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Genetic Discontinuity Between Local Hunter-Gatherers and Central Europe’s First Farmers

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After the domestication of animals and crops in the Near East some 11,000 years ago, farming had reached much of central Europe by 7500 years before the present. The extent to which these early European farmers were immigrants or descendants of resident hunter-gatherers who had adopted farming has been widely debated. We compared new mitochondrial DNA (mtDNA) sequences from late European hunter-gatherer skeletons with those from early farmers and from modern Europeans. We find large genetic differences between all three groups that cannot be explained by population continuity alone. Most (82%) of the ancient hunter-gatherers share mtDNA types that are relatively rare in central Europeans today. Together, these analyses provide persuasive evidence that the first farmers were not the descendants of local hunter-gatherers but immigrated into central Europe at the onset of the Neolithic.

Europe has witnessed several changes in archaeological cultures since anatomically modern humans displaced the Neandertal population 30,000 to 40,000 years ago (1, 2). Palaeolithic hunter-gatherers survived the Last Glacial Maximum (LGM) about 25,000 years ago in southern and eastern refugia (3) and resettled central Europe after the retreat of the ice sheets. With the end of the Ice Age at ~9600 B.C.E., their Mesolithic descendants or successors had recolonized large parts of the deglaciated northern latitudes (4, 5). From around 6400 B.C.E., the hunter-gatherer way of life gave way to farming cultures in a transition known as the Neolithic Revolution (6). The extent to which this important cultural transition was mediated by the arrival of new peoples, and the degree of Mesolithic and early Neolithic ancestry in Europeans today, have been debated for more than a century (7–10). To address these questions directly, we obtained mitochondrial DNA (mtDNA) types from 22 central and northern European post-LGM hunter-gatherer skeletal remains (Fig. 1) and compared 20 of these (those for which full sequence information was available) to homologous mtDNA sequences from 25 early farmers (11, 12) and 484 modern Europeans from the same geographic region (13). Our ancient sample spans a period from circa (ca.) 13,400 to 2300 B.C.E. and includes bones from Hohler Fels in the Ach valley (Late Upper Palaeolithic) and Hohlenstein-Stadel in the Lone valley (Mesolithic). Extensive precautions were taken to ensure sequence authenticity (14), including extracting independent samples from different skeletal locations of the same individuals and examining remains only from high latitudes or cave sites with good biomolecular preservation.

The sites are as follows: 1, Ostorf; 2, Bad Dürenberg; 3, Falkensteiner Höhle; 4, Hohler Fels; 5, Hohlenstein-Stadel; 6, Donkalnis; 7, Spiginas; 8, Dudka; 9, Kretuonas; 10, Drestwo; 11, Chekalino; 12, Lebyazhinka; 13, Unseburg; 14, Unterwiederstedt; 15, Derenburg/Meerenstieg; 16, Elsleben; 17, Halberstadt; 18, Seehausen; 19, Flomborn; 20, Vaithingen an der Enz; 21, Schwetzingen; 22, Asparn/Schletz; 23, Ecsegfalva.

Fig. 1. mtDNA types from prehistoric samples of hunter-gatherers and farmers. The green shading represents the first farming areas (dark green: early LBK, 5650 to 5400 calibrated years B.C.E. [calBC]; light green: LBK, 5400 to 4900 calBC) in central Europe, based on archaeological finds, whereas squares represent successfully analyzed Late Palaeolithic, Mesolithic, and Ceramist hunter-gatherers dating from 13,400 to 2300 B.C.E. The term “Neolithic” is sometimes applied to the Eastern European Ceramist culture because of their use of pottery, but this does not imply a farming economy (21). Previously analyzed (11, 12) LBK farming sites are marked with circles for comparison. The area of each square or circle is proportional to the number of individuals successfully investigated. In red are labeled archaeological sites with one or more U4/U5 individuals; in yellow, sites with other mtDNA types, highlighting the specificity of U types in the prehistoric hunter-gatherers.

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An analysis of the molecular variance (15) showed that our early farmers and hunter-gatherers were from two well-differentiated populations; the among-populations proportion of genetic variation (F\text{ST}) = 0.163, P < 10^{-6}. To put this value into perspective, we compared a range of modern human populations, randomly sampling 20 individuals from each. The maximum F\text{ST} value in all comparisons among eight modern European samples was 0.0327, and among 13 modern European, Middle Eastern, Indian, Chinese, Papua New Guinean, and Australian samples it was 0.133 (14). We also found that our modern European sample was significantly different from the early farmer (F\text{ST} = 0.0580, P = 10^{-5}) and hunter-gatherer (F\text{ST} = 0.0858, P < 10^{-8}) samples. To test whether these genetic differences can be explained under the null hypothesis of population continuity alone, we performed coalescent simulations across a wide range of ancestral population size combinations. We conservatively assumed a modern female effective population size of N_0 = 12,000,000 (one-tenth of the current female population size of central and northern Europe) and two periods of exponential growth: the first after the Upper Paleolithic colonization of Europe 45,000 years ago of female effective population size N_{1UP}, sampled from an ancestral African population of constant female effective size N_A = 5000; and the second after the Neolithic transition in central Europe 7500 years ago of effective population size N_N. We sampled sequences from each simulation according to the numbers (hunter-gatherer n = 20, early farmer n = 25, modern n = 484) and dates (Table 1) of the sequences presented here and found the proportion of simulated F\text{ST} values that were greater than those observed (P_{S>O} (14)). By exploring all combinations of 100 values for N_{1UP} (ranging from 10 to 5000) and 100 values for N_N (ranging from 1000 to 100,000), we found that the maximum P_{S>O} value between hunter-gatherers and early farmers was 0.022 (for N_{1UP} = 4960 and N_N = 1000), and the maximum P_{S>O} value between hunter-gatherers and modern central Europeans was 0.028 (for N_{1UP} = 3560 and N_N = 1000). Most P_{S>O} values were considerably lower (Fig. 2). These results allow us to reject direct continuity between hunter-gatherers and early farmers, and between hunter-gatherers and modern Europeans.

When we considered continuity between early farmers and modern Europeans, we did identify ancestral population size combinations where P_{S>O} > 0.05 (black shaded area in Fig. 2C). Thus, there are demographic conditions under which the observed genetic differences between early European farmers and modern Europeans can be explained by assuming population continuity. Those conditions include assuming N_N < 3000, an effective female population size that may be considered implausibly low and is certainly lower than the current archaeological census estimates of 124,000 (16). However, we note that (i) ancestral population sizes are notoriously difficult to estimate from archaeological data, and (ii) the relationship between effective and census population size is dependent on unknown factors, including mating systems and population substructure.

Most modern European mtDNA lineages can be assigned to one of the following clades or haplogroups: H, V, U (including K), J, or T, all derived from clade R; or I, W, or X, the descendants of clade N. Although some subclades, such as U5, are fairly specific to Europe, most are shared with adjacent areas of Asia and North Africa and are of uncertain antiquity in Europe. We are therefore cautious about treating specific clades as markers of particular past population groups or demographic episodes (17). Nonetheless, it is intriguing to note that 82% of our 22 hunter-gatherer individuals carried clade U (14 U5, 2 U4, and 2 unspecified U types; Table 1). A high incidence of U types (particularly those belonging to the U5 subclade) in Stone Age Europeans has been inferred from modern mtDNA (7), but the frequencies found here are surprisingly high. Europeans today have moderate frequencies of U5 types, ranging from about 1 to 5% along the Mediterranean coastline to 5 to 7% in most core European areas, and rising to 10 to 20% in northeastern European Uralic speakers, with a maximum of over 40% in the Scandinavian Saami. U4 types show frequencies between 1 and 5% in most parts of Europe, with Western Europe at the lower end of this range and northeastern Europe and central Asia showing percentages in excess of 7% (13).

The diversity among the hunter-gatherer U types presented here, together with their continued presence over 11 millennia, and the fact that U5 is rare outside Europe, raises the possibility that U types were common by the time of the post-LGM repopulation of central Europe, which started around 23,000 years ago (3). In a previous study, we showed that the early farmers of central Europe carried mainly N1a, but also H, HV, J, K,

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**Fig. 2.** Probabilities of obtaining observed genetic differences, as measured by F\text{ST}, between (A) hunter-gatherers and LBK early farmers, (B) hunter-gatherers and modern Europeans, and (C) LBK early farmers and modern Europeans, across a range of assumed ancestral population size combinations. Two phases of exponential growth were considered, the first after the initial colonization of Europe 45,000 years ago, of assumed effective female population size N_{1UP} (y axis), and ending when farming began in central Europe 7500 years ago, when the assumed effective female population size was N_N (x axis); and the second leading up to the present, when the assumed effective female population size is 12 million. The initial colonizers of Europe were sampled from a constant ancestral African population of 5000 effective females. The F\text{ST} values are those observed from the data presented in this study. Black shaded areas indicate probabilities >0.05.
Linearbandkeramik culture (LBK) and the earliest settlements of the Neolithic nature between the central European Mesolithic and the earliest settlements of the Neolithic. Thus, it seems that despite the exchange of stone artifacts, genetic exchange between both groups, at least on the female side, was initially limited. The only exception is the site Ostorf (northern Germany), where two individuals carried haplogroup T2, which is also found in our LBK sample. We are cautious about interpreting this as a signature of local admixture, particularly because the hunter-gatherer and early farmer T2 types belong to different sublineages, but it is notable that Ostorf is culturally a Mesolithic enclave surrounded by Neolithic funnel-beaker farmers and is the only hunter-gatherer site where any non-U mtDNA types were observed (Table 1). Further sampling from such local contexts should shed light on the details of Mesolithic-Neolithic interactions after the arrival of farming. We note that any genetic exchange between hunter-gatherers and early farmers at this site would reduce the overall genetic differentiation between the two groups, so inclusion of this site has, if anything, a conservative effect on our conclusions regarding continuity.

Taken together, our results indicate that the transition to farming in central Europe was accompanied by a substantial influx of people from outside the region who, at least initially, did not mix significantly with the resident female hunter-gatherers. We accept that alternative, more complex demographic scenarios, such as strong local population structure and high group extinction and fission rates, might also explain our data. However, the ubiquity of U types in our hunter-gatherer samples is inconsistent with extensive population structuring and indicates that the demographic processes that shaped the observed patterns of genetic variation extend beyond the local scale.

The extent to which modern Europeans are descended from incoming farmers, their hunter-gatherer forerunners, or later incoming groups remains unresolved. The predominant mtDNA types found in the ancient samples considered in this study are found in modern Europeans, but at considerably lower frequencies, suggesting that the diversity observed today cannot be explained by admixture between hunter-gatherers and early farmers at this site.

Table 1. Stone Age individuals and their mtDNA results. A, DNA of the archaeologists available for comparison; D, diagenetical analysis; M, multiple extractions and number of these; N, positive amplification of nuclear DNA; Rf, restriction fragment length polymorphism analysis; SNP, single-nucleotide polymorphisms from the coding region of mtDNA obtained by means of multiplex amplification; BP, before the present; ca., circa. The mtDNA was sequenced from nucleotide position (np) 15997 to np16409. mtDNA positions are numbered according to the revised Cambridge reference sequence (22), minus 16,000. Fourteen individuals did not yield results (table S1), whereas for two individuals the mtDNA sequences were not determined (n.d.) and thus not considered in the AMOVA analysis and simulations.

<table>
<thead>
<tr>
<th>Country</th>
<th>Site, skeleton</th>
<th>Basis of dating*</th>
<th>Dating calBC*</th>
<th>Analyses</th>
<th>mtDNA sequence</th>
<th>Clade</th>
</tr>
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<tbody>
<tr>
<td>Lithuania</td>
<td>Spingas 4</td>
<td>GIN-5571: 7470 ± 60 BP</td>
<td>ca. 6350 calBC</td>
<td>A, M3, C109, Q, Rf</td>
<td>356c</td>
<td>U4</td>
</tr>
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<td></td>
<td>Donkalnis 1</td>
<td>Cultural context</td>
<td>Mesolithic</td>
<td>A, D, M4, C79, N, RF, SNP</td>
<td>192t 270t</td>
<td>U5b2</td>
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<td></td>
<td>Kretuonas 3</td>
<td>OxA-5926: 5580 ± 65 BP</td>
<td>ca. 4450 calBC</td>
<td>A, M4, C72, N, RF, SNP</td>
<td>192t 270t</td>
<td>U5b2</td>
</tr>
<tr>
<td></td>
<td>Kretuonas 1</td>
<td>OxA-5935: 5350 ± 130 BP</td>
<td>ca. 4200 calBC</td>
<td>A, M5, C56, N, RF, SNP</td>
<td>192t 270t</td>
<td>U5b2</td>
</tr>
<tr>
<td>Poland</td>
<td>Dudka 2</td>
<td>14C date on charcoal</td>
<td>3650 calBC</td>
<td>A, M3, C80, N, RF</td>
<td>189c 270t</td>
<td>U5b1</td>
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<tr>
<td></td>
<td>Dudka 3</td>
<td>Cultural context</td>
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<td>189c 265 g 270t</td>
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<td>Drestwo 2</td>
<td>Ua-13085: 3805 ± 70 BP</td>
<td>ca. 2250 calBC</td>
<td>D, M4, C102, N, RF</td>
<td>192t 256t 270t</td>
<td>U5a</td>
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<td>Chekalino IVa</td>
<td>14C date on shell</td>
<td>7800 calBC</td>
<td>A, D, M2, C83, Rf</td>
<td>192t 256t 270t 294t</td>
<td>U5a</td>
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<td>Chekalino IVb</td>
<td>14C date on shell and cultural context</td>
<td>8000–7000 calBC</td>
<td>A, D, M2, C60, Rf</td>
<td>192t 241a/c</td>
<td>U5a1</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>192t 256t 270t 399 g</td>
<td></td>
<td></td>
<td></td>
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<td>Germany</td>
<td>Bad Dürrenberg 2</td>
<td>OxA-3136: 7930 ±90 BP</td>
<td>ca. 6850 calBC</td>
<td>A, D, M2, C 1 19, RF</td>
<td>356c</td>
<td>U4</td>
</tr>
<tr>
<td></td>
<td>Hohlenstein-Stadel, 5830a</td>
<td>ETH-5732: 7835 ± 80 BP</td>
<td>ca. 6700 calBC</td>
<td>M1, SNP</td>
<td>114a 192t</td>
<td>U5a1</td>
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<td>Hohlenstein-Stadel, 5830b</td>
<td>ETH-5732: 7835 ± 80 BP</td>
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<td>M1, SNP</td>
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<td>Magdalenián</td>
<td>M2, SNP</td>
<td>192t 270t</td>
<td>U5a</td>
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<td>(H 5312-4907: 12,770 ± 110 BP; H 5119-4601: 13,085 ± 95 BP) and cultural context</td>
<td>ca. 13,400 calBC</td>
<td></td>
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<td>n.d.</td>
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<td>(H 5312-4907: 12,770 ± 110 BP; H 5119-4601: 13,085 ± 95 BP) and cultural context</td>
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<td>Falkensteiner Höhle, FH</td>
<td>ETH-7615: 8185 ± 80 BP</td>
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<td>M2, SNP</td>
<td>n.d.</td>
<td>U5b2</td>
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<td>A, M2, C18</td>
<td>224c 311c</td>
<td>K</td>
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<td>A, M2, C16</td>
<td>270t</td>
<td>U5</td>
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<td>093y 153a 294t</td>
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<td>14C dates and context</td>
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<td>T2e</td>
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<td>14C dates and context</td>
<td>ca. 2950 calBC</td>
<td>A, M3</td>
<td>168t 192t 256t 270t 302 g</td>
<td>U5a</td>
</tr>
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*Radiocarbon dates with laboratory numbers refer to direct dates of the skeleton and were calibrated with the program CalPal (23) on the basis of Intcal04. Corrections of reservoir effects were applied where identified.
Ribosomal Protein S6 Kinase 1 Signaling Regulates Mammalian Life Span

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Caloric restriction (CR) protects against aging and disease, but the mechanisms by which this affects mammalian life span are unclear. We show in mice that deletion of ribosomal S6 protein kinase 1 (S6K1), a component of the nutrient-responsive mTOR (mammalian target of rapamycin) signaling pathway, led to increased life span and resistance to age-related pathologies, such as bone, immune, and motor dysfunction and loss of insulin sensitivity. Deletion of S6K1 induced gene expression patterns similar to those seen in CR or with pharmacological activation of adenosine monophosphate (AMP)–activated protein kinase (AMPK), a conserved regulator of the metabolic response to CR. Our results demonstrate that S6K1 influences healthy mammalian life span and suggest that therapeutic manipulation of S6K1 and AMPK might mimic CR and could provide broad protection against diseases of aging.

Genetic studies in Saccharomyces cerevisiae, Caenorhabditis elegans, and Drosophila melanogaster imply several mechanisms in the regulation of life span. These include the insulin and insulin-like growth factor 1 (IGF-1) signaling (IIS) pathway and the mammalian target of rapamycin (mTOR) pathway, which both activate the downstream effector ribosomal protein S6 kinase 1 (S6K1) (1, 2). Although the role of these pathways in mammalian aging is less clear, there is mounting evidence that IIS regulates life span in mice (1). Global deletion of one allele of the IGF-1 receptor (Igf1r), adipose-specific deletion of the insulin receptor (Insr), global deletion of insulin receptor substrate protein 1 (Insr1), or neuron-specific deletion of Insr2, all increase mouse life span (1). Life-span-extending mutations in the somatotropic axis also appear to work through attenuated IIS (3). Igf1r has also been implicated as a modulator of human longevity (4). However, the action of downstream effectors of IIS or mTOR signaling in mammalian longevity is not fully understood.

S6K1 transduces anabolic signals that indicate nutritional status to regulate cell size and

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14. Information on materials and methods is available as supporting material on Science Online.
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