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Kinship-based social inequality in Bronze Age Europe

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Revealing and understanding the mechanisms behind social inequality in prehistoric societies is a major challenge. By combining genome wide data, isotopic evidence as well as anthropological and archaeological data, we go beyond the dominating supra-regional approaches in archaeogenetics to shed light on the complexity of social status, inheritance rules and mobility during the Bronze Age. We apply a deep micro-regional approach and analyze genome wide data of 104 human individuals deriving from farmstead-related cemeteries from the Late Neolithic to the Middle Bronze Age in southern Germany. Our results reveal that individual households lasting several generations consisted of a high-status core family and unrelated low-status individuals, a social organization accompanied by patrilocality and female exogamy, and the stability of this system over 700 years.

Archaeogenetic research of human remains from Central Europe has generally focused on supra-regional and long-term genetic developments, revealing several major prehistoric genetic turnovers (1–3). These studies, mostly conducted on a continental scale, cannot fully uncover the complex role of individuals within these processes. It is assumed that the Early Bronze Age (EBA) saw an increase in hierarchical social structures as evidenced by the establishment of princely graves (4–6). Furthermore, isotopic evidence suggests the existence of a long-lasting exogamous marriage network that strengthened contacts over wide regions (7–9).

Here we present high-resolution genetic, archaeological and isotopic data from the southern German Lech River valley (Fig. 1 and figs. S1 to S4) which was densely populated with small farmsteads from the Late Neolithic to the Middle Bronze Age (MBA) (6). We produced genome-wide data for 118 ancient individuals by enriching DNA sequencing libraries for a panel of ~1.2 million single nucleotide polymorphisms (1240K SNP set) informative about genetic ancestry (6, 10) (tables S1 and S2). Employing standard quality criteria (6), 104 individuals were selected for pairwise kinship analysis, in a total of 13,806 analyzed pairs, which resulted in 3,633 usable pairs of individuals with more than 10,000 overlapping SNPs. Based on kinship results and more stringent quality criteria, 55 unrelated individuals were selected for population genetic analyses. Of these, two were associated

with the Corded Ware Culture (CWC; ca. 2750–2460 BC), ten with the Bell Beaker Complex (BBC, ca. 2480–2150 BC) (11), 34 with the EBA (ca. 2150–1700/1500 BC) and nine with the MBA (ca. 1700–1300 BC). We merged this dataset with previously published data from 993 ancient individuals (table S3), 1129 modern individuals typed on the Affymetrix Human Origins Array (1, 3, 12, 13) and 300 high coverage genomes from the Simons Genome Diversity Project (14). In addition, strontium and oxygen isotope data were generated for 139 Lech valley individuals to provide information on their mobility during lifetime (table S4).

We projected our samples together with previously published ancient individuals onto a scaffold of modern western Eurasian individuals via principal component analysis (PCA) (figs. S5A and S6). The Lech valley individuals fall within the European cline, stretching between Bronze Age pastoralists of the Pontic-Caspian steppe and Middle Neolithic and Chalcolithic Europeans. We quantified the variation along this cline using f_4 -statistics of the form $f_4(\text{Mbuti, Test}; \text{Yamnaya_Samara, Anatolia_Neolithic})$ and found that individuals carry significantly different amounts of Yamnaya_Samara- and Anatolia_Neolithic-related ancestries (Fig. 2A, figs. S5B and S7, and table S5), a variation that is significantly correlated to sample age ($P = 0.002$; t test for linear regression) (Fig. 2A) reflecting an increase over time in the proportion of Neolithic farmer ancestry. This is also seen

in the same f -statistic when grouping individuals by period (fig. S8). Estimating how many generations ago this admixture happened shows that the earlier dated individuals experienced more recent admixture in their ancestry in comparison to the individuals with younger dates (fig. S9 and table S6), suggesting pulse-like admixture rather than a long ongoing process. Using the *qpAdm/qpWave* framework (2, 12), we modeled the populations of the different time periods in the Lech valley as three-way mixtures of Western Hunter-Gatherers (WHG), Anatolian Neolithic farmers and Steppe pastoralists, confirming a gradual increase of Neolithic farmer-like ancestry (Fig. 2B and table S7) and revealing in the CWC individuals a significantly higher proportion of steppe-related ancestry on the autosomes when compared to the X-chromosome (z score = 3.13) (Fig. 2C and table S7). This is consistent with a proposed male sex bias for this ancestry in Central European Late Neolithic and Bronze Age populations (15). In contrast, the later Lech valley groups carry no significant sex bias. Most male individuals carry Y-chromosomal R1b-P312-lineage, the predominant male lineage in central and western Europe in the third millennium BC (2, 16) (table S8). Taken together, the evidence suggests that the population derived from a recent admixture of people of divergent ancestries, presumably incoming CWC-associated people with steppe-related ancestry, and locally established Middle Neolithic farmers (2, 13, 16). A possible explanation for the gradual increase of Neolithic farmer-like ancestry in the Lech valley is ongoing admixture with co-existing groups in other regions who experienced less gene flow from steppe-related populations (table S9).

Strontium and oxygen isotopic ratios revealed significantly more non-local females than males and children (figs. S10 and S11). Chi-square tests and ANOVA on Ranks confirmed that the isotope data of females and males as well as females and subadult individuals differed significantly, whereas differences between adult males and subadult individuals were not significant (6). This suggests patrilineal residential rules, with males predominantly staying, or at least being buried, with their families. Three of the adult males are exceptional as they exhibit a shift of strontium isotope ratios from their first to their third molars (fig. S12), indicating a movement away from their birthplaces during adolescence, and a return as adults. A similar analysis of early and late developing molars in females suggests that their movements from outside the Lech valley occurred in adolescence or later, as evidenced by non-local isotope ratios in early and late forming teeth (fig. S12).

To analyze kinship between individuals we used the software *lcMLkin* (17), as well as two additional approaches based on pairwise genetic differences (6, 18). *lcMLkin* estimates two key parameters from genotype likelihoods: the coefficient of relatedness, r , and the probability k_0 that no

alleles that are shared by a pair are identical-by-descent (IBD) (figs. S13 to S18 and table S10) (6). Together, the two parameters allow classification of pairs of individuals into (i) parent-offspring, (ii) siblings, (iii) second degree relatives, (iv) 3rd to 5th degree relatives, and (v) higher-order related and unrelated.

Almost all first- and second-degree relationships are found between pairs buried within the same burial site rather than individuals from different sites (38 of 39 total pairs) (fig. S16), while relationships between individuals buried at different sites are found to be only third-degree or higher with one exception of the half-sibling pair OBKR_76/POST_99 (fig. S16B). We reconstructed six pedigrees, three of which – at the EBA sites OBKR, WEHR and POST – span at least four generations (Fig. 3 and fig. S19). Of the ten parent-offspring pairs detected, six were between mother and offspring, and the offspring was male in all cases ($P = 0.001$, one-tailed binomial test), and in nine of the ten cases of adult age. This indicates that daughters rather than sons left their parental home, consistent with female exogamy/patrilineal residence as evidenced by the isotope data (figs. S20 to S25). Only one maternal lineage lasts longer than one generation (i.e., a mother and her children) based on mtDNA sharing, and the exception are two more distantly related females at AITI. In contrast, patrilineality is seen in a lineage at POST, which spans four or potentially five generations (Fig. 3). Moreover, male individuals who do not belong to the predominant paternal R1b-lineage have no close relatives buried at the same sites.

Certain types of grave goods, especially weapons (daggers, axes, chisels and arrow heads) in male graves and elaborate body adornments in female graves (large headdresses, massive leg rings) as well as pins in graves of both sexes are likely status-associated (18), according to the dominating view in archeology that rich burial goods indicate the deceased and/or their family's wealth and status (6). We observe a significant accumulation of grave goods among members of (multigenerational) families of both sexes within EBA cemeteries, evidenced by a correlation between the number of grave good types found and the rate of relatives of an individual ($P = 0.022$; t test for linear regression) (figs. S26 and S27 and table S11). When looking at males and females separately, this correlation remains significant for males ($P = 0.012$ vs. $P = 0.064$ for females; t test for linear regression) (fig. S27). Weapons appear significantly more often in graves of men with relatives than in the graves of men with no close relatives ($P = 0.025$, Fisher's exact test). At the site of WEHR only three of the sixteen individuals were very well equipped (fig. S1), a mother (WEHR_1586) and her two sons (WEHR_1474 and 1564), indicating that wealth and status were inherited by offspring from their parents. Subadults were also well-furnished and provided with high-status objects (e.g., POST_131,

OBKR_6, AITI_119) suggesting that their social status was inherited rather than acquired during their lifetime. Members of the core family were regularly buried in close spatial proximity (OBKR is an exception), highlighting their social cohesion (figs. S1 to S4). At POST, high status by grave goods is underlined by the construction of burial mounds (POST_50, POST_137) and marking of graves with alignments of wooden posts (POST_44, POST_50 and POST_137) (fig. S2). This indicates a connection between the affiliation to the core family and the elaborate form of burial practice.

Besides the group of biologically related and well-furnished burials, two other groups of burials were identified, which – according to radiocarbon dates – lived together with the members of the core families in each of the farmsteads (fig. S28). First, the group of non-local females with high strontium isotope values who arrived in the Lech valley from beyond the pre-Alpine lowlands (10) (figs. S10 to S25). These females are not part of any pedigree, but almost all of them were well furnished with burial goods (e.g., POST_32, OBKR_50) (fig. S25). Second, some individuals (e.g., AITI_50, UNTA85_1412) are not related to any other individual and poorly furnished in the grave. We find no significant differences in ancestry between these three groups (table S12 and fig. S29). Considering both grave furnishing and kinship, people of different status and biological relatedness likely lived together in the same household, which should therefore be seen as complex and socially stratified institutions.

We used our reconstructed family trees to improve direct dating of individuals by imposing constraints on age differences between individuals in a Bayesian approach (6, 19). In the cemetery at POST (Fig. 3 and table S13), pedigree-based Bayesian modeling decreased the calibrated ranges of the ¹⁴C ages in all individuals from an average 2-sigma error of 154 years with conventional calibration to 105 years on average an improvement of around 30% on average, confining the dating range of the entire family from 233 years to 169 years within the 2-sigma range (fig. S30).

The examination of ancient family structures and social inequality are key aspects of understanding social organization of ancient populations (18, 20–22). Conventionally, status differences in the EBA were assumed to exist between a large number of peasants and a small number of outstanding elites, which could have been wealthy farmers or princely leaders and their kin group who exerted social and economic control over large areas or populaces (6, 23). Here, we show a different kind of social inequality in prehistory, i.e., complex households that consisted of i) a higher-status core family, passing on wealth and status to descendants, ii) unrelated, wealthy and high-status non-local women and iii) local, low-status individuals. Based on comparisons of grave goods, several of the high-status non-local females could have come from areas inhabited by the Únětice culture (6), i.e.,

from a distance of at least 350 km. As the EBA evidence from most of Southern Germany is very similar to the Lech valley, we suggest that social structures comparable to our micro-region existed in a much broader area. The EBA households in the Lech valley, however, seem similar to the later historically known *oikos* (24), the household sphere of classic Greece, as well as the Roman *familia*, both comprising the kin-related family and their slaves (25). Only now, the deep history of intra-household inequality has become visible.

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SUPPLEMENTARY MATERIALS

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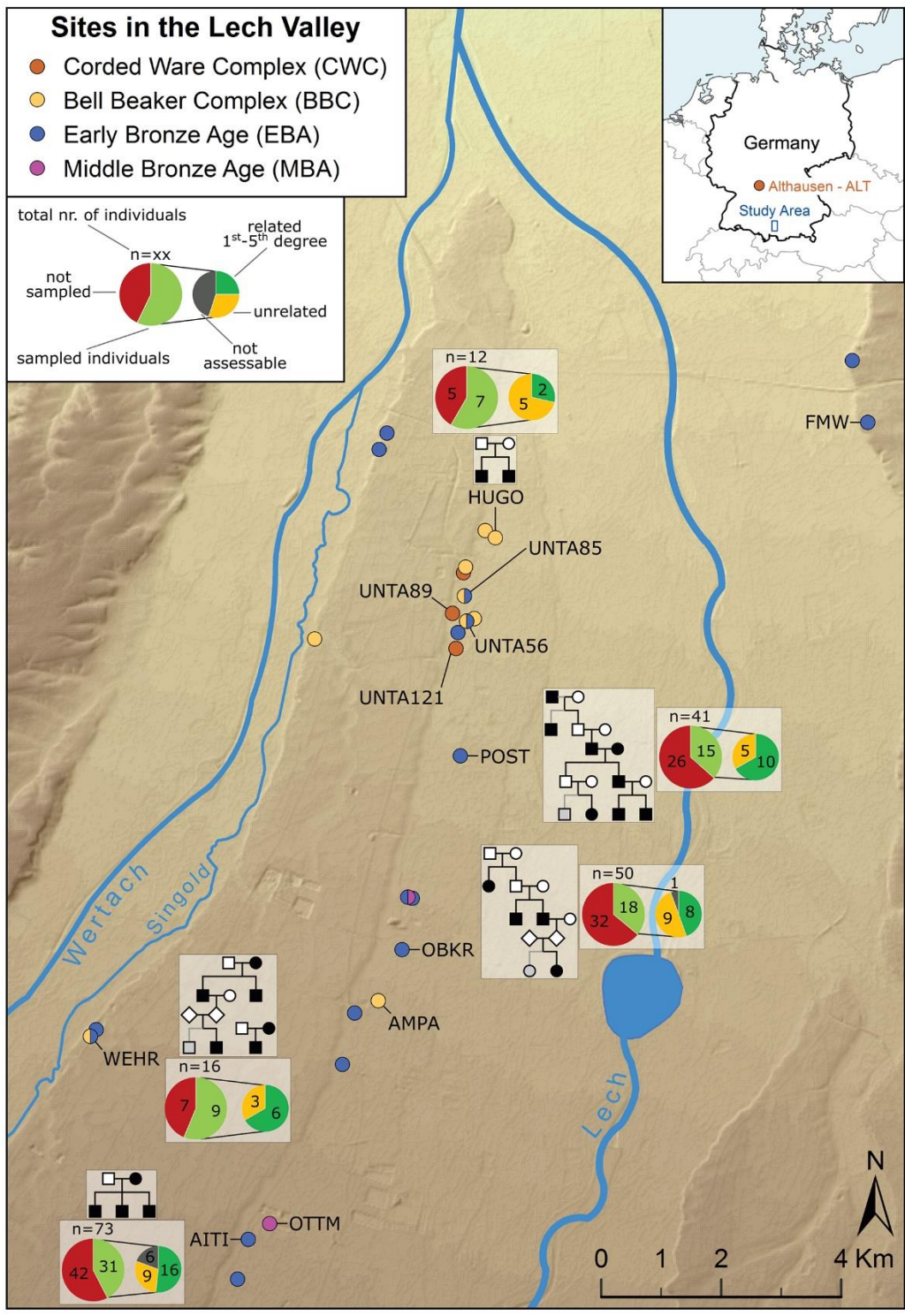


Fig. 1. The studied micro-region of the Lech valley in southern Germany. All sites of the region are mapped and marked according to their chronological assignment, sampled sites are labeled. Studied sites are supplemented by the established family trees and aDNA sample composition and results. Map generated with ArcGIS 10.5 using Copernicus data and information funded by the European Union – EU-DEM layers as a base map.

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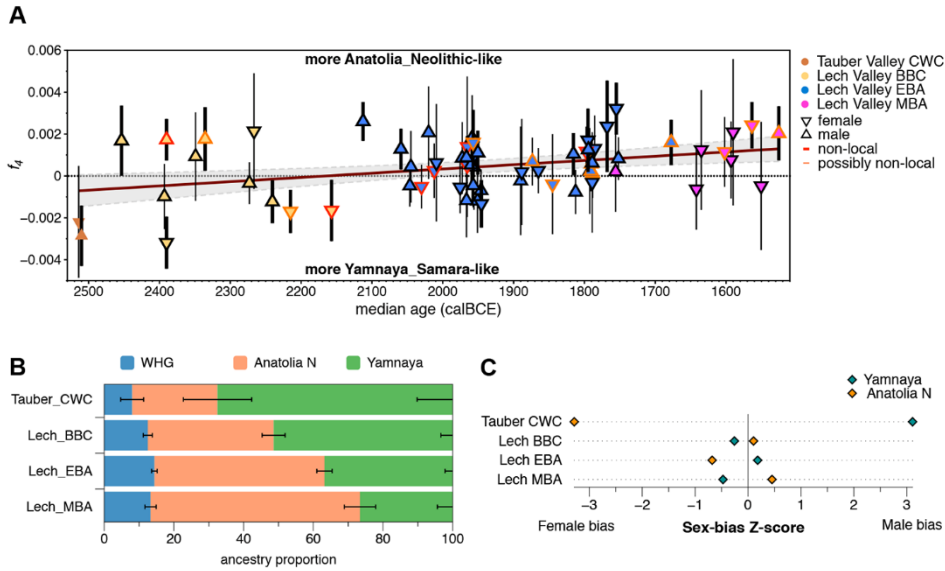


Fig. 2. Changes in ancestry over time. (A) Median ages of individuals plotted against z scores of f_4 (Mbuti, Test; Yamnaya_Samara, Anatolia_Neolithic) show increase of Anatolian farmer-related ancestry (indicated by more positive z scores) and decrease of variation in ancestry over time. Grey shading indicates significant z scores, red line shown linear correlation ($r = -0.35971$; $P = 0.003$) and dotted lines the 95% confidence interval. (B) ancestry proportions on autosomes calculated with *qpAdm*. (C) Sex-bias z scores between autosomes and X chromosomes show significant male bias for steppe-related ancestry in the CWC.

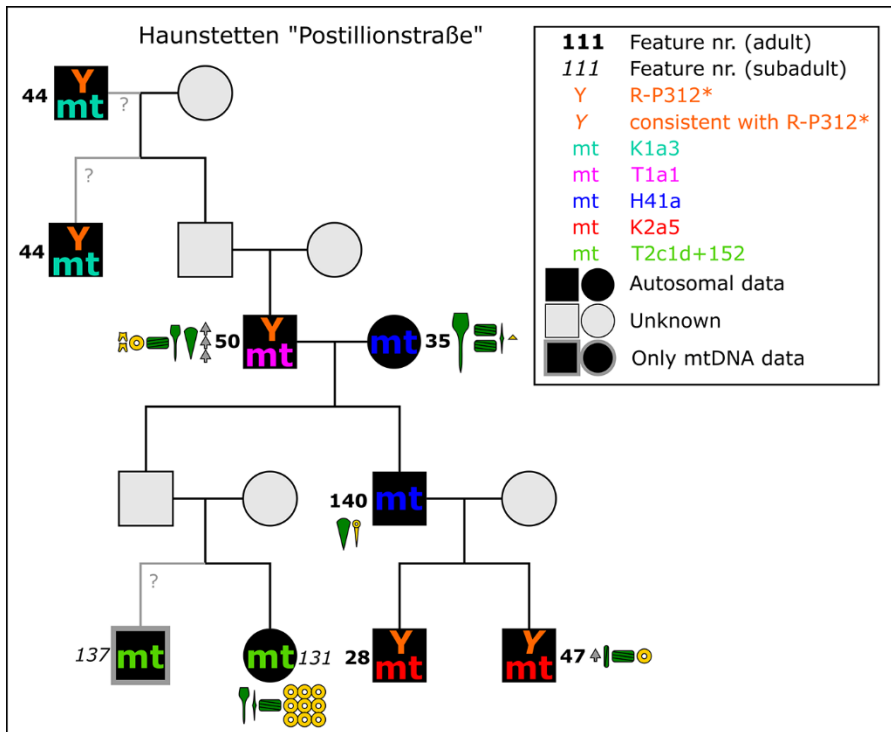


Fig. 3. Multigenerational pedigree found at the site POST. In this burial site at least four generations connected by a paternal lineage can be identified. Shared mtDNA haplotypes (table S1) are marked in the same color and where assignable the Y-haplogroup is indicated (table S8). Adult individuals are denoted by bold lettering and subadult individuals by italics. Kinship connections with a question mark are proposed on the basis of mtDNA haplotype sharing but not confirmed by nuclear DNA (Feat. 137) or represent several different possibilities to resolve the pedigree (Feat. 44). Grave goods associated with the individuals are shown alongside the position in the family tree.

Kinship-based social inequality in Bronze Age Europe

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