

2-1-2012

Cranial variation and the transition to agriculture in Europe

Ron Pinhasi

Department of Archaeology, University College Cork, Cork, Ireland, ei.ccu@isahniP.R

Noreen Von Cramon-Taubadel

Department of Anthropology, School of Anthropology and Conservation, University of Kent, Canterbury, UK, N.Von-Cramon@kent.ac.uk

Recommended Citation

Open access pre-print, subsequently published as Pinhasi, Ron and Von Cramon-Taubadel, Noreen (2012) "A Craniometric Perspective on the Transition to Agriculture in Europe," *Human Biology*: Vol. 84: Iss. 1, Article 10.
Available at: http://digitalcommons.wayne.edu/humbiol_preprints/11

This Open Access Preprint is brought to you for free and open access by the WSU Press at DigitalCommons@WayneState. It has been accepted for inclusion in Human Biology Open Access Pre-Prints by an authorized administrator of DigitalCommons@WayneState.

Cranial variation and the transition to agriculture in Europe

Pinhasi, R.¹, von Cramon-Taubadel, N.²

¹Department of Archaeology, University College Cork, Cork, Ireland

²School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NR,
United Kingdom

Abstract

Debates surrounding the nature of the Neolithic demographic transition in Europe have historically centred on two opposing models; a ‘demic’ diffusion model whereby incoming farmers from the Near East and Anatolia effectively replaced or completely assimilated indigenous Mesolithic foraging communities and an ‘indigenist’ model resting on the assumption that ideas relating to agriculture and animal domestication diffused from the Near East, but with little or no gene flow. The extreme versions of these dichotomous models have been heavily contested primarily on the basis of archaeological and modern genetic data. However, in recent years there has been a growing acceptance of the likelihood that both processes were ongoing throughout the Neolithic transition and that a more complex, regional approach is required to fully understand the change from a foraging to a primarily agricultural mode of subsistence in Europe. Craniometric data have been particularly useful for testing these more complex scenarios, as they can reliably be employed as a proxy for the genetic relationships amongst Mesolithic and Neolithic populations. In contrast, modern genetic data assume that modern European populations accurately reflect the genetic structure of Europe at the time of the Neolithic transition, while ancient DNA data are still not geographically or temporally detailed enough to test continent-wide processes. Here, with particular emphasis on the role of craniometric analyses, we review the current state of knowledge regarding the cultural and biological nature of the Neolithic transition in Europe.

Introduction: The European Neolithic Debate

Over the past two decades, the excavation and analysis of archaeological sites in the Levant and Anatolia have demonstrated that the emergence of agriculture was a slow and complex process involving major intra- and inter-regional variation in settlement types and pattern, the mode of subsistence, architecture, technology, arts, and mortuary practices (Aurenche and Kozłowski 1999; Bar-Yosef 1998; Kuijt and Goring-Morris 2002; Özdoğan 1997; Özdoğan 2005). The emergence of different types of Neolithic communities in these core regions is associated with several maritime dispersals of farmers into Cyprus, Crete, Italy, Sardinia, Corsica and further west, and by land via northwest Anatolia into southeast Europe (Cherry 1990; Perlès 2001; Runnels 2003; Van Andel and Runnels 1995; Zilhão 2001; Zvelebil 1986; Zvelebil 2001).

In the past, interpretations of the transition to agriculture in Europe have tended to be polarized between two dominant approaches:

- (1) A 'demic diffusion' model views the transition as being predominantly the outcome of the dispersal of Near Eastern/Anatolian farmers into Europe. According to this model, agriculture emerges in various parts of Europe mainly as the outcome of the dispersal of Near Eastern/Anatolian farmers into European territories. Under this model, the exogenous farmers brought with them a 'Neolithic package', which includes domesticated crops, livestock (i.e., cattle, sheep, goat, pig), ceramic and housing technologies, and certain figurative and stylistic attributes particularly characteristic of western Anatolian farmers. The basic contention of this model was that the demographic profile of farming populations differed from that of hunter-

gatherers. Population growth resulted in the expansion of local populations in all directions and at a relatively steady rate. Support for this model comes from archaeological, chronological, and geographic distance data, and diffusion rates were calculated on the basis of geographic distances and radiocarbon dates. Subsequently, genetic data were used to support arguments for this putative population expansion (e.g., Ammerman and Cavalli-Sforza 1984; Barbujani et al. 1998; Cavalli-Sforza et al. 1993; Cavalli-Sforza et al. 1994; Sokal et al. 1991). The strongest adherents of this view have been Colin Renfrew (Renfrew 1992) and Luca Cavalli-Sforza (Cavalli-Sforza 1996), who have also suggested strong correlations between linguistic patterns (e.g., Indo-European language families), modes of subsistence, and modern distributions of genetic alleles.

- (2) Conversely, an 'indigenist' model views the transition to agriculture in Europe as the outcome of a local transition in which indigenous European hunter-gatherer populations adopt farming, either as a parallel and independent innovation, or as an outcome of the cultural diffusion of some aspects of the Neolithic package (herds of domesticated animals, domesticated seeds of key crops, etc.) by Near Eastern/Anatolian farmers. Supporters of this model view the transition as a process that did not involve major demic input from the Near East/Anatolia. The spread of farming under this model is, therefore, seen as an economic and cultural transformation in which indigenous European hunter-gatherers adopt the Neolithic life (Dennell 1983; Whittle 1996; Whittle and Cummings 2007).

However, it is clear that these two approaches need not be mutually exclusive. The

demic diffusion model does not rule out the possibility that in some regions of Europe local hunter-gatherers adopted agriculture, perhaps as a cultural response to the emergence of farming by incoming exogenous populations. In the case of the ‘indigenist’ approach, many of its proponents agree that at least in southeast Europe, agricultural transitions were mainly the outcome of a major influx of exogenous Anatolian/Near Eastern farmers. However, a major point of contention is whether the transition in major parts of Europe involved genetic input from farmers of Anatolian/Near Eastern descent. As we will further discuss below, this point is of particular relevance to genetic studies that explore genetic variation and phylogenies of both present and past Europeans.

What, therefore, was the demographic and genetic impact of Near Eastern/Anatolian populations to the gene pool of European populations? According to proponents of the demic diffusion model (Ammerman and Cavalli-Sforza 1971; Ammerman and Cavalli-Sforza 1973; Ammerman and Cavalli-Sforza 1984; Pinhasi et al. 2005), the dispersion of farmers into Europe involved the replacement of local hunter-gatherer bands with only a minimal-to-moderate amount of admixture in the regions of southeast and central Europe. This model was long accepted for the ‘Danubian’ Neolithic cultures of central Europe (e.g. Childe 1957; Clark 1965a; Clark 1965b; Piggott 1965). Ammerman and Cavalli-Sforza’s ‘wave-of-advance’ model (Ammerman and Cavalli-Sforza 1971; Ammerman and Cavalli-Sforza 1973; Ammerman and Cavalli-Sforza 1984) suggests a gradual process of population expansion by farming communities northwards and westwards which is triggered by logistic population growth of the Near Eastern/Anatolian farming populations (see also (Bocquet-Appel 2011). As pointed out by Pinhasi and Pluciennik (Pinhasi and

Pluciennik 2004), the basic contention of this model was that the demographic profile of farming populations differed from that of hunter-gatherers. It can, however, be difficult to obtain a reliable estimate of demographic parameters on the basis of archaeological data (although see Chamberlain, 2009). Estimating settlement patterns in terms of site size, density, and estimated length of occupation etc. on the basis of surveys, test excavations, and published reports is fraught with difficulties and biases (see for example Webb & Frankel, 2004 in regards to Bronze Age Cyprus). First, it has to take into account intra- and inter- regional differences in the detection of sites, especially in the case of submerged coastal settlements but also in the case of sites which were destroyed by recent land use, eroded, or buried under meters of alluvium (in particular sites in Thrace and Macedonia). Second, major contrasts in the life style, especially subsistence strategies, of Mesolithic and Neolithic populations means that the former left less material culture traces than the latter. This is clear when one considers the size and depth of cultural layers in major tell sites in comparison to the average Mesolithic camp site. Third, it is difficult to determine population size and density parameters on the basis of numbers of structures in a given site, or its overall size. This is because we do not know how many individuals inhabited each (presumably domestic) structure and we often do not know the original boundaries of archaeological settlements (see for example Flannery, 1972, 2002).

Furthermore, as has been demonstrated by various researchers (cf. various contributions in (J-P Bocquet-Appel and Bar-Yosef 2008) that the genetic input of a given founding population to a local indigenous population depends not only on the original size of each population, but also on other demographic parameters such as fertility and mortality rates. Hence, a relatively small founding population of

Anatolian farmers, with a high fertility rate (relative to indigenous hunter-gatherers), may have had a major genetic impact on the gene pool of local Mesolithic populations. Taking the above into consideration, it is evident that a clear model-bound evolutionary approach is required to accurately infer past demography from archaeological data (cf. Steele and Shennan, 2009; Shennan, 2009).

Another major issue to consider is the nature and extent of contact between hunter-gatherer bands and incoming farmers. Contact between these populations could obviously have only occurred in places where both populations coexisted. Zvelebil and Rowley-Conwy (Zvelebil and Rowley-Conwy 1984; Zvelebil and Rowley-Conwy 1986), therefore, proposed a three-stage model for the adoption of agriculture which takes into consideration periods of interaction between dispersing farming populations and indigenous hunter-gatherers along established frontiers. During the initial 'availability' phase, hunter-gatherers will adopt a limited number of farming economy elements their subsistence but otherwise retain their indigenous economic basis and associated lifestyle. During the following 'substitution' phase, hunter-gatherers will enter a process in which a growing percentage of their economy will be based on farming products. During the final 'consolidation' phase, hunter-gatherers will no longer just adopt part of the Neolithic economy and products but will transform their economic basis and some of the related social and technological aspects, thus emerging as a 'new' farming society. This three-stage process is hypothesised to typically occur along a 'frontier' region at which dispersing farmers interact with local hunter-gatherers. As we discuss below, the archaeological records of southeast, Mediterranean and Central Europe do not provide much evidence for frontier regions (but see Zilhão 2001 for coastal regions of Portugal). It therefore

follows that different geographic regions of Europe will vary in the extent of their farmer/hunter-gatherer interaction, thereby altering the expectation of possible genetic admixture between them.

One of the major problems is that the dichotomization of the two predominant approaches undermines the complexity of the issue at hand. On the basis of the chronological data alone, it is clear that the neolithisation of Europe, as a demographic process, took place over a period of more than four millennia. Taking this into consideration, it is unrealistic to assume that the same demographic and historical processes that characterise the transition to farming in the parts of Europe where agriculture was introduced during the 7th millennium BC, were the same as those in the peripheral regions of northwest Europe (for example, the British Isles). Assuming a figure of 20 years per human generation and no contribution of local hunter-gatherers to the dispersing farmer's gene pool, the first farmers arrived in the British Isles (e.g. Collard et al. 2010) at least 200 generations after the original dispersal of the founding population from the Near East/Anatolia. Any absorption of local hunter-gatherers into the expanding farming populations during this period would have left a genetic trace on the descendants prior to them colonising new peripheral regions.

Archaeological Record of Neolithic dispersals into Europe

The Pre-Pottery Neolithic/Aceramic period in the Near East and Anatolia began after the onset of the Holocene more than 11,000 years ago and lasted for 3000-4000 years (cf. Bar-Yosef 1998; Bar-Yosef and Meadow 1995; Blockley and Pinhasi 2011; Kuijt and Goring-Morris 2002; Özdoğan 1997). During this long period, the archaeological

record indicates maritime colonisation of Cyprus, Crete and mainland Greece (Thessaly and the Argolid) by more than one wave of Near Eastern/Anatolian migrants (Cherry 1990; Manning et al. 2010; Perlès 2001; Perlès 2005). In the case of these regions, evidence for Mesolithic occupation is either limited or non-existent. At the same time, with the exception of Cyprus, evidence for an early aceramic Neolithic is also only documented in Knossos level X in Crete, and Franchthi Cave, Argissa and Sesklo in the Peloponnese (Perlès 2001). The Early Neolithic (Pottery) archaeological records of Greece and the Balkans show a clear contrast in that the Balkan sites reveal a large array of typical Anatolian elements (pottery types, multi-legged pottery vessels, etc.) that are absent in Greece (Perlès 2005)

The first appearance of the Neolithic in central and western Europe is associated with the Linear Bandkeramik Culture (LBK) (Bogucki 2003) that originated in western Hungary and eastern Austria c. 5600-5500 BC and then spread rapidly westwards to France and northwards to Poland and Germany (Whittle 1996). The initial expansion of the LBK was a rapid event which took place over ≈ 350 years. During its middle/late phase, the LBK continued to expand in three distinct movements. One was through the loess lands along the upper Danube into the Neckar Basin and the middle Rhineland. A second was via Moravia and Bohemia into central Germany, eventually reaching the lower Rhine and Meuse. A third occurred along the shoreline of the Baltic Sea (Thomas and Rowlett 1992), where the tempo of expansion was slower. On the western fringe of the LBK distribution and further west towards the Atlantic the archaeological record has yielded Limburg and La Hoguette pottery assemblages that display differences with the LBK proper, possibly involving indigenous hunter-gatherers responding to interaction with incoming farmers (Allard 2007).

In southern Europe, Impressed and Painted Ware sites first appear along the western coasts of Greece, Albania, Dalmatia, south Italy and Sicily at around 6200/6000 BC (Skeates 2003). In these regions, there is a hiatus between late Mesolithic and earliest Neolithic dates (Pluciennik 1997). The archaeological record of the western Mediterranean indicates an arrival of Cardial/Impressed Ware Neolithic farmers in coastal regions between 5800 and 5300 BC (Zilhao 2003). In Corsica, the Cardial Neolithic is dated to 5700-5300 BC (Tykot 1994). In Sardinia, a human presence is confirmed by 8th millennium BC via radiometric dates for human remains from Grotta Corbeddu. However, early Neolithic dates from Sardinia fall in the mid 6th millennium BC and suggest a hiatus of close to 1000 years between the Mesolithic and Neolithic occupations of the island (Pluciennik 1997). The scarcity of dates from central Italy does not allow much discussion regarding the spread of farming in this region, but secure dates fall around the middle of the sixth millennium BC.

In the case of the Iberian peninsula, the rapid spread of the Cardial culture along the western Mediterranean coastline suggests leapfrog colonisation by pioneering maritime Neolithic groups with late Mesolithic and early Neolithic sites located around the peripheral coastal regions of the peninsula (Zilhao 2003). Along the southwestern coast of Portugal, late Mesolithic populations survived for as long as 500 years after the first arrival of Neolithic farmers in the estuaries of the Tagus, Sado and Mira rivers, while contemporaneous Neolithic populations inhabited the limestone massifs of central Estremadura and the Algarve (Zilhao 2003).

The Genetic Evidence for the Demographic Transition to Agriculture in Europe

Given the patchiness and paucity of archaeological data, much of the research into the nature of the transition to agriculture in Europe has focused on the use of biological (genetic and phenotypic) data. As discussed in greater detail below, there is a growing

recognition that phenotypic (especially skeletal) data can yield important insights into the microevolutionary processes underlying this transition, but the majority of research to date has been genetic in nature. Studies of DNA markers have yielded diverse and often conflicting results regarding the contribution of indigenous late hunter-gatherers and exogenous Near Eastern/Anatolian farmers to the gene pool of modern European populations (Deguilloux et al. 2011). Estimates for the contribution of Near Eastern farmers have varied greatly, ranging from 20% to 70% (Belle et al. 2006a; Dupanloup et al. 2004; Richards 2003; Richards et al. 1996; Richards et al. 2000; Richards et al. 2002; Torroni et al. 1998; Torroni et al. 2000).

More than 30 years ago, a seminal study by Menozzi et al. (Menozzi et al. 1978) examined (via principal components analysis) whether the geographic pattern of 39 gene frequencies indicated a spatial pattern that would support or reject in its direction the ‘wave of advance’ model. The underlying assumption was that migrations of farmers into an area sparsely populated by local hunter-gatherers would generate circular gradients (clines) of gene frequencies around the origin of dispersal (Cavalli-Sforza et al. 1993; Cavalli-Sforza et al. 1994). Synthetic maps based on PC scores displayed a southeast to northwest cline which Menozzi and colleagues (Menozzi et al. 1978) attributed to the ‘wave of advance’ or ‘demic diffusion’ of farmers from the Near East into Europe with gradual changes in allele frequencies believed to be due to the absorption of local hunter-gatherer populations into the farming communities. This study was extended and corroborated by Cavalli-Sforza and collaborators (Cavalli-Sforza et al. 1993; Cavalli-Sforza et al. 1994) using data on allelic frequencies of European populations for over 130 markers.

In the last two decades, the validity and reliability of these maps has been questioned (see Fix 1999; Bellwood and Renfrew 2002; Jobling et al. 2004; Jobling and Tyler-Smith 2003; Renfrew and Boyle 2000 and references therein). In particular, Sokal and colleagues (Sokal et al. 1999) pointed out that the synthetic gene frequency maps originally produced by Menozzi and colleagues (Menozzi et al. 1978) were derived by reducing the data set of allele frequencies into a selected number of principal components that required the interpolation of missing surfaces. According to analyses by Sokal et al. (1999), this results in artificial spatial autocorrelation, making it difficult to discern if any observed clinal pattern is the outcome of 'true' biological factors (see also (Novembre and Stephens 2008)).

Many studies have focused on the extent to which modern patterns of mitochondrial DNA (mtDNA) haplotypes (and haplogroups) can be explained on the basis of (1) the colonisation of Europe by anatomically modern humans approximately 40,000 years ago, (2) post Late Glacial Maximum (LGM) expansions out of refugia occurring approximately 18,000-14,000 years ago and/or, (3) the expansion of farming populations out of the Near East approximately 10,000 years ago. Results regarding these questions have varied greatly with some studies supporting a major demic diffusion of farmers (e.g. (Belle et al. 2006a; Chikhi et al. 1998; Simoni et al. 2000)) while others arguing that the genetic contribution of Near Eastern/Anatolian is less than 15% (cf. (Richards et al. 2000; Richards et al. 2002; Richards et al. 1998; Soares et al. 2010 and references therein)).

Studies of Y chromosome markers have suggested that haplogroup J2 is the most important marker for the spread of farming into southeast Europe (Di Giacomo et al. 2004; Semino et al. 2000). However, as in the case of mtDNA studies, the pattern of

Y chromosome diversity among modern European populations has also been ascribed to the Upper Palaeolithic colonisation by anatomically modern humans (Rosser et al. 2000; Semino et al. 2000). Conversely, Chikhi et al. (Chikhi et al. 2002) indicates that the average contribution of Near Eastern/Anatolian farmers to the modern European gene pool was much higher ($\approx 65\%$). Analyses of Y-chromosome spatio-temporal patterns have also led to conflicting results. Congruent with a demic diffusion model, Balaresque et al. (Balaresque et al. 2010) found that spatial patterns in the frequency of haplogroup R1b among present day Europeans demonstrated an east-west cline with lowest frequency (12%) in eastern Turkey and highest frequency (85%) in Ireland. In contrast, Morelli et al. (Morelli et al. 2010) report results that indicate that Y chromosome diversity among modern-day Sardinians is best explained by a pre-Neolithic dispersal. While a study by Myres et al. (Myres et al. 2011) indicates that two R1 sub-clades show distinctive geographic distributions: R1a-M420 varieties are most frequent in eastern Europe and the R1b-M343 sub-clade is more common in western Europe, while a further sub-clade of R1b, defined by the mutation M269, is the most common Y-chromosome haplogroup throughout western Europe ((Myres et al. 2011).

There are also discrepancies between the results from mtDNA and Y-chromosome studies, which might reflect a disparity in sex-specific patterns (see also Bentley et al. 2009) with unequal contribution of male and female Neolithic farmers to the local European hunter-gatherer gene pool (e.g., higher male farmer reproductive success, Balaresque et al. 2010). This would lead to the expansion of incoming Y lineages, but it cannot explain the limited evidence for the contribution of Neolithic females, unless the founding dispersal out of the Near East/Anatolia was predominantly one of male

farmers. We must, therefore, consider the extent to which a lack of consensus regarding the causes of modern European genetic diversity patterns is a true reflection of a complex demographic history, as opposed to a reflection of inherent limitations in the analysis of the available genetic datasets.

One apparent limitation in the case of some studies is that they were not model-based and as such their analyses do not involve the specific testing of a set of alternative hypotheses/models. The use of a model-based approach which applies simulations (e.g. Barbujani et al. 1995a; Barbujani et al. 1995b; Belle et al. 2006b; Currat and Excoffier 2005; Dupanloup et al. 2003; Excoffier and Ray 2008; Ghirotto et al. 2009; Itan et al. 2009; Ray et al. 2005; Ray and Excoffier, 2009; Bentley et al. 2009) has the potential to assess the validity of different scenarios rather than relying on ad-hoc interpretative explanations of observed patterns. As pointed out by Burger and Thomas (2011, pp 7-8); “The challenge in population genetic inference is to understand, in a statistical framework, what historical scenarios could have given rise to that tree and geographic location of samples. The solution to this problem is to explore different historical scenarios and find the conditions where the data has the highest probability of arising, or some summary description of the simulated data fits best to the observed data”.

In a model-free mode of enquiry it is often difficult to assess which is the most likely explanation when several are possible. For example, genetic gradients may result from stochastic processes, such as genetic drift, but also potentially from variable selective pressures (cf. Fix 1999). Likewise, the assumption that a relatively low percentage of contribution of exogenous Neolithic farmers to European populations is

in accord with a cultural rather than demic diffusion model (e.g., Belle et al. 2006a, p. 1595) is not necessarily valid. In any case, the study of intra- and inter-genetic variability among modern day populations can at best make conclusive statements only about modern day variability. Inferences regarding past demographic processes can be drawn from modern data, but only with reference to specific models, which take into account temporal and geographic variation, as well as the underlying evolutionary processes of mutation, migration, genetic drift and possible selection.

As such, the recent expansion of available ancient DNA (aDNA) data from Mesolithic and Neolithic samples is a welcome analytical and methodological advancement. As we will discuss further below, the few aDNA studies of Mesolithic and Neolithic European individuals clearly demonstrate genetic discontinuity in some regions not only between (Neolithic) farmers and their (Mesolithic) predecessors, but also between the former and modern populations from the given region (see e.g., Bramanti et al. 2009), suggesting that there is no ‘one size fits all’ model which explains the transition from a hunter-gatherer to a farming subsistence strategy across all of Europe.

The main advantage of aDNA analysis is that it allows the direct study specimens from the specific regions and periods of interest. However, aDNA analyses also suffer from certain limitations such as authenticity, reliability, representativeness of samples, and assessment of their absolute age (Cooper and Poinar 2000 ; Gilbert et al. 2005; Handt et al. 1994; Hofreiter 2008; Hofreiter et al. 2001; Kolman and Tuross 2000; Montiel et al. 2001; Paabo et al. 2004; Rohland and Hofreiter 2007a; Rompler et al. 2006; Willerslev and Cooper 2005). Recent improvements in extraction methods maximize the yield of endogenous DNA from fossil specimens, and the introduction of ultra high throughput next generation sequencing (NGS) (Rohland and Hofreiter

2007b; Schuster 2008) are ideally suited to small fragment retrieval, utilizing aDNA fragments as short as 40-50 bp (Green et al. 2010; Poinar et al. 2006), thus, allowing improved detection and removal of non-endogenous data at the post-sequencing stage.

Most aDNA studies have focused on the analysis of short DNA fragments, mainly from the HVR-1 region of the mtDNA genome. The study by Haak et al. 2005 (Haak et al. 2005) involved the analysis of mtDNA segments from 24 LBK Neolithic specimens from Central Europe. They found that 25% of the Neolithic farmers had the N1a mtDNA haplogroups in comparison to modern Europeans in which the frequency of this type is only 0.2%. This result suggests that LBK farmers did not have a strong genetic influence on modern European female lineages. At this stage no Mesolithic or Upper Palaeolithic specimens were analysed but the authors hypothesized that the high frequency of N1a type is in best agreement with a European Palaeolithic rather than Near Eastern/Anatolian Neolithic ancestry for the LBK farmers.

In a more recent paper, Bramanti et al. (Bramanti et al. 2009) analysed 22 mtDNA sequences of Late Upper Palaeolithic, Mesolithic and Neolithic Linienbandkeramik specimens (spanning in time from 13400 cal BC to 2300 cal BC) and compared these to homologous mtDNA sequences from 25 LBK farmers and 484 modern Europeans from the same geographic region. Results show that 82% of 22 hunter-gatherer individuals carried clade U but there was also a distinct diversity of U haplogroups. The results also indicate that in genetic terms, the LBK sample and the hunter-gatherer sample were significantly different. Higher F_{ST} values, were obtained between the Mesolithic and LBK groups ($F_{ST}=0.163$) than between modern global

populations ($F_{ST} = 0.133$) (Burger and Thomas 2011). Serial coalescent simulations were then applied in order to assess whether F_{ST} values for simulated lineages sampled in various points in space and time can be used to reject the null hypothesis of population continuity. The null hypothesis was rejected as none of the simulated scenarios yielded similar or higher F_{ST} values.

In southern Scandinavia, the archaeological record indicates that the first farming Funnel Beaker Cultural complex (also known as the Trichterbecher Kultur [TRB]) and the late hunter-gatherer Pitted Ware Culture (PWC) coexisted between 5000-4000 years ago. A recent study by Malmström and colleagues (Malmström et al. 2009) examined the genetic affinities of individuals from these two cultures by analyzing ancient mtDNA sequences (316 bp of the D-loop) from the skeletons of 22 individuals; 19 PWC and 3 TRB. Results show that there is not population continuity between individuals from the two cultures and between the PWC specimens and modern Scandinavians. It is hence clear that the PWC hunter-gatherers were not the direct ancestors of modern Swedes, Norwegians or Saami. Since mtDNA haplogroups were only available for 3 TRB individuals, it was not possible to assess the potential contribution of the Scandinavian farmers to the modern Scandinavian populations.

Sampietro et al. (Sampietro et al. 2007) retrieved HVRI and diagnostic coding SNPs from the mtDNA genomes of 11 Neolithic remains from Granollers (Catalonia, northeast Spain) dated to 5500 years ago. A correspondence analysis indicated genetic continuity between the early Neolithic individuals and modern day populations from Iberia. Genealogical continuity between Neolithic and modern-day mtDNA gene pools has also been suggested for the Alpine regions (Di Benedetto et al. 2000). This

contrasts with discontinuity between Neolithic farmers and modern day inhabitants in the case of Central Europe (Bramanti et al. 2009) and gives credence to models suggesting that the Neolithic transition in Europe involved a mosaic of different demographic and cultural processes varying by region (see e.g., Pinhasi and Pluciennik 2004; Zvelebil 2001). A simulation analysis of mtDNA variation in ancient and modern Sardinians (Ghirotto et al. 2009) showed evidence of continuity between Bronze Age specimens and modern populations from the Ogliastra region, yet discontinuity between the former and modern populations from the Gallura region, suggesting a complex scenario in which two geographically close populations evolved under different demographic conditions.

In sum, we are still some way from a truly detailed understanding of the genetic and demographic changes surrounding the Neolithic transition across Europe. As Ghirotto et al. 2009, p 884) point out: “In studies of admixture, allele frequencies of modern populations are often considered to approximate the unknown allele frequencies of the past... Although algorithms have been developed to somehow take into account the effect of genetic drift through time ... a genealogical continuity between the people occupying a certain region in the past and in the present is still a very common assumption.” But as the preceding review indicates, regional aDNA studies do not unanimously support this assumption. At this stage, the available data do not allow us to address this question with sufficient resolution since studies have focused predominantly on mtDNA sequences that only provide information on variability in the maternal line.

Craniometric Studies

Given the wealth of genetic material available, approaching the Neolithic question from the point of view of craniometric data may seem a comparatively unsophisticated means of enquiry. However, in recent years, research into global patterns of human craniometric variation has consistently found that the majority of cranial shape variation in modern human populations is the result of neutral microevolutionary factors (e.g., González-José et al. 2004; Harvati and Weaver 2006a; Harvati and Weaver 2006b; Relethford 1994; Relethford 2002; Relethford 2004; Roseman 2004; Roseman and Weaver 2004; Roseman and Weaver 2007; Smith 2009; Smith 2011; von Cramon-Taubadel and Weaver 2009; von Cramon-Taubadel 2009a; von Cramon-Taubadel 2009b; von Cramon-Taubadel, 2011). What this suggests is that, on average, diversification of cranial shape differences within and between human populations has been the result of mutation, gene flow and genetic drift, rather than being subjected to strong diversifying natural or sexual selection. Moreover, studies comparing matrices of genetic and craniometric distances directly have found a strong level of congruence between them, indicating that in the absence of genetic data, craniometric information can serve as a useful proxy for past population history (e.g. Hubbe et al. 2011; Konigsberg 1990a; Konigsberg 1990b; Strauss and Hubbe 2010; von Cramon-Taubadel and Weaver 2009).

Genetic analyses of modern European populations suffer from the problem that more recent demographic changes (e.g. the expansion of empires, transcontinental migrations and invasions etc.) are likely to have partially erased the genetic signature of any Neolithic transition. Moreover, while the analysis of ancient DNA sampled directly from archaeological remains has the potential to yield important insights into the genetic structure of Mesolithic and Neolithic populations, we do not, as yet, have the chronological or geographical coverage for ancient DNA samples as we do for

craniometric ones. Therefore, the analysis of craniometric variation patterns makes an important contribution to our understanding of the complex transition from hunting and gathering to farming in Europe.

It is also possible to apply a specifically model-bound approach to quantitative craniometric traits in much the same way as it possible with genetic allele data (e.g. Cheverud 1982; Relethford and Blangero 1990; Relethford and Lees 1982). Recent studies by Pinhasi and von Cramon-Taubadel (Pinhasi and von Cramon-Taubadel 2009; von Cramon-Taubadel and Pinhasi 2011) have used model-fitting methods to explicitly test the demic versus indigenist models for the transition to agriculture in southeastern, central and eastern Europe. Pinhasi and von Cramon-Taubadel (Pinhasi and von Cramon-Taubadel 2009) found that the affinities between early Neolithic populations in central Europe and the Near East could best be explained by a demic diffusion model from the Levant/Anatolia rather than the indigenous adoption of farming by central European Mesolithic communities. The models were conservatively based on a null model of isolation-by-geographic and temporal distance, such that all populations were connected via gene flow, the strength of which varied depending on how temporally or geographically distant any pair of populations was. Thereafter, this null model was altered to reflect different scenarios of active migration by Near Eastern farmers into central Europe. It is worth noting that the results do not imply complete replacement of any indigenous hunter-gatherer community but rather that indigenous hunter-gatherers did not undergo extensive gene flow with incoming farming populations, thus effectively creating two separate lineages living contemporaneously in central Europe. The craniometric data show a strong separation between Near Eastern/Neolithic populations on the one hand and

Mesolithic populations on the other, irrespective of their temporal or geographic differences.

The more recent analysis by von Cramon-Taubadel and Pinhasi (von Cramon-Taubadel and Pinhasi 2011) elaborated on this initial finding by testing the hypothesis that later ‘Forest Neolithic’ populations living in the Eastern and Baltic regions actually represent indigenous hunter-gatherer populations who had adopted some cultural elements from contemporaneous ‘true’ Neolithic populations living in the region, as had been suggested on the basis of archaeological data (Zvelebil 1996; Zvelebil 2001). We expanded the initial dataset to include later populations from the Baltic/eastern European region, as well as later Neolithic populations from across Europe. Using an explicitly model-based approach, our results found that ‘Forest Neolithic’ populations showed greater affinities with earlier Mesolithic populations from across Europe and the Near East than they did with contemporaneous Neolithic populations living in central Europe and Scandinavia. What these results suggest, is that in these outlying regions of Europe indigenous hunter-gatherer populations were adopting cultural elements from contemporaneous farming communities but without associated levels of gene flow. The results of this study taken in combination with Pinhasi and von Cramon-Taubadel (2009) strongly support the notion that the transition to agriculture was a more complex process than the dichotomous use of the ‘demic diffusion’ versus the ‘indigenist’ models would suggest. Therefore, future studies need to take greater account of this complex demographic change, which requires a more sensitive regional approach as advocated by Pinhasi and colleagues (Pinhasi 2004; Pinhasi 2006; Pinhasi and Pluciennik 2004).

The first formal morphological analysis examining inter-population affinities of Near Eastern/Anatolian Epipaleolithic and early Neolithic populations to early farmers

from southeastern, Mediterranean and central Europe was carried out by Pinhasi and colleagues ((Pinhasi 2004; Pinhasi and Pluciennik 2004). These studies focused on principal components analyses of craniometric dimensions of the vault, face, cranial base, teeth and mandibles. Results demonstrated a considerable degree of morphometric heterogeneity among the Pre-Pottery Neolithic specimens from the Levant (Jericho, Basta, Abu Hureyra), Cyprus (Khirokitia) and southeast Anatolia (Çayönü). This heterogeneity contrasted with the homogeneity of specimens from Central Anatolia (Çatal Höyük), Greece (Nea Nikomedeia), the Balkans (Karanovo, Starčevo), Hungary (Körös), Romania (Çris) and Germany (LBK). In the western Mediterranean results were less clear with heterogeneity among the Cardial/Impressed Ware Neolithic groups and the absence of a strong pattern of differentiation between Mesolithic and Neolithic groups.

However, these analyses were limited in regards to several aspects: (1) the inclusion of Khirokitiamay biased the results as it was documented that a large number of the individuals from this site showed evidence of artificial cranial deformation (Angell 1953). While the deformed skulls were excluded from the PCA runs, it is likely that the remaining set also underwent some artificial deformation and since the data were collated from a publication and not by re-measuring these specimens, it was not possible to verify, (2) some of the specimens included were originally assumed to be of Early Neolithic context but this assumption was later shown to be incorrect (e.g. Condeixa in Portugal), (3) these analyses aimed to maximize the number of crania included, resulting in a compromise regarding the number of cranial dimensions that could be included in each set (due to a high proportion of missing data). The outcome was that PCA runs utilised at most 10 cranial variables (cf. (Pinhasi and Pluciennik 2004), and while these variables capture the principal dimensionality of the cranium,

this set does not allow one to assess more intra- and inter- population variability in specific morphological structures (i.e. face versus vault etc.).

Hence, we present here an analysis of cranial shape variation utilising the dataset employed by von Cramon-Taubadel and Pinhasi (von Cramon-Taubadel and Pinhasi 2011) (Figure 1), and which is free of the problems mentioned above. We employed standard principal components analysis (PCA) to investigate which of the 15 cranial variables were most important in distinguishing between the Neolithic and Mesolithic/Forest Neolithic groupings (see Figure 3, von Cramon-Taubadel and Pinhasi 2011).

--INSERT FIGURE 1 HERE--

Figure 2 shows a plot of the first two principal components extracted from the PCA, which together explain almost 45% of the total variance. Although there is a great deal of overlap amongst and between specimens from different sites, a clear distinction emerges between Mesolithic and 'Forest Neolithic' hunter-gatherer crania (open and light symbols) and Neolithic farmer crania (dark and filled symbols) on the first PC axis. Examination of the component matrix demonstrated that the variables most strongly correlated with positive end of PC1 (Neolithic) were measures of vault height, vault length and frontal breadth, while the variables most strongly correlated with the negative end of PC1 (Mesolithic) were measures of facial breadth and height, and vault breadth. These results demonstrate that European hunter-gatherer and early farming populations differed craniometrically (and presumably genetically) irrespective of their geographical location or their chronology.

--INSERT FIGURE 2 HERE--

Conclusion

Pinhasi & Pluciennik (Pinhasi and Pluciennik 2004) analysed the relationship between Early Neolithic specimens from Cyprus, Greece, and Anatolia and Late Upper Palaeolithic and Mesolithic specimens from Italy, Greece (Mediterranean Mesolithic), and the Danube Gorge (Vlasac and Lepenski Vir Mesolithic) using a limited set of only seven cranial variables. The scatterplot of PC 1 and PC 2 did not show a clear separation between the Neolithic and Mesolithic specimens, although it was evident that the majority of Çatal Höyük were located close to Nea Nikomedeia with relatively long, narrow vaults. Similarly, a PCA analysis of Neolithic and Mesolithic specimens from the Mediterranean region did not show any clear pattern of hunter-farmer differentiation. In retrospect, the lack of differentiation between foragers and farmers in the case of these analyses may be attributed to the limited number of variables utilised. However, as is evident in the case of the current analysis, patterns of differentiation between foragers and farmers are complex but can nonetheless be discerned when examining a larger data set and utilising a relatively large number of cranial variables. The overlap between these groups is anticipated when we take into consideration expected intra-population variation (e.g. Relethford, 1994; 2002). Nonetheless, the craniometric analysis allows us to discern certain patterns. For example, the 'Forest Neolithic' specimens are clearly much more similar to other Mesolithic hunter-gatherers than to Neolithic farmers in terms of their craniometric shape, suggesting a large degree of cultural diffusion in this region. However, it is also evident that the earliest potential colonisers of southeast and central Europe are very similar to the Anatolian Çatal Höyük population, congruent with an initial demic diffusion from the Near East/Anatolia.

The apparently conflicting conclusions reached on the basis of modern genetic studies are due in part to an inclination to underestimate the complexity of historical processes, and to equate and conflate cultural and biological populations (Zvelebil 2000). The assumption that common patterns will emerge from the utilisation of model-free genetic analyses of haplogroup variation is problematic since observed ‘patterns’ are easily over-interpreted and in many cases coalescence times are automatically attributed to presumed major dispersal events such as the spread of farming into Europe (see e.g. Rosenberg and Feldman, 2002; Weaver and Roseman, 2008; Balloux, 2010). As reviewed in detail above, model-bound analyses of the rich osteological record associated with the Neolithic transition have the potential to yield important insights into the biological and cultural nature of this change. Moreover, these craniometric analyses in concert with the analysis of aDNA are demonstrating that the dichotomous use of a ‘demic’ versus an ‘indigenist’ model of change are no longer sufficient for describing this complex demographic transition. The archaeological record attests that the introduction of agriculture in Europe involved several dispersal mechanisms: (1) the directional movement of a whole population from one region to another; (2) demic diffusion by means of a wave of advance; (3) leapfrog colonization by small groups targeting optimal areas to form an enclave surrounded by indigenous inhabitants; (4) frontier mobility, or exchange between farmers and foragers at agricultural frontier zones; (5) regional contact, involving trade and exchange of ideas but no demic input; and (6) infiltration of communities by small number of specialists, or a social elite (Zvelebil 2001). Each of these mechanisms will have exerted different impacts on the genetic and phenotypic makeup of Neolithic and post-Neolithic European populations. Some dispersal mechanisms, such as leapfrog colonisation, do not usually entail migration of large

population numbers and hence will not necessarily leave detectable genetic or biological traces. In any case, in some parts of Europe the arrival of exogenous farmers may have involved rather major and abrupt cultural transformations, while in others the process did not entail population replacement, or any drastic cultural change affecting the local Mesolithic populations.

At present, there are only a limited number of aDNA studies of Mesolithic and Neolithic European populations, examining relatively small samples and focusing predominantly on the study of HVR-I mtDNA haplogroups. The costs and technical complexities associated with the successful extraction, amplification and analysis of authentic endogenous DNA limits the results to specific regions as opposed to detecting pan-European patterns. Therefore, we argue that a model-bound craniometric approach taken together with the direct genetic analysis of specimens from specific geographic regions and time periods holds the potential to fill existing lacuna in regards to the population history of Europeans. Given the success with which craniometric data has been used to address specific questions surrounding the Neolithic transition in Europe, we anticipate future analyses of the rich bioarchaeological record to yield further insight into the microevolutionary history of Europe.

Acknowledgments

This research was supported by the European Research Council Starting Grant (ERC-2010-StG 263441).

References

- Allard P. 2007. The Mesolithic-Neolithic transition in the Paris Basin: a review. In: Whittle A, editor. *Going Over the Mesolithic-Neolithic Transition in North West Europe*. Oxford: Oxford University Press. p 211-223.
- Ammerman AJ, and Cavalli-Sforza LL. 1971. Measuring the rate of spread of early farming in Europe. *Man NS* 6:674-688.
- Ammerman AJ, and Cavalli-Sforza LL. 1973. A population model for the diffusion of early farming in Europe. In: Renfrew C, editor. *The Explanation of Culture Change*. London: Duckworth.
- Ammerman AJ, and Cavalli-Sforza LL. 1984. *The Neolithic Transition and the Genetics of Populations in Europe*. Princeton, NJ: Princeton University Press.
- Angell LJ. 1953. The human remains from Khirokitia,” In: Dikaios P, editor. *Khirokitia: Final report on the excavation of a Neolithic settlement in Cyprus on behalf of the Department of Antiquities, 1936-1946*. Oxford University Press: Oxford. pp. 416–30.
- University Press. In: Dikalos P, editor. *Khirokitia: Final report on the excavation of a Neolithic settlement in Cyprus on behalf of the Department of Antiquities, 1936–1946*. Oxford: Oxford University Press.
- Aurenche O, and Kozlowski SK. 1999. *La naissance du Néolithique au Proche Orient, ou le paradis perdu*. Paris: Errance.
- Balaresque P, Bowden GR, Adams SM, Leung H-Y, King TE, Rosser ZH, Goodwin J, Moisan J-P, Richard C, Millward A et al. . 2010. A Predominantly Neolithic Origin for European Paternal Lineages. *PLoS Biol* 8(1):e1000285.
- Balloux F. 2010. The worm in the fruit of the mitochondrial DNA tree. *Heredity* 104:419-420.

- Bar-Yosef O. 1998. The transition to agriculture in the Old World. *The Review of Archaeology* 19(2):1–5.
- Bar-Yosef O, and Meadow R. 1995. The origins of agriculture in the Near East. In: Price TD, and Gebauer AB, editors. *Last Hunters, First Farmers: New Perspectives on the Prehistoric Transition to Agriculture*. Santa Fe: School of American Research Press. p 39–94.
- Barbujani G, Bertorelle G, Capitani G, and Scozzari R. 1995a. Geographical structuring in the mtDNA of Italians. *Proc Natl Acad Sci U S A* 92(20):9171-9175.
- Barbujani G, Bertorelle G, and Chikhi L. 1998. Evidence for Paleolithic and Neolithic gene flow in Europe. *Am J Hum Genet* 62(2):488-492.
- Barbujani G, Sokal RR, and Oden NL. 1995b. Indo-European origins: a computer-simulation test of five hypotheses. *Am J Phys Anthropol* 96(2):109-132.
- Belle EM, Landry PA, and Barbujani G. 2006a. Origins and evolution of the Europeans' genome: evidence from multiple microsatellite loci. *Proc Biol Sci* 273(1594):1595-1602.
- Belle EM, Ramakrishnan U, Mountain JL, and Barbujani G. 2006b. Serial coalescent simulations suggest a weak genealogical relationship between Etruscans and modern Tuscans. *Proc Natl Acad Sci U S A* 103(21):8012-8017.
- Bellwood P, and Renfrew C, editors. 2002. *Examining the Farming/Language Dispersal Hypothesis*. Cambridge: McDonald Institute for Archaeological Research. 505 p.
- Blockley SPE, and Pinhasi R. 2011. A revised chronology for the adoption of agriculture in the Southern Levant and the role of Lateglacial climatic change. *Quaternary Science Reviews* 30(1-2):98-108.

- Bocquet-Appel J-P. 2011. When the world's population took off: the springboard of the Neolithic Demographic Transition. *Science* 333:560-561.
- Bogucki P. 2003. Neolithic dispersals in riverine interior central Europe. In: Ammerman AJ, and Biagi P, editors. *The Widening Harvest The Neolithic Transition in Europe: Looking Back, Looking Forward*. Boston: Archaeological Institute of America. p 249-272.
- Bramanti B, Thomas MG, Haak W, Unterlaender M, Jores P, Tambets K, Antanaitis-Jacobs I, Haidle MN, Jankauskas R, Kind C-J et al. . 2009. Genetic discontinuity between local hunter-gatherers and Central Europe's first farmers. *Science* 326:137-140.
- Burger J, and Thomas MG. 2011. The palaeopopulationgenetics of humans, cattle and dairying in Neolithic Europe. In: Pinhasi R, and Stock JT, editors. *HUMAN Bioarchaeology of the Transition to Agriculture*. New York: Wiley & Sons. p 371-384.
- Cavalli-Sforza LL. 1996. The spread of agriculture and nomadic pastoralism: insights from genetics, linguistics, and archaeology. In: Harris D, editor. *The Origins and Spread of Agriculture and Pastoralism in Eurasia*. London: UCL Press. p 51-69.
- Cavalli-sforza LL, Menozzi P, and Piazza A. 1993. Demic expansions and human evolution. *Science* 259:639-646.
- Cavalli-Sforza LL, Menozzi P, and Piazza PA. 1994. *The History and Geography of Human Genes*. Princeton, N.J.: Princeton University Press.
- Chamberlain A. 2009. Archaeological demography. *Human Biology* 81:275-286.
- Cherry J. 1990. The first colonisation of the Mediterranean islands: a review of recent research. *Journal of Mediterranean Archaeology* 3:145-221.

- Cheverud JM. 1982. Phenotypic, Genetic, and Environmental Morphological Integration in the Cranium. *36:499-516*.
- Chikhi L, Nichols RA, Barbujani G, and Beaumont MA. 2002. Y genetic data support the Neolithic demic diffusion model. *Proc Natl Acad Sci U S A 99(17):11008-11013*.
- Childe VG. 1957. *The Dawn of European Civilisation*. Bungay, Suffolk: Chaucer Press.
- Clark G. 1965a. Radiocarbon dating and the expansion of farming culture from the Near East over Europe. *Proceedings of the Prehistoric Society 31(n.s.):58-73*.
- Clark G. 1965b. Radiocarbon dating and the spread of farming economy. *Antiquity 39:45-48*.
- Collard M, Edinborough K, Shennan S, and Thomas MG. 2010. Radiocarbon evidence indicated that migrants introduced farming to Britain. *Journal of Archaeological Science 37:866-870*.
- Cooper A, and Poinar HN. 2000 Ancient DNA: Do it right or not at all. *Science 289:1139*.
- Curat M, and Excoffier L. 2005. The effect of the Neolithic expansion on European molecular diversity. *Proc Biol Sci 272(1564):679-688*.
- Deguilloux M-F, Soler L, Pemonge M-H, Scarre C, Jousaume R, and Laporte L. 2011. News from the west: Ancient DNA from a French megalithic burial chamber. *American Journal of Physical Anthropology 144(1):108-118*.
- Dennel R. 1983. *European Economic Prehistory: A New Approach* Orlando, FL: Academic Press.
- Di Benedetto G, Nasidze IS, Stenico M, Nigro L, Krings M, Lanzinger M, Vigilant L, Stoneking M, Pääbo S, and Barbujani G. 2000. Mitochondrial DNA sequences

- in prehistoric human remains from the Alps. *European Journal of Human Genetics* 8:669-677.
- Di Giacomo F, Luca F, Popa LO, Akar N, Anagnou N, Banyko J, Brdicka R, Barbujani G, Papola F, Ciavarella G et al. . 2004. Y chromosomal haplogroup J as a signature of the post-neolithic colonization of Europe. *Hum Genet* 115(5):357-371.
- Dupanloup I, Bertorelle G, Chikhi L, and Barbujani G. 2004. Estimating the impact of prehistoric admixture on the genome of Europeans. *Mol Biol Evol* 21(7):1361-1372.
- Dupanloup I, Pereira L, Bertorelle G, Calafell F, Prata MJ, Amorim A, and Barbujani G. 2003. A recent shift from polygyny to monogamy in humans is suggested by the analysis of worldwide Y-chromosome diversity. *J Mol Evol* 57(1):85-97.
- Excoffier L, and Ray N. 2008. Surfing during population expansions promotes genetic revolutions and structuration. *Trends Ecol Evol* 23(7):347-351.
- Fix AG. 1999. *Migration and Colonization in Human Microevolution*. Cambridge, UK: Cambridge University Press.
- Flannery KV. 1972. The origins of the village as a settlement type in Mesoamerica and the Near East: a comparative study. In: Ucko PJ, Tringham R, Dimbleby GW, editors. *Man, Settlement, and Urbanism*. Duckworth, London. pp 23-53.
- Flannery KV. 2002. The origins of the village revisited: from nuclear to extended households. *American Antiquity* 67:417-433.
- Ghirotto S, Mona S, Benazzo A, Papparazzo F, Caramelli D, and Barbujani G. 2009. Inferring Genealogical Processes from Patterns of Bronze-Age and Modern DNA variation in Sardinia. *Mol Biol Evol*.

- Gilbert MT, Bandelt HJ, Hofreiter M, and Barnes I. 2005. Assessing ancient DNA studies. *Trends Ecol Evol* 20(10):541-544.
- González-José R, Van Der Molen S, González-Pérez E, and Hernández M. 2004. Patterns of phenotypic covariation and correlation in modern humans as viewed from morphological integration. *American Journal of Physical Anthropology* 123(1):69-77.
- Green RE, Krause J, Briggs AW, Maricic T, Stenzel U, Kircher M, Patterson N, Li H, Zhai W, Fritz MH-Y et al. . 2010. A Draft Sequence of the Neandertal Genome. *Science* 328(5979):710-722.
- Haak W, Forster P, Bramanti B, Matsumura S, Brandt G, Tanzer M, Villems R, Renfrew C, Gronenborn D, Alt KW et al. . 2005. Ancient DNA from the First European Farmers in 7500-Year-Old Neolithic Sites. *Science* 310(5750):1016-1018.
- Handt O, Hoss M, Krings M, and Paabo S. 1994. Ancient DNA: methodological challenges. *Experientia* 50(6):524-529.
- Harvati K, and Weaver TD. 2006a. Human cranial anatomy and the differential preservation of population history and climate signatures. *Anatomical Record* 288A:1225-1233.
- Harvati K, and Weaver TD. 2006b. Reliability of cranial morphology in reconstructing Neanderthal phylogeny. In: Harvati K, and Harrison TL, editors. *Neanderthals revisited: new approaches and perspectives*. Dordrecht: Springer. p 239-254.
- Hofreiter M. 2008. Palaeogenomics. *Comptes Rendus Palevol* 7(2-3):113-124.
- Hofreiter M, Serre D, Poinar HN, Kuch M, and Paabo S. 2001. Ancient DNA. *Nat Rev Genet* 2(5):353-359.

- Hubbe M, Harvati K, and Neves W. 2011. Paleoamerican morphology in the context of European and East Asian late Pleistocene variation: Implications for human dispersion into the new world. *American Journal of Physical Anthropology* 144(3):442-453.
- Itan Y, Powell A, Beaumont MA, Burger J, and Thomas MG. 2009. The Origins of Lactase Persistence in Europe. *PLoS Comput Biol* 5(8):e1000491.
- J-P Bocquet-Appel J-P, and Bar-Yosef O, editors. 2008. *The Neolithic Demographic Transition and Its Consequences*. New York: Springer.
- Jobling MA, Hurles ME, and Tyler-Smith C. 2004. *Human Evolutionary Genetics: Origins, Peoples and Disease*.
- Jobling MA, and Tyler-Smith C. 2003. The human Y chromosome: An evolutionary marker comes of age. *Nature Reviews Genetics* 4(8):598-612.
- Kolman CJ, and Tuross N. 2000. Ancient DNA analysis of human populations. *Am J Phys Anthropol* 111(1):5-23.
- Konigsberg LW. 1990a. Analysis of prehistoric biological variation under a model of isolation by geographic and temporal distance. *Human Biology* 62:49-70
- Konigsberg LW. 1990b. Temporal aspects of biological distance: serial correlation and trend in a prehistoric skeletal lineage'. *American Journal of Physical Anthropology* 82:45-52.
- Kuijt I, and Goring-Morris N. 2002. Foraging, farming, and social complexity in the Pre-Pottery Neolithic of the southern Levant: a review and synthesis *Journal of world prehistory* 16(4):361-440.
- Malmström H, Gilbert MTP, Thomas MG, Brandström M, Storå J, Molnar P, Andersen PK, Bendixen C, Holmlund G, Götherström A et al. . 2009. Ancient

- DNA Reveals Lack of Continuity between Neolithic Hunter-Gatherers and Contemporary Scandinavians. *Current Biology* 19(20):1758-1762.
- Manning SW, McCartney C, Kromer B, and Stewart ST. 2010. The earlier Neolithic in Cyprus: recognition and dating of a Pre-Pottery Neolithic A occupation. *Antiquity* 84:693–706.
- Menozi P, Piazza A, and Cavalli-Sforza L. 1978. Synthetic maps of human gene frequencies in Europeans. *Science* 201(4358):786-792.
- Montiel R, Malgosa A, and Francalacci P. 2001. Authenticating ancient human mitochondrial DNA. *Hum Biol* 73(5):689-713.
- Morelli L, Contu D, Santoni F, Whalen MB, Francalacci P, and Cucca F. 2010. A Comparison of Y-Chromosome Variation in Sardinia and Anatolia Is More Consistent with Cultural Rather than Demic Diffusion of Agriculture. *PLoS ONE* 5(4):e10419.
- Myres NM, Rootsi S, Lin AA, Jarve M, King RJ, Kutuev I, Cabrera VM, Khusnutdinova EK, Pshenichnov A, Yunusbayev B et al. . 2011. A major Y-chromosome haplogroup R1b Holocene era founder effect in Central and Western Europe. *Eur J Hum Genet* 19(1):95-101.
- Novembre J, and Stephens M. 2008. Interpreting principal component analyses of spatial population genetic variation. *Nat Genet* 40(5):646-649.
- Özdoğan M. 1997. The beginning of Neolithic economies in southeastern Europe: an Anatolian perspective. *Journal of European Archaeology* 5(2):1–33.
- Özdoğan M. 2005. Westward expansion of the Neolithic way of life: what we know and what we do not know. In: Lichter C, editor. *How Did Farming Reach Europe? Anatolian-European Relations from the Second Half of the 7th*

- through the First Half of the 6th Millennium Cal BC Istanbul: BYAZ 2. p 13–28.
- Paabo S, Poinar H, Serre D, Jaenicke-Despres V, Hebler J, Rohland N, Kuch M, Krause J, Vigilant L, and Hofreiter M. 2004. Genetic analyses from ancient DNA. *Annual Review of Genetics* 38:645-679.
- Perlès C. 2001. *The Early Neolithic in Greece*. Cambridge, UK.: Cambridge University Press.
- Perlès C. 2005. From the Near East to Greece: let's reverse the focus - Cultural elements that didn't transfer. In: Lichter C, editor. *How did farming reach Europe?: Anatolian-European relations from the second half of the 7th through the first half of the 6th millennium cal BC Istanbul: BYZAS 2*. p 275-290.
- Piggott S. 1965. *Ancient Europe*. Edinburgh.: Edinburgh University Press.
- Pinhasi R. 2004. A new model for the spread of the first farmers in Europe. *Documenta Praehistorica* 30:1-76.
- Pinhasi R. 2006. Neolithic skull shapes and demic diffusion: a bioarchaeological investigation into the nature of the Neolithic transition. *Documenta Praehistorica* 33:61-70.
- Pinhasi R, Fort J, and Ammerman AJ. 2005. Tracing the Origin and Spread of Agriculture in Europe. *PLoS Biology* 3(12):e410.
- Pinhasi R, and Pluciennik M. 2004. A Regional Biological Approach to the Spread of Farming in Europe Anatolia, the Levant, South-Eastern Europe, and the Mediterranean. *Current Anthropology* 45(54):59-82.
- Pinhasi R, and von Cramon-Taubadel N. 2009. Craniometric Data Supports Demic Diffusion Model for the Spread of Agriculture into Europe. *PLoS ONE* 4(8):e6747.

- Pluciennik M. 1997. Radiocarbon determinations and the Mesolithic-Neolithic transition in Southern Italy. *Journal of Mediterranean Archaeology* 10:115–150.
- Poinar HN, Schwarz C, Qi J, Shapiro B, MacPhee RDE, Buigues B, Tikhonov A, Huson DH, Tomsho LP, Auch A et al. . 2006. Metagenomics to Paleogenomics: Large-Scale Sequencing of Mammoth DNA. *Science* 311(5759):392-394.
- Ray N, Currat M, Berthier P, and Excoffier L. 2005. Recovering the geographic origin of early modern humans by realistic and spatially explicit simulations. *Genome Res* 15:1161-1167.
- Ray N, and Excoffier L. 2009. Inferring past demography using spatially explicit population genetic models. *Human Biology* 81:141-157.
- Relethford JH. 1994. Craniometric variation among modern human populations. *Am J Phys Anthropol* 95(1):53-62.
- Relethford JH. 2002. Apportionment of global human genetic diversity based on craniometrics and skin color. *American Journal of Physical Anthropology* 118:393–398.
- Relethford JH. 2004. Global patterns of isolation by distance based on genetic and morphological data. *Human Biology* 76:499-513.
- Relethford JH, and Blangero J. 1990. Detection of differential gene flow from patterns of quantitative variation. *Human Biology* 62(1):5-25.
- Relethford JH, and Lees FC. 1982. The use of quantitative traits in the study of human population structure. *American Journal of Physical Anthropology* 25(S3):113-132.

- Renfrew C. 1992. Archaeology, genetics and linguistic diversity. *Man (NS)* 27:445-478.
- Renfrew C, and Boyle K, editors. 2000. *Archaeogenetics: DNA and the population prehistory of Europe*. Cambridge: McDonald Institute for Archaeological Research. 45-56 p.
- Richards M. 2003. The Neolithic invasion of Europe. *Annual Review of Anthropology* 32(1):135-162.
- Richards M, Corte-Real H, Forster P, Macaulay V, Wilkinson-Herbots H, Demaine A, Papiha S, Hedges R, Bandelt HJ, and Sykes B. 1996. Paleolithic and neolithic lineages in the European mitochondrial gene pool. *Am J Hum Genet* 59(1):185-203.
- Richards M, Macaulay V, Hickey E, Vega E, Sykes B, Guida V, Rengo C, Sellitto D, Cruciani F, Kivisild T et al. . 2000. Tracing European founder lineages in the Near Eastern mtDNA pool. *Am J Hum Genet* 67(5):1251-1276.
- Richards M, Macaulay V, Torroni A, and Bandelt HJ. 2002. In search of geographical patterns in European mitochondrial DNA. *Am J Hum Genet* 71(5):1168-1174.
- Richards MB, Macaulay VA, Bandelt HJ, and Sykes BC. 1998. Phylogeography of mitochondrial DNA in western Europe. *Ann Hum Genet* 62(Pt 3):241-260.
- Rohland N, and Hofreiter M. 2007a. Ancient DNA extraction from bones and teeth. *Nature Protocols* 2(7):1756-1762.
- Rohland N, and Hofreiter M. 2007b. Comparison and optimization of ancient DNA extraction. *Biotechniques* 42(3):343-352.
- Rompler H, Dear PH, Krause J, Meyer M, Rohland N, Schoneberg T, Spriggs H, Stiller M, and Hofreiter M. 2006. Multiplex amplification of ancient DNA. *Nature Protocols* 1:720-728.

- Roseman CC. 2004. Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. *Proceedings of the National Academy of Sciences* 101(35):12824-12829.
- Roseman CC, and Weaver TD. 2004. Multivariate apportionment of global human craniometric diversity. *American Journal of Physical Anthropology* 125(3):257-263.
- Roseman CC, and Weaver TD. 2007. Molecules versus morphology? Not for the human cranium. *BioEssays* 29:1185-1188.
- Rosenberg NA, and Feldman MW. 2002. The relationship between coalescence times and population divergence times. In: Slatkin M, and Veuille M, editors. *Modern developments in theoretical population genetics*. Oxford: Oxford University Press. p 130-164.
- Rosser ZH, Zerjal T, Hurles ME, Adojaan M, Alavantic D, Amorim A, Amos W, Armenteros M, Arroyo E, Barbujani G et al. . 2000. Y-chromosomal diversity in Europe is clinal and influenced primarily by geography, rather than by language. *Am J Hum Genet* 67(6):1526-1543.
- Runnels C. 2003. The origins of the Greek Neolithic: a personal review. In: Ammerman AJ, and Biagi P, editors. *The Widening Harvest The Neolithic Transition in Europe: Looking Back, Looking Forward*. Boston: Archaeological Institute of America. p 121-132.
- Sampietro ML, Lao O, Caramelli D, Lari M, Pou R, Marti M, Bertranpetit J, and Lalueza-Fox C. 2007. Palaeogenetic evidence supports a dual model of Neolithic spreading into Europe. *Proc Biol Sci* 274(1622):2161-2167.
- Schuster SC. 2008. Next-generation sequencing transforms today's biology. *Nat Meth* 5(1):16-18.

- Semino O, Passarino G, Oefner PJ, Lin AA, Arbuzova S, Beckman LE, De Benedictis G, Francalacci P, Kouvatsi A, Limborska S et al. . 2000. The genetic legacy of Paleolithic Homo sapiens sapiens in extant Europeans: a Y chromosome perspective. *Science* 290(5494):1155-1159.
- Shennan S. 2009. Evolutionary demography and the population history of the European Early Neolithic. *Human Biology* 81:339-355.
- Simoni L, Calafell F, Pettener D, Bertranpetit J, and Barbujani G. 2000. Geographic patterns of mtDNA diversity in Europe. *Am J Hum Genet* 66(1):262-278.
- Skeates R. 2003. Radiocarbon dating and interpretations of the Mesolithic-Neolithic transition in Italy. In: Ammerman AJ, and Biagi P, editors. *The Widening Harvest The Neolithic Transition in Europe: Looking Back, Looking Forward*. Boston: Archaeological Institute of America. p 157-188.
- Smith HF. 2009. Which cranial regions reflect molecular distances reliably in humans? Evidence from three-dimensional morphology. *American Journal of Human Biology* 21:36-47.
- Smith HF. 2011. The role of genetic drift in shaping modern human cranial evolution: a test using microevolutionary modeling. *International Journal of Evolutionary Biology* Article ID 145262:1-11.
- Soares P, Achilli A, Semino O, Davies W, Macaulay V, Bandelt HJ, Torroni A, and Richards MB. 2010. The archaeogenetics of Europe. *Current biology : CB* 20(4):R174-183.
- Sokal RR, Oden NL, and Thomson BA. 1999. A problem with synthetic maps. *Human Biology* 71:1-13.
- Sokal RR, Oden NL, and Wilson C. 1991. Genetic evidence for the spread of agriculture in Europe by demic diffusion. *Nature* 351(6322):143-145.

- Steele J, and Shennan S. 2009. Introduction: Demography and cultural macroevolution. *Human Biology* 81:105-119.
- Strauss A, and Hubbe M. 2010. Craniometric Similarities Within and Between Human Populations in Comparison with Neutral Genetic Data. *Human Biology* 82:315-330.
- Thomas HL, and Rowlett ES-J. 1992. The archaeological chronology of Northern Europe. In: Ehrich RW, editor. *Chronologies in Old World Archaeology*, Vol 1. Chicago: University of Chicago Press. p 345-355.
- Torroni A, Bandelt HJ, D'Urbano L, Lahermo P, Moral P, Sellitto D, Rengo C, Forster P, Savontaus ML, Bonne-Tamir B et al. . 1998. mtDNA analysis reveals a major late Paleolithic population expansion from southwestern to northeastern Europe. *Am J Hum Genet* 62(5):1137-1152.
- Torroni A, Richards M, Macaulay V, Forster P, Villems R, Norby S, Savontaus ML, Huoponen K, Scozzari R, and Bandelt HJ. 2000. mtDNA haplogroups and frequency patterns in Europe. *Am J Hum Genet* 66(3):1173-1177.
- Tykot RH. 1994. Radiocarbon dating and absolute chronology in Sardinia and Corsica. In: Skeates R, and Whitehouse R, editors. *Radiocarbon Dating and Italian Prehistory*. Rome: Archaeological Monographs of the British School at Rome No. 14. p 115-145.
- Van Andel T, and Runnels C. 1995. The earliest farmers in Europe. *Antiquity* 69:481-500.
- von Cramon-Taubade IN, and Weaver TD. 2009. Insights from a quantitative genetic approach to human morphological evolution. *Evolutionary Anthropology* 18:237-240.

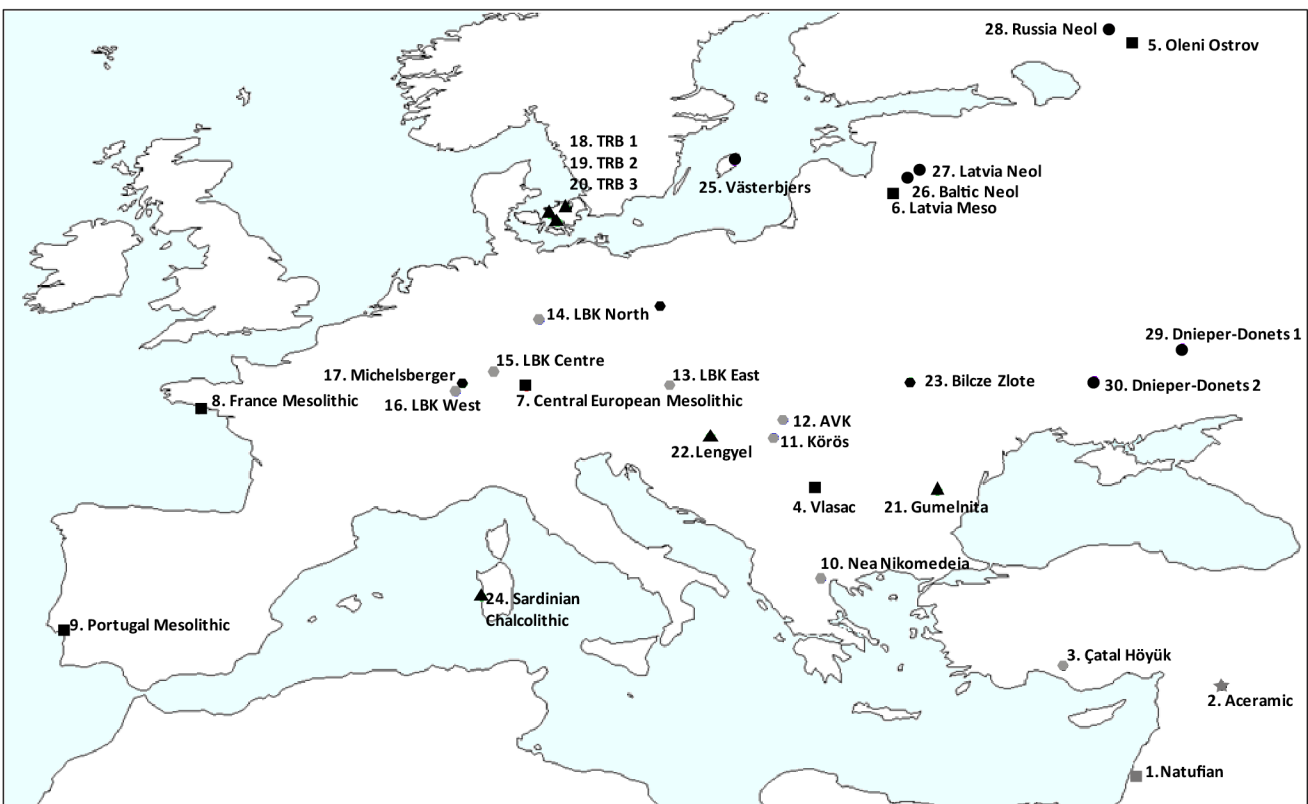
- von Cramon-Taubadel N. 2009. Congruence of individual cranial bone morphology and neutral molecular affinity patterns in modern humans. *American Journal of Physical Anthropology* 140:205-215.
- von Cramon-Taubadel N. 2009b. Revisiting the homoiology hypothesis: The impact of phenotypic plasticity on the reconstruction of human population history from craniometric data. *Journal of Human Evolution* 57:179-190.
- von Cramon-Taubadel N. 2011. The relative efficacy of functional and developmental cranial modules for reconstructing global human population history. *American Journal of Physical Anthropology* 146:83-93.
- von Cramon-Taubadel N, and Pinhasi R. 2011. Craniometric data support a mosaic model of demic and cultural Neolithic diffusion to outlying regions of Europe. *Proceedings of the Royal Society, B* In Press:doi:10.1098/rspb.2010.2678.
- Weaver TD, and Roseman CC. 2008. New developments in the genetic evidence for modern human origins. *Evolutionary Anthropology* 17:69-80.
- Webb J, and Frankel D. 2004. Intensive site survey. Implications for estimating settlement size, population and duration in prehistoric Bronze Age Cyprus. *British School at Athens Studies*, 11: 125-137.
- Whittle A. 1996. *Europe in the Neolithic: The Creation of New Worlds*. Cambridge University Press.
- Whittle A, and Cummings V, editors. 2007. *Going Over the Mesolithic-Neolithic Transition in North West Europe*. Oxford: Oxford University Press. 400 p.
- Willerslev E, and Cooper A. 2005. Ancient DNA. *Proc Biol Sci* 272(1558):3-16.
- Zilhao J. 2003. The Neolithic transition in Portugal and the role of demic diffusion in the spread of agriculture across west Mediterranean Europe. In: Ammerman AJ, and Biagi P, editors. *The Widening Harvest The Neolithic Transition in*

- Europe: Looking Back, Looking Forward. Boston: Archaeological Institute of America. p 207-226.
- Zilhão J. 2001. Radiocarbon evidence for maritime pioneer colonization at the origins of farming in west Mediterranean Europe. *Proceedings of the National Academy of Sciences of the United States of America* 98(24):14180-14185.
- Zvelebil M. 1986. Mesolithic societies and the transition to farming: problems of time, scale and organisation. In: Zvelebil M, Dennerll R, and Domanka L, editors. *Hunters in transition: Mesolithic societies of temperate Eurasia and their transition to farming*. Cambridge, UK: Cambridge University Press. p 167-188.
- Zvelebil M. 1996. The agricultural frontier and the transition to farming in the circum-Baltic area. In: Harris DR, editor. *The origins and spread of agriculture and pastoralism in Eurasia*. London, UK: UCL Press. p 323–345.
- Zvelebil M. 2000. The social context of the agricultural transition in Europe. In: Renfrew C, and Boyle K, editors. *Archaeogenetics: DNA and the population prehistory of Europe*. Cambridge: McDonald Institute for Archaeological Research. p 57–79.
- Zvelebil M. 2001. The agricultural transition and the origins of Neolithic society in Europe. *Documenta Praehistorica* 28:1-26
- Zvelebil M, and Rowley-Conway P. 1984. Transition to farming in Northern Europe: a hunter-gatherer perspective. *Norwegian Archaeological Review* 17:104-128.
- Zvelebil M, and Rowley-Conway P. 1986. Foragers and farmers in Atlantic Europe. In: Zvelebil M, editor. *Hunters in Transition*. Cambridge: Cambridge University Press. p 67-93.

Figure captions

Figure 1. Map showing the geographic locations of the 30 Mesolithic, Neolithic and 'Forest Neolithic' OTUs examined for cranial shape variation. The map is a modified version of that published in von Cramon-Taubadel and Pinhasi (2011).

Figure 2. Plot of the first two PC axes (explaining 27.35% and 17.41% of the total variance, respectively) of cranial shape data based on 15 measured variables. Specimens are coded according to the archaeological grouping provided von Cramon-Taubadel and Pinhasi (2011). The major shape differences separating hunter-gatherer Mesolithic populations and farming Neolithic populations are coded by PC1 with Neolithic specimens having longer and taller vaults, and Mesolithic specimens having larger, and broader faces. Variables illustrated by dashed lines have a lesser influence on PC1 with a correlation co-efficient of less than $r = 0.100$.



Legend

- ▲ Late Neolithic/Chalcolithic
- Forest Neolithic
- Early Neolithic
- ★ Aceramic Neolithic
- Natufian
- Mesolithic

