are able to compensate for, changes in cellular metabolite (essentially, pyruvate) concentrations brought about by a carbohydrate-rich diet. The number of mitochondria within a cell (typically 100s to 1000s) is affected by caloric intake and, in addition, calorie-rich diets appear to generate excess quantities of reactive oxygen species (free radicals) through the oxidative phosphorylation pathway. These are toxic to the cell in general, have been linked with various degenerative diseases, and are responsible for the high rates of mutagenesis in the mitochondrial genome (Wallace *et al.* 1995, 1999; Wallace 1999, 2005; Loeb *et al.* 2005). Hence, hunter-gatherer populations making the shift to a carbohydrate-rich diet at the Neolithic transition may have experienced disruption to cellular energy management with potentially pathological consequences. It has been postulated that inheriting mitochondria predisposed to 'uncoupled' functioning could not only aid cold-climate existence, but could also alleviate the effects of a carbohydrate-rich diet (Wallace 2005). Interestingly, not only are the J and T haplogroups among those associated with such a mitochondrial action, they are also recognized as being the archetypal haplogroups representing Neolithic demic diffusion from the Near East.

Despite the hypothetical nature of the link between dietary change and mitochondrial genome selection, it is possible to imagine a situation where the spread of advantageous features could have interpretational consequences for modern-day researchers of ancient DNA. A haplogroup or haplotype that confers a survival advantage on the carrier is likely to spread at a higher rate than one that does not. To the researcher, *in situ* proliferation of advantageous haplogroups would be indistinguishable from the large-scale influx of people carrying that haplogroup. Thus, the prediction would be that positive natural selection could create an impression of substantial demic diffusion in ancient populations.

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