Cranial variation and the transition to agriculture in Europe

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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
Cranial variation and the transition to agriculture in Europe

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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 Kozlowski 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
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-Conwey 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-gathers 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 (≈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 Linenbandkeramik 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 Plucienik 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 Nikomedea), 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.
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 Nikomedea 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).
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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 $r = 0.100$. 