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Response to Comment on “Ancient DNA from the First European Farmers in 7500-Year-Old Neolithic Sites”

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The discovery of mitochondrial type N1a in Central European Neolithic skeletons at a high frequency enabled us to answer the question of whether the modern population is maternally descended from the early farmers instead of addressing the traditional question of the origin of early European farmers.

Our study (1) described the discovery of the mitochondrial type N1a in 6 out of 24 Central European Neolithic skeletons, which was unexpected because today this type is found at 150-times lower frequency in Europe. We offered two possible explanations for our observations. First, female Early Neolithic farmers could have been replaced by immigrant women after the early Neolithic (post-early-Neolithic replacement theory). Second, the female early Neolithic farmers could have been genetically diluted by resident native hunter-gatherers (Paleolithic survival theory). Both interpretations are compatible with our genetic data. Because there is so far no archaeological evidence for a major post-early-Neolithic population replacement, we suggested that the Paleolithic survival theory is more likely.

In their comment, Ammerman *et al.* (2) raise concerns about our study and call for further ancient DNA studies. First, the authors may have misread the central question asked in our study. We tackled the question of the fate of the early European farmers [as represented by the Neolithic skeletons of the Linear pottery culture (LBK)], that is, whether modern central Europeans are descended from them or not. In contrast, Ammerman *et al.* imply that our study deals with questions on the origin of the early European farmers, such as whether the female lineages in the farmer skeletons were immigrants from southeastern Europe or whether they were local Mesolithic women who intermarried with incoming males. Irrespective of this misunderstanding, the origin of the farmers remains an important question, and the plight of the early farmers' descendants outlined in our study, along with the intriguing ancient DNA data, may one day contribute to a better understanding of farming origins.

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We believe it is worthwhile to clarify the points that Ammerman and colleagues usefully raise. Regarding the point that we should have

analyzed far more than 24 samples, we point out that our main conclusions (1) were based on statistically significant results. Furthermore, we carefully examined the sample locations and mitochondrial DNA types to exclude the possibility of biased sampling. Ammerman *et al.* (2) are correct that one of our 24 skeletons, namely the one from Ecsegfalva, is not a “first” farmer but only an “early” farmer, as far as eastern Hungary is concerned. We included this skeleton in our analysis because it is culturally and chronologically closely related to our actual focus, the first farmers in the LBK area of neighboring Central Europe (Fig. 1). The other 23 skeletons represent the first full farming populations in their local LBK regions; this is particularly the case for the Flomborn site, which is among the first LBK colonies west of the Rhine and is also the type-site for the “Flomborn”

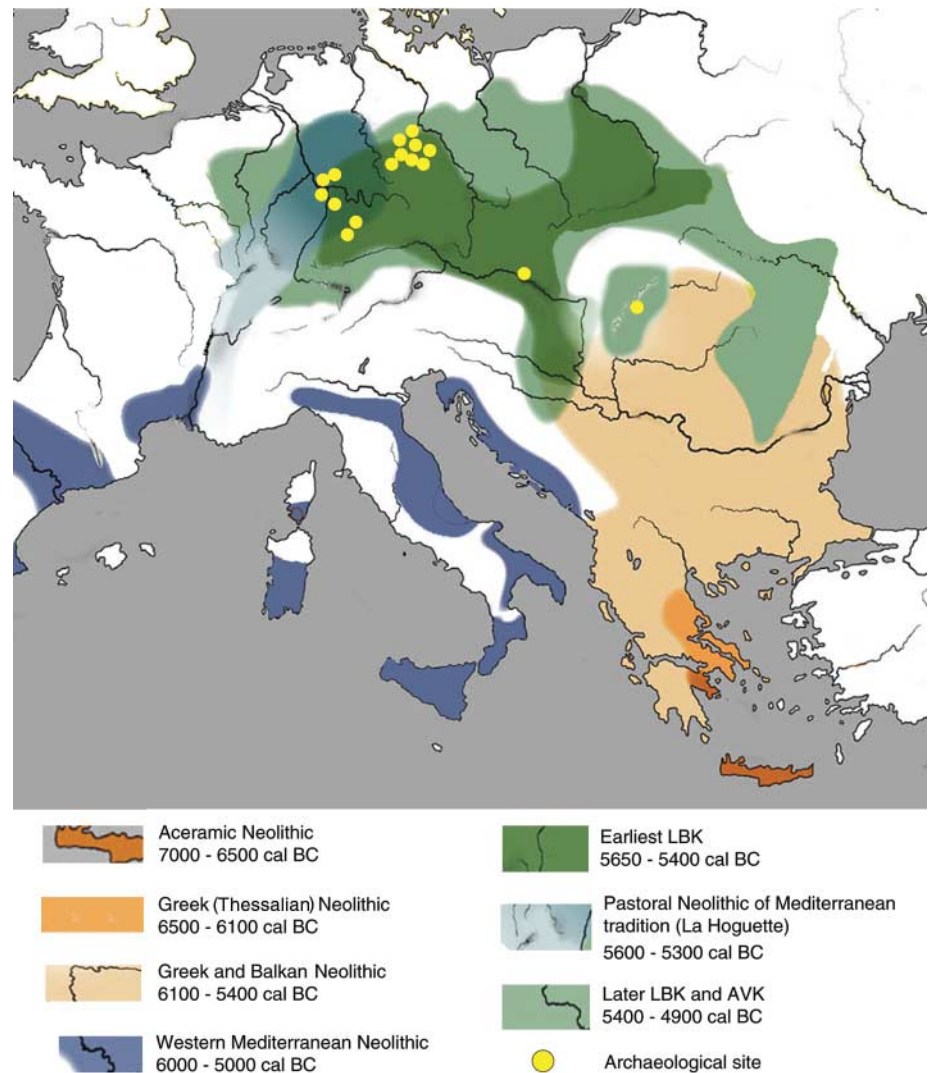


Fig. 1. The spread of farming across Europe. The colors indicate time scales for the spread of the early Neolithic in Europe. All 24 samples of our ancient DNA study belong to the same LBK/AVK (Linear pottery and Alföld linear pottery culture) chronostratum, representing the first farmers in much of central Europe.

phase, which we calculate to have started around 5400 cal BC (3).

Ammerman *et al.*'s hypothesis that immigrant male farmers would take local hunter-gatherer wives is based on mostly Central and Southern African ethnography; it is entirely unproven for the LBK. On the contrary, the western areas of the LBK area—where this topic has been studied intensively—indicate that male and female members of local pastoralist and/or hunter-gatherer communities lived side-by-side with members of immigrant farming societies (immigrants from Transdanubia and southwestern Slovakia) in multitraditional communities, which only at a coarse archaeological resolution appear to be “LBK villages” (4). Incidentally, Ammerman and colleagues' choice of words distinguishing “farmers” from “wives and daughters of farmers” is unfortunate, invit-

ing the misreading that women were not farmers. Further, we were aware that the situation in other European regions (particularly in the south and east of Europe) could have been quite different, and therefore we used as controls present-day individuals only from the LBK area.

Finally, Ammerman *et al.* suggest analyzing more samples and further (i.e., nonmitochondrial) genetic loci. We encourage such projects to help illuminate aspects of European prehistory that were not the focus of our more modest study. We caution, however, that in our experience, only about 15% of morphologically well-preserved skeletons contain amplifiable nuclear DNA. Thus, on average, we would expect Y-chromosomal DNA from only about 7.5% of a skeletal sample. The logistic challenge of such a project is not inconsiderable, although new data would be most welcome.

Finally, we agree with Ammerman and colleagues that morphological data are useful, for example, for examining the Paleolithic survival theory (5).

References

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