

'Aegean' and 'Anatolian' first farmers: ambiguous labelling or research blind spot?

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Abstract

While ancient DNA has convincingly shown that Early Neolithic farmers throughout Europe were descended from populations that once lived in the Aegean Basin and Anatolia, the labelling of the 'Neolithic' ancestry has remained ambiguous. Depending on sources, this ancestry has been described as 'Aegean', 'Northwest Anatolian' or simply 'Anatolian'. The lack of a unified terminology, it is argued here, betrays unresolved questions regarding the source of that ancestry – a problem that Volker and I raised in our 2011 article for the *Praehistorische Zeitschrift* (Brami & Heyd 2011). Whole-genome ancient DNA research has since confirmed the importance of migration as a driver for agricultural dispersals in Europe. But the closer we get to the source of that ancestry, the more the picture becomes blurred and difficult to interpret.

Keywords: Neolithic, ancient DNA, labelling, migration, Aegean, Anatolia

13.1 Introduction

Traditionally cast as one of the most essential tipping points in human history, the 'Neolithic revolution' (Childe 1936) is the shift from an appropriative economy based on hunting, gathering and fishing, to a productive economy based on plant cultivation and animal husbandry. The starting date of the Neolithic is more or less arbitrary, but is often thought to coincide with the start of the Holocene in southwest Asia, c 11,600 years ago, when humans settled down, built the first permanent villages, and developed new engagements with nature, through processes that eventually led to morphological changes in plant and animal domesticates (Fig. 1). Changes associated with the 'Neolithic revolution' took place within a fairly restricted geographic area initially – the Fertile Crescent, as well as the Taurus-Zagros Mountain foothills and highlands – parts of present-day Turkey, Syria, Iraq, Iran, Lebanon, Israel, Palestine and Jordan (Bar-Yosef 2011; Zeder 2011).

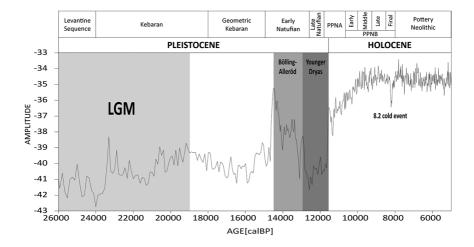


Figure 1. Temperature fluctuations in the Northern Hemisphere, based on Greenland Ice Cores (curve GISP2.180 in CalPal 2019.9), and Levantine chronology (sequence adapted from Zeder 2011: Fig. 2).

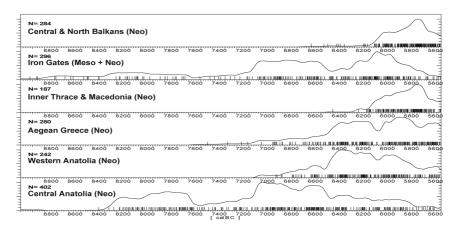


Figure 2. Summed probability distributions of n=1691 calibrated radiocarbon dates associated with Neolithic contexts ('food producing' sites) during the interval 9500–5500 calBC, with calibrated ages plotted by the Barcode Method (Weninger et al. 2014). Each small vertical line shows the median value of the corresponding calibrated 14C age. For the Danube Gorges, dates relating to both Mesolithic and Neolithic occupations are displayed.

An important question raised by ongoing archaeological investigations in the region is how the Neolithic, once formalized into a coherent pattern of existence, became portable and spread across large stretches of Europe, Asia and Africa, eventually giving rise to the complex societies in which we live today. While farming was introduced piecemeal in Cyprus and central Anatolia, at the latest by the 9th millennium BC, possibly supported in places by local domestication events, the westward expansion of the Neolithic beyond that 'core zone' or 'zones' appears to have proceeded differently, starting about two thousand years later (Fig. 2). In the Aegean Basin, first farming communities emerged fully-fledged in the 7th millennium BC (Brami 2015; 2019). All aspects of the Neolithic 'Bauplan' described by Childe and others (Childe 1936; Zeder 2009) were present from the start of occupation, suggesting the introduction of one or more Neolithic 'packages' in regions that were previously dominated by foragers (Özdoğan 2011).

Based on 14C dates and the distribution of specific ceramic wares, Volker and I suggested in our 2011 article three dispersal routes out of Anatolia in the 7th and 6th millennia BC, each associated with a slightly different Neolithic 'package': 1) the northwestern expansion of the Dark Faced Burnished Ware (DFBW) horizon to the region of Marmara (Fikirtepe tradition); 2) the westward expansion of the Red Slipped Burnished Ware (RSBW) horizon to the Aegean coast of Turkey, Greece and Turkish Thrace; and 3) a maritime koiné linking Impresso-decorated ceramic traditions in the eastern Mediterranean Basin and the Aegean (Brami & Heyd 2011). Our paper also hinted at yetto-confirm pre-ceramic Neolithic dispersals in places like Küçükçekmeçe near Istanbul, on the basis of the occurrence in low frequency of specific tool types, such as opposed platform bidirectional cores, which are found among some aceramic Neolithic communities of Cappadocia. While our article proved controversial at the time of release due to the equation made between communities of practices and population dispersals, the idea of large-scale migrations at the outset of the Neolithic expansion has been largely vindicated by recent biomolecular approaches.

13.2 Early agricultural dispersals confirmed by genetics

Since the late 2000s, whole-genome and genome-wide ancient DNA analyses have revolutionized research on prehistoric migrations by providing direct biomarkers from the skeletons excavated and robust statistical methods to compare populations and infer ancestry. At first sight, the picture presented by recent palaeogenomic studies is relatively straightforward, with well-differentiated early farmer and hunter-gatherer populations at the onset of agriculture in Europe (Mathieson et al. 2015; 2018; Hofmanová et al. 2016). European foragers are now thought to have occasionally admixed with incoming farm-

ers, leading to asymmetric mating patterns in places like Lepenski Vir in the Danube's Iron Gates or the Blätterhöhle Cave in northwestern Germany (Bollongino et al. 2013; Lipson et al. 2017; Brami et al. 2022; Hofmanová et al. 2022). However, the hunter-gatherer contribution to the farming gene pool remains small, amounting to no more than about c 10% in the early phases of the European Neolithic (Mathieson et al. 2015; Hofmanová et al. 2016; Lipson et al. 2017). In other words, the spread of agriculture in Europe was primarily driven by population expansion and demic diffusion (Shennan 2018), as initially suggested by Childe (Childe 1936) and later Ammerman and Cavalli-Sforza (1984) in their influential 'wave of advance' model.

While a two-population admixture model generally summarizes well patterns of interactions observed at continental level in Neolithic Europe, demographic modelling using the neutral portion of the genome that is not affected by selection in high-coverage ancient genomes has recently offered unprecedented insights into the post-glacial demographic history of the ancestors of the world's first farmers (Marchi et al. 2022). Despite Mesolithic genomes like those from Loschbour in Luxembourg and Vlasac in Serbia falling close on a PCA plot, the model proposed by Marchi et al. identified a deep split c 23,000 years ago between two branches of what is usually described as the 'Western Hunter-Gatherer' ancestry in Europe. Europe's first farmers can themselves be shown to be descended from Western Hunter-Gatherers and Southwest Asian populations that admixed in Anatolia or in the Taurus Foothills c 14,000 years ago and subsequently experienced a massive drift, maybe linked to range expansion among small settled communities (Marchi et al. 2022). It was this population, supported by agriculture and recurrent Neolithic Demographic Transition events, that expanded into Europe, making its way to places as far away as the British Isles (Brace et al. 2019).

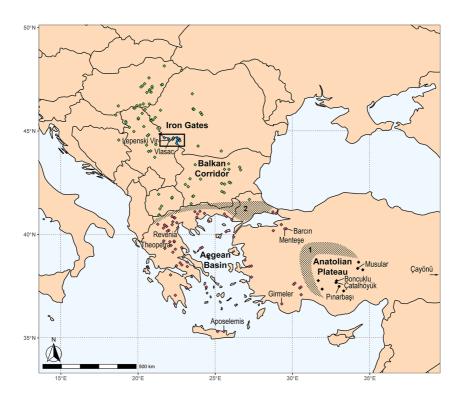
The picture prior to the arrival of agriculture in Europe was both complex and dynamic, with populations splitting into refugia, admixing during periods of climatic amelioration, contracting in size and expanding, depending on resources availability (Marchi et al. 2022). For now it looks like the Anatolian and Danubian mating pools remained broadly distinct until c 6200 BC, when

agriculture spread to the central Balkans (Brami et al. 2022). Nonetheless, these regions shared a common recent demographic history since the end of the last Ice Age and were never isolated *stricto sensu*.

13.3 Anatolian or Aegean first farmers?

While the genomic origins of Europe's first farmers are thus to be found somewhere in Anatolia and neighbouring regions, pinpointing the exact source of that ancestry is proving challenging. The term 'Anatolia' itself is confusing and deserves a brief explanation. Anatolia, in a strict sense, corresponds to the peninsular part of modern Turkey or Asia Minor. Many archaeologists today are content nonetheless to use the term 'Anatolia' in a broad sense to refer to the Asian part of Turkey, including those regions east of the Amanus Mountains, in the Taurus Foothills, i.e. 'Southeast Anatolia'. Since the Ancient Greek term 'Avatolá' refers to the direction of sunrise, or the East, the term 'Anatolia' could also be construed as referring to those lands to the east of Greece, beyond the coastline, the Anatolian Plateau.

The first Neolithic genomes in Turkey to be sequenced came from the sites of Barcin and Menteşe (Fig. 3) in the eastern Marmara region (Mathieson et al. 2015; Hofmanová et al. 2016) – two inland sites that nonetheless display similarities in material traditions with so-called 'Fikirtepe' sites on the coast of Marmara (Özdoğan 2011; Özbal & Gerritsen 2019). Whereas Mathieson et al. (2015) described those sampled individuals as 'Anatolian Neolithic farmers', Hofmanová et al. (2016) called them 'Aegean farmers', the latter term applying equally well to an Early Neolithic genome from the site of Revenia in northern Greece. Six new genomes from the cemetery of Aposelemis in Crete, radiocarbon-dated to c 6100–5800 BC, have recently confirmed that communities all over the Aegean Basin were involved in regular mating interactions throughout the Neolithic period (Skourtanioti et al. 2023). As two mitochondrial genomes from Greek Mesolithic (8th millennium BC)



3. Distribution of radiocarbon-dated sites in four regions of Anatolia and southeast Europe. The location of major agricultural frontier zones is indicated by 1 and 2 (tentative). Important sites mentioned in the text are listed here.

skeletons at Theopetra Cave in Thessaly belonged to lineages (K1) normally observed among Europe's first farmers, a local transition from Mesolithic to Neolithic communities in the Aegean Basin could not be excluded (Hofmanová et al. 2016).

Meanwhile, archaeogenetic research on the Anatolian Plateau (with samples from 9th millennium BC Boncuklu, among other sites) led to two important conclusions: Central Anatolian first farmers (1) belonged to the same

gene pool as Europe's first farmers (Kılınç et al. 2016); and (2) were directly descended from local Epipalaeolithic communities (14th millennium BC Pınarbaşı), suggesting a limited role for migration in the emergence of agriculture on the Plateau (Feldman et al. 2019). Given that genetic diversity increased over time, from the Aceramic to the Ceramic Neolithic period, additional gene flow at the time of Çatalhöyük East and the westward spread of agriculture appears likely (Yaka et al. 2021). New genomes from Musular in Cappadocia demonstrate that Central Anatolian farmers were already involved in broader mating interactions with Southern Levantine and Zagros and/or Caucasus populations at the end of the Aceramic Neolithic period, c 7400-7000 BC (Koptekin et al. 2023). The recent publication of 9th/8th millennium BC genomes from Çayönü in the Tigris Basin has not fundamentally altered this picture, suggesting that Upper Mesopotamian genomes were marginally closer to Anatolian genomes than expected under a linear isolation-by-distance model, in which genes mirror geography, but unlikely to have been the ultimate source of the ancestry observed in Anatolia (Ezgi Altınışık et al. 2022).

13.4 Conclusion

The Neolithic transition in Europe is often described as the low-hanging fruit of recent aDNA research, due to the relatively contrasted genetic profile of Europe's first farmers and hunter-gatherers, suggesting large-scale migration as a driver for agricultural dispersals. Yet, several questions remain: if hunter-gatherer populations in the Danubian region were significantly different from hunter-gatherer populations in Anatolia, where was the boundary between these two mating networks? Was the transition from Mesolithic to Neolithic societies in the Aegean Basin driven by migration or by acculturation? Did Northern Levantine communities play any significant role in the dispersal of Neolithic lifeways? At present, there is no firm answer to any of

these questions, hence the confusion between 'Aegean' and 'Anatolian' ancestry labels when referring to Europe's first farmers.

Both Anatolia and the Aegean Basin remain strong contenders as places of genetic origins of Europe's first farmers. The difficulty to pinpoint the exact source of European 'Neolithic' ancestry is compounded by the fact that: 1) little is known about the genetic makeup of Mesolithic populations in the Aegean Basin, and 2) migration and acculturation scenarios are difficult to distinguish if populations in Anatolia and the Aegean Basin remained close genetically throughout the 9th and 8th millennia BC. That picture might be about to change. A newly-reported genome from the settled forager site of Girmeler near Fethiye in southwest Turkey, dated to c 7738–7597 BC, just outside the Aegean Basin, clusters on PCA with both Epipaleolithic and Early Neolithic Central Anatolians (Koptekin 2022). Pending further investigations, this new discovery suggests that significant biological interactions took place across the Anatolian-Aegean farming frontier, at a time when agriculture was already practised on the Anatolian Plateau, but not yet in the Aegean Basin (Fig. 2).

Acknowledgements

It was Volker who set me on the research path that I am on today, by suggesting back in 2006 that I write an essay on 'The Early Neolithic in Greece' for his 'Neolithic and Copper Age Societies' class at Bristol University. I was a 2nd year undergraduate then, discovering prehistory. Volker's singular vision of prehistoric Europe, as a continuously changing interconnected whole, made a lasting impression on me and still guides my work today. The ongoing aDNA revolution in archaeology has shown many of his intuitions to be correct.

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