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A Craniometric Perspective on the Transition to Agriculture in Europe

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Abstract

Debates surrounding the nature of the Neolithic demographic transition in Europe have historically centered 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 were heavily contested primarily on the basis of archeological and modern genetic data. However, in recent years a growing acceptance has arisen 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 were particularly useful for testing these more complex scenarios, as they can reliably be employed as a proxy for the genetic relationships among 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.

Keywords

Craniometry, Neolithic, Mesolithic, Model-Bound Approaches, Demic Diffusion, Cultural Diffusion, Ancient DNA, Modern European DNA

Cover Page Footnote

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A Craniometric Perspective on the Transition to Agriculture in Europe

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Abstract Debates surrounding the nature of the Neolithic demographic transition in Europe have historically centered 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 were heavily contested primarily on the basis of archeological and modern genetic data. However, in recent years a growing acceptance has arisen 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 were particularly useful for testing these more complex scenarios, as they can reliably be employed as a proxy for the genetic relationships among 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.

The European Neolithic Debate

Over the past two decades, the excavation and analysis of archeological sites in the Levant and Anatolia 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, 2005). The emergence of

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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, 2001).

In the past, interpretations of the transition to agriculture in Europe 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. Under this model, the exogenous farmers brought with them a "Neolithic package," which includes domesticated crops, livestock (i.e., cattle, sheep, goats, pigs), 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 archeological, chronological, and geographic distance data, and diffusion rates were calculated on the basis of geographic distances and radiocarbon dates. The analysis of the latter (e.g., Clark 1965a,b), and in particular the application of systematic quality protocols for the selection of dates and Bayesian modeling, was shown to be a particularly fruitful area of research (e.g., Blockley and Pinhasi 2011).

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, 1994; Sokal et al. 1991). The strongest adherents of this view were Colin Renfrew (1992) and Luca 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 way of life (Dennell 1983; Whittle 1996; Whittle and Cummings 2007).

However, clearly 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 southeastern 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. This question rests on the basic assumption that Near Eastern farmers were genetically (as well as culturally) distinct from indigenous European hunter-gatherer populations. 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, 1973, 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 southeastern and central Europe. This model was long accepted for the "Danubian" Neolithic cultures of central Europe (e.g., Childe 1957; Clark 1965a,b; Piggott 1965). Ammerman and Cavalli-Sforza's (1971, 1973, 1984) "wave-of-advance" model suggests a gradual process of population expansion by farming communities northward and westward 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 (2004), the basic contention of this model was that the demographic and biological profile of farming populations differed from that of hunter-gatherers. To obtain a reliable estimate of demographic parameters (Zimmermann et al. 2009) on the basis of archeological data (although see Chamberlain 2009), however, can be difficult. 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 (e.g., see Webb and Frankel 2004 regarding Bronze Age Cyprus). First, estimations have 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 that 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 lifestyle, especially subsistence strategies, of Mesolithic and Neolithic populations mean 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, to determine population size and density parameters on the basis of the number of structures in a given site, or its overall size, is difficult. 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 archeological settlements (e.g., see Flannery 1972, 2002).

Furthermore, as various researchers have demonstrated (cf. contributions in Bocquet-Appel and Bar-Yosef 2008), 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, evidently a clear model-bound evolutionary approach is required to accurately infer past demography from archeological data (cf. Shennan 2009; Steele and 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 only have occurred in places where both populations coexisted. Zvelebil and Rowley-Conwy (1984, 1986) proposed a three-stage model for the adoption of agriculture that 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 into their subsistence strategy 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 hypothesized to typically occur along a "frontier" region at which dispersing farmers interact with local hunter-gatherers. As we discuss below, the archeological records of southeastern, Mediterranean, and central Europe do not provide much evidence for frontier regions (but see Zilhão 2001 for coastal regions of Portugal). Therefore, different geographic regions of Europe will vary in the extent of their farmer/hunter-gatherer interaction, thereby altering the expectation of a 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, clearly the "neolithization" of Europe took place over a period of more than four millennia. Taking this into consideration, to assume that the same demographic and historical processes that characterize the transition to farming in the parts of Europe where agriculture was introduced during the seventh millennium BC were the same as those in the peripheral regions of northwestern Europe (for example, the British Isles) is unrealistic. Assuming a figure of 20 years per human generation and no contribution of local hunter-gatherers to the dispersing farmers' 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 colonizing new peripheral regions.

Archeological 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 archeological record indicates maritime colonization 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, 2005). In the case of these regions, evidence for Mesolithic occupation is either limited or nonexistent. 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).

No direct evidence exists for continuity between Mesolithic and Neolithic in Bulgaria (Todorova 1995), and most Early Neolithic sites are in the east, belonging to the Karanovo I phase at Azmak, Čevdar, and Karanovo. Contemporary settlement occurred at Eleshnitsa and Gulubnik in the upper and central Struma Valley in western Bulgaria. A progression of Neolithic farmers spread northward along the Struma and Mesta valleys in western Bulgaria, and northward along the Ardas valley in Macedonia and southeastern Bulgaria. Most of this settlement occurred between 6500 and 6000 BC. On the Great Hungarian Plain, evidence for Mesolithic occupation is lacking (Whittle 1996), and Early Neolithic sites date to the first half of the sixth millennium BC. Between 5500 and 5000 BC, a relative explosion of settlement numbers occurred in the eastern and northeastern regions of the Carpathian Basin (Whittle 1996).

The Early Neolithic archeological 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, bone spoons), whereas they are absent in Greece (Perlès 2005). Neolithic cultural and stylistic heterogeneity on the Greek Islands is most likely the outcome of various long-distance sea-borne movements from the coastlines of Anatolia and the Levant (Perlès 2001). Van Andel and Runnels (1995) propose that the Larissa Plain in Thessaly was colonized by relatively small numbers, followed by local demographic growth and subsequent spread as a wave of advance.

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 westward to France and northward 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 toward the Atlantic, the archeological record has yielded Limburg and La Hoguette pottery assemblages that display differences with the LBK proper, possibly indicating 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, a hiatus is present between the late Mesolithic and the earliest Neolithic dates (Pluciennik 1997). The archeological record of the western Mediterranean indicates an arrival of Cardial/Impressed Ware Neolithic farmers in coastal regions between 5800 and 5300 BC (Zilhão 2003). In Corsica, the Cardial Neolithic is dated to 5700−5300 BC (Tykot 1994). In Sardinia, a human presence is confirmed by eighth millennium BC via radiometric dates for human remains from Grotta Corbeddu. However, early Neolithic dates from Sardinia fall in the mid sixth 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 leap-frog colonization by pioneering maritime Neolithic groups with late Mesolithic and early Neolithic sites located around the peripheral coastal regions of the peninsula (Zilhão 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 (Zilhão 2003).

The Genetic Evidence for the Demographic Transition to Agriculture in Europe. Alongside research into the available archeological and chronological context, 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, a growing recognition exists that phenotypic (especially cranial) 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 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. 2006;

Dupanloup et al. 2004; Richards 2003; Richards et al. 1996. 2000, 2002; Torroni et al. 1998, 2000).

More than 30 years ago, a seminal study by 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, 1994). Synthetic maps based on PC scores displayed a southeastern to northwestern cline which was attributed (Menozzi et al. 1978) to the "wave of advance" or "demic diffusion" of farmers from the Near East into Europe. This study was extended and corroborated by Cavalli-Sforza and collaborators (1993, 1994) using allelic frequency data for over 130 classical markers. In the last two decades, the validity and reliability of these maps were questioned (see e.g., Bellwood and Renfrew 2002; Fix 1999; Jobling and Tyler-Smith 2003; Jobling et al. 2004; Renfrew and Boyle 2000). In particular, Sokal et al. (1999) provided evidence that the original synthetic gene frequency maps could be due to 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).

Subsequently, many studies focused on the extent to which modern patterns of DNA haplotypes (and haplogroups) can be explained on the basis of (1) the colonization 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., Balaresque et al. 2010; Belle et al. 2006; Chikhi et al. 1998, 2002; Simoni et al. 2000) while others argue that diversity among modern European populations is mainly due to the Paleolithic colonization by anatomically modern humans (e.g., Morelli et al. 2010; Richards et al. 1996, 1998, 2000, 2002; Soares et al. 2010).

Also discrepancies exist 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). 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 data sets (see also Balloux 2010; Barbujaniet al. 1998; Chikhi 2009).

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. The use of a model-based approach which applies simulations (e.g., Barbujani et al. 1995; Belle et al. 2006; Bentley et al. 2009; Currat and Excoffier 2005; Dupanloup et al. 2004; Excoffier and Ray 2008; Galeta et al. 2011; Ghirotto et al. 2010; Itan et al. 2009; Ray et al. 2005; Ray and Excoffier 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 inquiry, to assess which is the most likely explanation when several are possible is often difficult. For example, genetic gradients may result from stochastic processes, such as genetic drift, but also potentially from variable selective pressures (cf. Fix 1999). As reviewed by Chikhi (2009), the common practice of using the age of particular DNA haplotypes to estimate the relative contributions of Paleolithic or Neolithic populations to the modern European gene pool or to date particular dispersal events is in itself problematic on theoretical grounds (see also Balloux 2010; Barbujani et al. 1998). Moreover, European populations have been subject to contractions, expansions, and dispersals during the millennia following the Mesolithic−Neolithic transition (Chikhi 2009), and consequently the study of intra- and intergenetic variability among modern-day populations can at best make conclusive statements only about modern-day variability. One can draw inferences from modern data regarding past demographic processes, but only with reference to specific models, which take into account temporal and geographic variations, 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. The aDNA studies of Mesolithic and Neolithic European individuals (e.g., Bramanti et al. 2009; Deguilloux et al. 2009; Haak et al. 2005, 2010; Lacan et al. 2011; Malmström et al. 2009; Sampietro et al. 2007) 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). This suggests that no "one size fits all" model exists 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, in contrast with modern European DNA, it allows the direct study of 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; Pääbo 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) is 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 nonendogenous data at the post-sequencing stage.

While ancient DNA studies of the Neolithic transition in Europe (e.g., Bramanti et al. 2009; Deguilloux et al. 2009; Haak et al. 2005, 2010; Lacan et al. 2011; Malmström et al. 2009; Sampietro et al. 2007) are continually improving our understanding of this complex demographic, biological and cultural transition, aDNA data sets are not currently chronologically or geographically detailed enough to provide a truly comprehensive understanding of the genetic and demographic changes surrounding the Neolithic transition across Europe. As Ghirottto 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." However, the results of published regional aDNA do not unanimously support this assumption. At this stage, the available data do not allow us to address this question with sufficient resolution also because studies have focused predominantly on mtDNA sequences that only provide information on variability in the maternal line.

In summary, 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 biological changes associated with the Neolithic transition. Moreover, while the analysis of ancient DNA sampled directly from archeological 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 alternative phenotypic (i.e., craniometric) variation patterns has the potential to make important contributions to our understanding of the complex transition from hunting and gathering to farming in Europe.

Craniometric Studies of the Mesolithic−Neolithic Transition. 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 inquiry. However, before the advent of molecular genetics, the biological history of Europeans was examined mainly via traditional anthropometric, and especially craniometric, methods. During the 19th century and the early part of the 20th century, the prevailing consensus among anthropologists and anatomists was that the main transition in cranial morphology occurring at the Mesolithic–Neolithic transition entailed a shift from dolicocephalic to brachycephalic morphology (Sardi et al. 2004a). This assumption persisted during most of the 20th century especially among European physical anthropologists (cf. various contributions in Schwidetzky 1973). Much of the 20th century literature on the craniometry of Mesolithic and Neolithic populations employs the use of racial typology, with divisions such as "Palaeoeuropean" (or "Cromagnoides"), Mediterranean, and Nordic races (see e.g., Ferembach, 1973a,b; Morant 1930; Riquet 1970, 1973; Roth-Lutra 1968; Saller 1925, 1926, 1927; Szombathy 1927; von Bonin 1935). The general supposition was that racial types existed (see also Ulrich 1945) and that these could be differentiated mostly on the basis of the assessment of the cranial index (vault breadth/length x 100). Interestingly, more recent work has shown that, in fact, Upper Paleolithic/Mesolithic crania differ for the most part from Neolithic crania in cranial height and facial dimensions rather than by the breadth and length dimensions (Menk 1981; Sardi et al. 2004a,b).

Earlier craniometric studies also tended to focus on descriptive statistics and basic comparisons of minimum/maximum, averages, and standard deviations of single linear dimensions. It was assumed that these largely univariate comparisons could highlight the craniometric affinities between racial types and that, following the initial onset of an agricultural lifestyle in a given region, changes in vault dimensions must reflect an in situ "gracilisation" or "degracilisation" of the vault and/or face (e.g., Schwidetsky 1962, 1969). These typological studies grossly underestimated the extent of intra-population variability and the extent of morphological overlap between populations/groups. One of the first researchers to apply a more rigorous multivariate approach to the analysis of Neolithic crania was Roland Menk (1981). Menk examined whether racial typology holds true in terms of multivariate differences between crania when utilizing a large data set of cranial series from across Europe. His principal component analyses indicated that cranial typology ceased to exist when one examines cranial morphology multivariately, as all "racial types" overlap in their multivariate dimensions indicating that the extent of intra-type variation by far exceeds inter-type differences (see also Constandse-Westermann 1974; Henke 1981, 1983).

The combination of a theoretical shift toward using populations/demes as the unit of analysis alongside the methodological approach of multivariate craniometry approach opened up the possibility of directly studying Mesolithic–Neolithic population affinities within the cultural and biological context of the transition to farming in Europe (e.g., Jackes et al. 1997; Lalueza-Fox, 1996; Lalueza-Fox et al. 1996; Pinhasi 2006; Pinhasi and Pluciennik 2004; Sardi et al. 2004b). Two comprehensive craniometric studies by Pinhasi and Pluciennik (2004) and Pinhasi (2006) focused on two issues: (1) the evidence for potential Mesolithic–Early Neolithic affinities and (2) whether southeastern and central

European Early Neolithic specimens shared any craniometric affinities with the Anatolian specimens from Çatal Höyük or the Pre-Pottery Near Eastern populations. These studies applied a range of multivariate methods (principal components analysis, discriminant function analysis, and squared Mahalanobis distance analysis) to various sets of specimens based on their archeological cultures, time period, and geographic location. All analyses utilized a set of 10 craniometric measurements which captured the basic dimensionality of the cranial vault and face. Results indicated (1) little similarity between Mesolithic/ Epipaleolithic hunters and Early Neolithic farmers in any region but with evidence of local continuity between Mesolithic and Neolithic populations in the Danube Gorges and (2) morphometric similarities between Çatal Höyük and early Neolithic mainland Greek and southeastern European groups. However, the craniometric affinities between circum-Mediterranean Early Neolithic series (Cardial/Impresso) did not reveal any clear patterns, mainly because of the small number of available relatively complete crania and unclear provenance for some of the specimens employed. These results did not provide support for a local transition to agriculture in southeastern or central Europe as no evidence for hunter−farmer craniometric affinities existed. It, therefore, seemed plausible to hypothesize on the basis of these results that the founding population of Early Neolithic Europeans was Çatal Höyük (or some Anatolian/Near Eastern early farming population). However, an assessment was not possible on the basis of these results as to whether the observed craniometric patterns best fit a demic diffusion model, a stochastic microevolutionary model (such as isolation-by-distance), or any other non-neutral (i.e., selective) model.

A more recent study by Brace et al. (2006) included a craniometric analysis of Upper Paleolithic, Mesolithic, Neolithic as well as modern European populations. On the basis of a Neighbor-joining analysis, they found that modern European populations from central and northern Europe were not similar to Neolithic populations from the same regions. While the overall results of the analysis support a model of demic diffusion from the Near East, they also suggest that modern central and northern populations were formed via an extensive admixture between incoming Near Eastern farmers and indigenous hunter-gatherer groups.

One of the theoretical aspects missing from this earlier work was an explicit a priori expectation of the extent to which craniometric data could be a useful or reliable proxy for genetic relationships. Hypotheses relating to the nature of the transition to agriculture must contend with two potentially confounding evolutionary processes: non-neutral dispersal (which disrupts neutral gene flow patterns) and potential non-neutral selection in response to changes in subsistence strategy and/or climate (either via phenotypic plasticity or natural selection). The substantial changes in food processing associated with the shift to farming were hypothesized to have a knock-on effect on the relative size and shape of the masticatory apparatus (e.g., Pinhasi et al. 2008; Sardi et al. 2004b), although most studies of this kind have focused on the forager−farmer transitions in other regions of the world (e.g., Carlson and Van Gerven 1977; González-José et al. 2005; Paschetta et al. 2010; Sardi et al. 2006). Employing craniometric data as a reliable proxy for neutral genetic data is reliant upon the assumption that cranial morphology is evolving neutrally (Brace et al. 2006) and, therefore, is not likely to be confounded by selective factors relating to climate, diet, or other environmental forces.

Fortunately, in recent years a growing body of 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 (González-José et al. 2004; Harvati and Weaver 2006a,b; Relethford 1994, 2002, 2004; Roseman 2004; Roseman and Weaver 2004, 2007; Smith 2009, 2011; von Cramon-Taubadel and Weaver 2009; von Cramon-Taubadel 2009a,b, 2011). What this suggests is that, on average, diversification of cranial shape differences within and between human populations was 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,b; Strauss and Hubbe 2010; von Cramon-Taubadel and Weaver 2009).

While cranial shape strongly fits a null model of neutral expectation, aspects of cranial size were shown to fit a model of climatic differences (e.g., Harvati and Weaver 2006a; Smith et al. 2007), consistent with the predictions of Bergmann's (1847) thermoregulatory rule. Given that Europe will have experienced considerable climatic fluctuations during the time of the Mesolithic/Neolithic transition, taking potential thermoregulatory adaptation into consideration is important. For this reason, studies which analyze scale-adjusted shape data are likely to capture the neutral aspects of cranial variation (and therefore the signal of past population history) more accurately than those based on raw measurements.

While the cranium appears to be acting relatively neutrally, and therefore may be used as a proxy for modeling population history analogous to neutral genetic data (Roseman and Weaver 2007; von Cramon-Taubadel and Weaver 2009), global patterns of mandibular variation were shown to be non-neutral (Smith 2011; von Cramon-Taubadel 2011b), correlating instead with differences in subsistence economy between hunter gatherer and agriculturalist populations (see also Carlson et al. 1977; González-José et al. 2005; Holmes and Ruff 2011; Paschetta et al. 2010; Pinhasi et al. 2008; Sardi et al. 2006). Therefore, the mandible is likely quite phenotypically plastic, remodeling during growth in response to differing dietary (biomechanical) stresses (e.g., Lieberman 2008). It is important to note that this plastic dietary effect does not extend to the cranium in general, with other "masticatory" regions of the skull still reflecting neutral population history, despite their functional involvement with chewing behavior (von Cramon-Taubadel 2009b, 2011b). Hence, while mandibular variation between Mesolithic and Neolithic populations might be useful for testing hypotheses about the dietary transition of foraging to farming, the cranium can be used reliably to test hypotheses about past microevolutionary processes such as migration, drift, gene flow, etc.

It is also possible to apply a specifically model-bound approach to quantitative craniometric traits in much the same way as is possible with genetic allele data (e.g., Cheverud 1982; Konigsberg 1990a,b; Konigsberg and Ousley 1995; Relethford 1982; Relethford et al. 1997; Relethford and Lees 1982; Relethford and Blangero 1990; Williams-Blangero et al. 1990). Recent studies by Pinhasi and von Cramon-Taubadel (2009; von Cramon-Taubadel and Pinhasi 2011) used model-fitting methods to explicitly test the demic vs. indigenist models for the transition to agriculture in southeastern, central, and eastern Europe. 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. Worth noting is 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 (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 was suggested on the basis of archeological data (Zvelebil 1996, 2001). We expanded the initial data set 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, 2006; Pinhasi and Pluciennik 2004).

Conclusion

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 utilization of model-free genetic analyses of haplogroup variation is problematic since observed "patterns" are easily overinterpreted, 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., Balloux 2010; Barbujani et al. 1998; Chihki 2009; Rosenberg and Feldman 2002; Weaver and Roseman 2008). As reviewed 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 is no longer sufficient for describing this complex demographic transition. The archeological 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) leap-frog 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 a 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 leap-frog colonization, do not usually entail the 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 may not have affected the local Mesolithic populations.

At present, only a limited number of aDNA studies exist 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 limit 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 regarding the population history of Europeans. Given the success with which craniometric data were used to address specific questions surrounding the Neolithic transition in Europe, we anticipate future analyses of the rich bioarcheological record to yield further insight into the microevolutionary history of Europe.

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