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Solutions or illusions? An analysis of the available palaeogenetic evidence from the origins of the Neolithic in the Iberian Peninsula

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1. Introduction

The "Sisyphus' rock" of Human Sciences could be the wide array of circumstances, interpretations and processes generated by human beings and their numberless organizations, groups, communities, collectives, languages or "cultures" that determine their interpretations. Thus, when (pre)historians and social scientist in general have the chance to resort to *hard* sciences, they cling tightly to it, sometimes even with a blind trust, in the hope of finding a reference point for their intrinsically human —and therefore multidimensional and multifocal— interpretations, open to different possible solutions.

In recent years the study of the past has placed its trust in dating techniques, —particularly in 14C—, in statistical analyses and in genetic studies, among other such possibilities, in a way that they could be considered as the new "guide fossils" in prehistorical research. For instance, the chronology of a domestic animal or plant would be taken as an undeniable marker of the "Neolithic" period, and something similar could be said of the hypothetical presence of a Near Eastern haplogroup in a VI millennium BC European individual (Balsera et al., 2015; Bernabeu-Aubán et al., 2016, 2015; Fernández-Eraso et al., 2015; García-Martínez de Lagrán, 2017; Martins et al., 2015); for example from the Iberian Peninsula). However, from a (pre)historic viewpoint, things are not so clear or so "hard".

The present paper focuses on the analysis of the palaeogenetic data available for the Neolithisation process and the Early Neolithic period in the Iberian Peninsula. We have considered the information from a historical and anthropological perspective in an attempt to understand and complement the interpretations derived from the geneticists themselves. Moreover, a part of the paper is devoted to explain the archaeological consequences of the types of analysis carried out and the results of such studies. The final goal would be to broaden the possible interpretations of the Neolithisation process and the Early Neolithic period in this territory.

2. Palaeogenetic evidence of the Mesolithic-Neolithic transition in Europe

Understanding the jargon commonly used in genetics can be challenging for an unfamiliar audience, this being probably the main cause of misinterpretation of genetic data by non-experts. With this in mind, the main concepts used in population genetic studies have been compiled in supplementary information and explained in a simple way, starting from the very basics (Supplementary Information 1).

During the last few years we have witnessed an exponential increase in the quantity (and quality) of prehistoric human paleogenetic data. Two main factors have contributed to this fact, namely the development of a new genotyping technique -the so-called Next Generation Sequencing or NGS- and a new sampling strategy targeting the densest of the bones -the petrous (pars petrosa of the temporal bone)-, which proved to contain up to 183 times more DNA than any other skeletal element (Gamba et al., 2014). These advances have not passed unnoticed for the archaeological community and our knowledge of different archaeological cultures and periods has improved greatly, including the old question of the nature of the spread of the Neolithic in Europe. In this regard, genetics has come to challenge us in different ways and while these scientific techniques are overall very welcome, their interpretations

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have left some scholars with discomfort (Hofmann, 2014; Linden, 2016).

Inspired by Thomas Lindahl's article title “Facts and Artifacts in ancient DNA” (Lindahl, 1997), we will focus in this section on the “facts” aka main conclusions of published ancient DNA studies on the European Mesolithic-Neolithic transition to further discuss some of their “artifacts”, understood in this case as partial interpretations needing of a wider archaeological discussion, with a particular focus on Iberia.

2.1. The European pre-Neolithic genetic background

Early ancient mitochondrial DNA studies already suggested that the genetic background of pre-Neolithic european populations might have been dramatically different from that found in the Early Neolithic (Bramanti et al., 2009), a suspicion that became a fact once that more and more data of both groups was made available (Gamba et al., 2014; Hervella et al., 2015; Posth et al., 2016; Sánchez-Quinto et al., 2012). These were indeed good news, as this finding would potentially allow for phenomena of acculturation, admixture, or assimilation to be identified, something that would have been unachievable if both groups had been genetically homogeneous or even similar.

These studies painted a picture of a uniform hunter-gatherer population across Europe, mainly dominated by U-type haplogroups: U, U2, U4, U5 and U8 (Bramanti et al., 2009; Gamba et al., 2014; Lazaridis et al., 2014; Sánchez-Quinto et al., 2012). More recent contributions have proposed a more complex scenario, with a higher mtDNA diversity in pre-Late Glacial Maximum samples, including representatives of U haplogroups but also members of the haplogroup R in Northern Italy and, surprisingly, of the macrohaplogroup M in France and Belgium, a clade that is nowadays restricted to Asia, Australasia and America (Posth et al., 2016). This post-LGM reduction in diversity was interpreted by the authors as evidence of 1) a genetic bottleneck during the LGM resulting from extreme climatic conditions, followed by a re-expansion after the ice sheets retracted and 2) a genetic turn-over of the post-LGM population by a distinct group of an unknown origin, maybe from a different LGM refugia, dominated by haplogroup U5 (Posth et al., 2016). These post-LGM groups are the immediate ancestors of the populations that would later interact with the Neolithic farmers. Even though this interpretation is based on a small subset of complete mitochondrial sequences (N = 55) from different locations, cultures and ages, it raises concerns about the use of hunter-gather sequences regardless of their age as proxies of Mesolithic populations (Bramanti et al., 2009).

Genome-wide DNA studies contradict this apparent uniformity, showing a clear distinction between Western, Eastern and Scandinavian hunter-gatherers (Haak et al., 2015; Lazaridis et al., 2016; Olalde et al., 2015. It is important to note the differences in sample size, chronology and geographical representativity of the data obtained with each approach.

Fig. 1 illustrates the location of archaeological sites that have provided paleogenetic data from Mesolithic and Early Neolithic periods. As it can be seen in the figure, data are still very scarce and biased towards certain regions. Even though we acknowledge that the only way forward is to work with the available information, its limitations and uncertainties should be clearly stated, especially when attempting direct comparisons between Mesolithic and Early Neolithic specimens from different regions. In fact, Olalde et al., 2015 recognize that the Early Neolithic sample of Cova Bonica (Catalonia, Spain) is genetically closer to a Hungarian Mesolithic-type DNA than to the two samples of La Braña-Arintero (León, Spain).

2.2. The European Neolithic genetic background and possible interactions with hunter-gatherer populations

The mitochondrial DNA landscape of the European Neolithic is overall dominated by haplogroups K, N*, N1a, T2, X2, H and J, most of which can be traced back to Early Neolithic Anatolia and the Levant (Fig. 2). In the absence of information on the local Mesolithic genetic background, assumptions need to be made based upon similarities with the genetic stock of the first farming Near Eastern populations, which has only become available very recently (Fernández et al., 2014; Kılınç et al., 2016; Lazaridis et al., 2016; Mathieson et al., 2015). Even though this dataset is still scarce and does not account for the geographical and chronological complexity of the first emergence of the Neolithic in the Near East, interesting patterns have arisen: 1) Levantine, Anatolian and Zagros farmers represent three different genetic stocks (albeit with certain common mtDNA haplogroups) clearly distinguished at genome-wide and Y chromosome levels and 2) Early Neolithic populations across Europe that have been studied up to date show striking similarities at genome-wide level to the Anatolian Neolithic (Boncuklu Höyük, Menteşe and Barcın), but not to the populations of the Southern Levant (Ain Ghazal, Motza) and the Zagros region in Iran (Ganj Dareh). Even though a Southern Levantine ancestry of Early Neolithic European populations has been excluded considering the information above, mitochondrial DNA analyses of samples of the Northern Levant have shown intriguing similarities with both LBK and Cardial/Epicardial groups, proposing an early dispersal of farmers through Cyprus and the Aegean sea (Fernández et al., 2014). Southern and Northern Levantine populations share haplogroups K and R0, and both also lack haplogroups N1a and X2,characteristic of Anatolian populations.

Moving towards Europe, the most Southwestern point with Early Neolithic DNA data is the site of Revenia, in Northern Greece (6438-6264 cal BC).[1] Mitochondrial data is also available from two individuals of the Mesolithic site of Theopetra in Thessaly (7605–7529 and 7288–6771 respectively) (Hofmanová et al., 2016). The two Neolithic individuals harbour mtDNA haplogroup X2 and Y Chromosome haplogroup G2a, both present in Anatolian Pottery Neolithic sites (Barcın and Menteşe), while the two hunter-gatherers from Theopetra have been identified as members of mitochondrial haplogroup K1. No genomic or Y chromosome data could be retrieved from these two hunter-gatherer individuals. While an Anatolian origin has been claimed for the Early Neolithic Revenia sample based upon their similarities at genome-wide level, it is surprising that the two studied Mesolithic individuals carry typically Neolithic mytotypes. As pointed out in (Fernández-Domínguez and Reynolds, 2017), in the absence of Mesolithic genomic data from the region both a common Mesolithic genetic background for Anatolia and Greece and the Greek samples being direct descendants of Neolithic Anatolians as a result of migration are suitable explanations.

From there on, the bulk of data corresponds to the Danubian route of Neolithic spread, with representatives of the Körös, Starčevo, Çris, Transdanubian (Hungarian) LBK and German LBK (Brandt et al., 2013; Brotherton et al., 2013; Gamba et al., 2014; Haak et al., 2015, 2010; Hervella et al., 2015; Szécsényi-Nagy et al., 2015). The mitochondrial DNA composition of the Anatolian datasets mirrors the Starčevo-Çris-Körös, Transdanubian and German LBK data, displaying a set of common haplogroups: K, N1a, T2, X2, H and J (Fig. 2). These populations also harbour a high frequency -usually over 50%- of the Y chromosome haplogroup G2a. Similarly, the genomic DNA for the Körös and Starčevo samples

[1] The chronological references in the text are cal BC.

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