

ANCIENT SOCIOLOGY

Kinship-based social inequality in Bronze Age Europe

Alissa Mittnik^{1,2,3*}, Ken Massy⁴, Corina Knipper⁵, Fabian Wittenborn⁶, Ronny Friedrich⁵, Saskia Pfrengle², Marta Burri¹, Nadine Carlich-Witjes⁷, Heidi Deeg⁸, Anja Furtwängler², Michaela Harbeck⁹, Kristin von Heyking⁷, Catharina Kociumaka¹⁰, Isil Kucukkalpci², Susanne Lindauer⁵, Stephanie Metz^{6,11}, Anja Staskiewicz¹², Andreas Thiel¹³, Joachim Wahl¹⁴, Wolfgang Haak¹, Ernst Pernicka⁵, Stephan Schiffels¹, Philipp W. Stockhammer^{1,4*}, Johannes Krause^{1,2*}

Revealing and understanding the mechanisms behind social inequality in prehistoric societies is a major challenge. By combining genome-wide data, isotopic evidence, and anthropological and archaeological data, we have gone beyond the dominating supraregional approaches in archaeogenetics to shed light on the complexity of social status, inheritance rules, and mobility during the Bronze Age. We applied a deep microregional approach and analyzed 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 individual households, lasting several generations, that 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 supraregional 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 (tables S1 and S2) (6, 10). Using standard quality criteria (6), 104 individuals were selected for pairwise kinship analysis, in a total of 13,806 analyzed pairs, which resulted in 3633 usable pairs of individuals with more than 10,000 overlapping SNPs. On the basis of 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 Complex (CWC; ~2750 to 2460 BCE), 10 with the Bell Beaker Complex (BBC; ~2480 to 2150 BCE) (11), 34 with the EBA (~2150 to 1500 BCE), and nine with the MBA (~1700 to 1300 BCE). 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 by means of principal components 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 -statistics of the form $f_4(\text{Mbuti}, \text{Test}; \text{Yamnaya_Samara}, \text{Anatolia_Neolithic})$ 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 with 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), 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 with 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). By 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 BCE (table S8) (2, 16). 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 coexisting groups in other regions who experienced less gene flow from steppe-related populations (table S9).

Strontium and oxygen isotopic ratios revealed significantly more nonlocal females than males and children (figs. S10 and S11). χ^2 tests and analysis of variance 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 patrilocal residential rules, with males predominantly staying, or at least being buried, with their families. Three of the adult males are exceptional because 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

¹Department of Archaeogenetics, Max Planck Institute for the Science of Human History, 07745 Jena, Germany. ²Institute for Archaeological Sciences, Eberhard Karls University Tübingen, 72070 Tübingen, Germany. ³Department of Genetics, Harvard Medical School, Boston, MA 02115, USA. ⁴Institute for Pre- and Protohistoric Archaeology and Archaeology of the Roman Provinces, Ludwig-Maximilian University Munich, 80799 Munich, Germany. ⁵Curt Engelhorn Center for Archaeometry gGmbH, 68159 Mannheim, Germany. ⁶Heidelberg Academy of Sciences, 69117 Heidelberg, Germany. ⁷AnthroArch GbR, 82284 Grafath, Germany. ⁸Museumsverein Bad Mergentheim eV, 97980 Bad Mergentheim, Germany. ⁹State Collection for Anthropology and Palaeoanatomy, Bavarian Natural History Collections, 80333 Munich, Germany. ¹⁰Private address, 86672 Thierhaupten, Germany. ¹¹Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Direktion Landesarchäologie-Außenstelle Trier, 54290 Trier, Germany. ¹²Private address, 81247 Munich, Germany. ¹³State Office for Cultural Heritage Management Baden-Württemberg, 73728 Esslingen, Germany. ¹⁴State Office for Cultural Heritage Management Baden-Württemberg, 78467 Konstanz, Germany. *Corresponding author. Email: alissa_mittnik@hms.harvard.edu (A.M.); philipp.stockhammer@lmu.de (P.W.S.); krause@shh.mpg.de (J.K.)

by nonlocal 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) third- to fifth-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), whereas 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 Königsbrunn-Obere Kreuzstraße (OBKR), Wehringen-Hochfeld (WEHR), and Haunstetten-Postillionstraße (POST)—span at least four generations (Fig. 3 and fig. S19). Of the 10 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 10 cases was of adult age. This indicates that daughters rather than sons left their parental home, which is consistent with female exogamy and patrilocality, as evidenced by the isotope data (figs. S20 to S25). Only one maternal lineage lasts longer than one generation (a mother and her children) according to mitochondrial DNA (mtDNA) sharing, and the exception are two more distantly related females at Kleinaitingen-Gewerbegebiet Nord (AITI). By contrast, patrilocality 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 arrowheads) in male graves and elaborate body adornments in female graves (large headdresses and massive leg rings) as well as pins in graves of both sexes are likely status-associated, according to the dominating view in archeology that rich burial goods indicate the deceased and/or their family's wealth and status (6). We observed 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 ($P = 0.012$ versus $P = 0.064$ 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 16 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 (for example, POST_131, OBKR_6, and AITI_119), suggesting that their social status was inherited rather than acquired during their lifetime. Members of the core family were regularly buried in

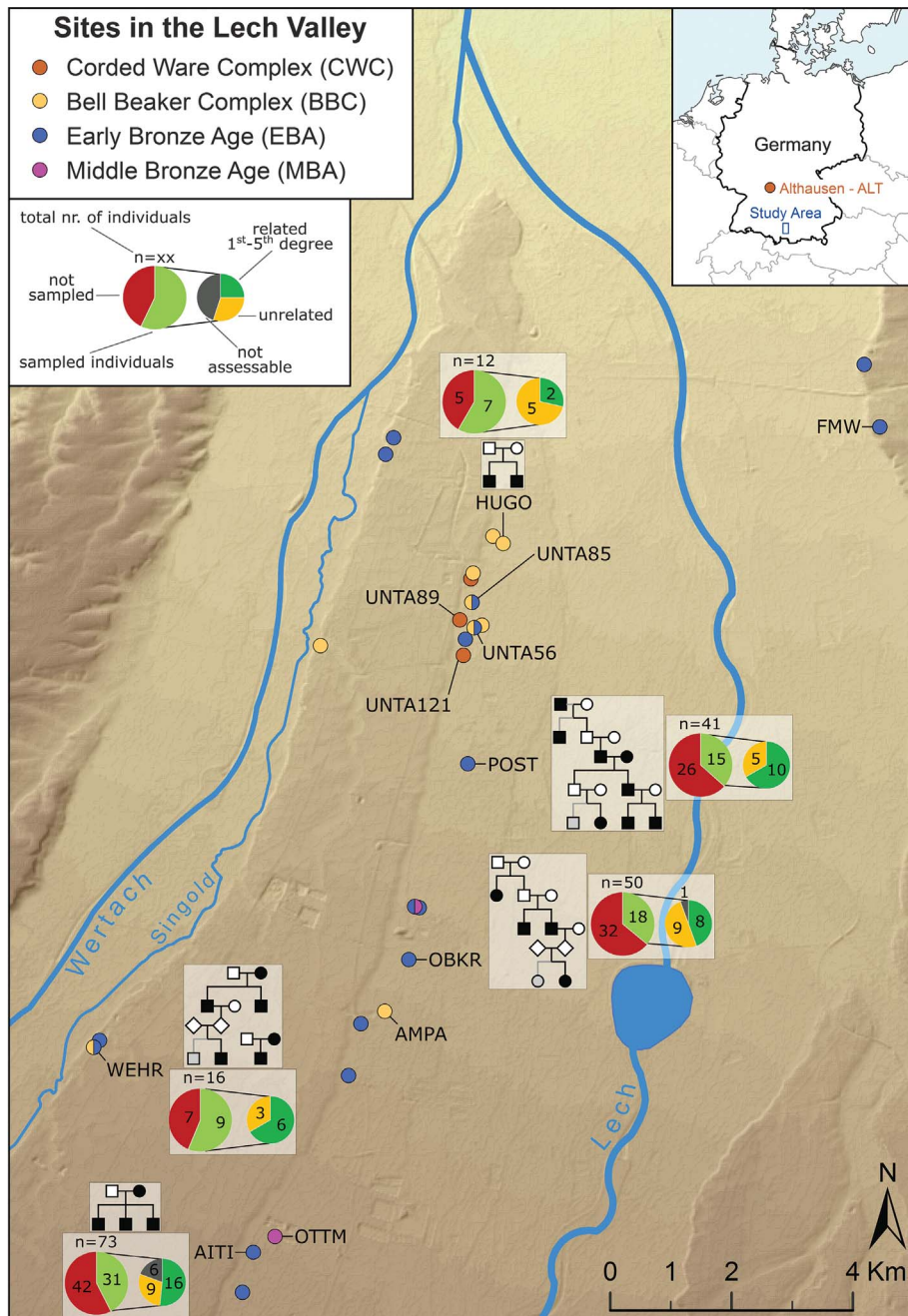
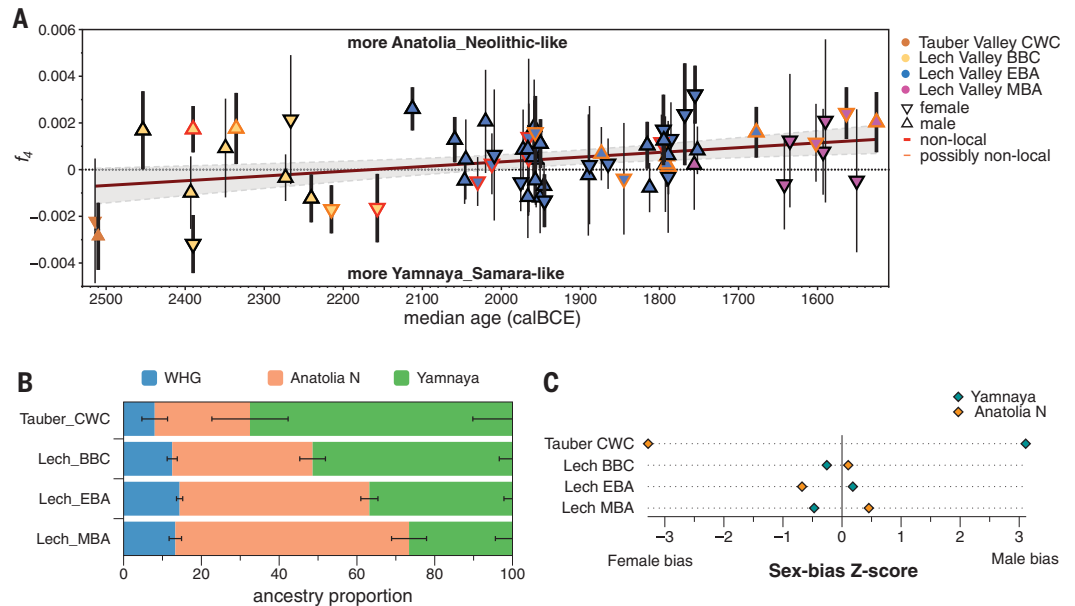


Fig. 1. The studied microregion of the Lech valley in southern Germany. All sites of the region are mapped and marked according to their chronological assignment; sampled sites are labeled. Studied sites are supplemented by the established family trees and ancient DNA sample composition and results.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

Fig. 2. Changes in ancestry

over time. (A) Median ages of individuals plotted against f_4 (Mbuti, Test; Yamnaya_Samara, Anatolia_Neolithic) show increase of Anatolian farmer-related ancestry (indicated by more positive f_4 values) and decrease of variation in ancestry over time. Error bars represent three times the standard error, thick error bars indicate significant z scores, the red line shown shows linear correlation ($r = -0.37481$; $P = 0.002$), and dotted lines indicate 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.



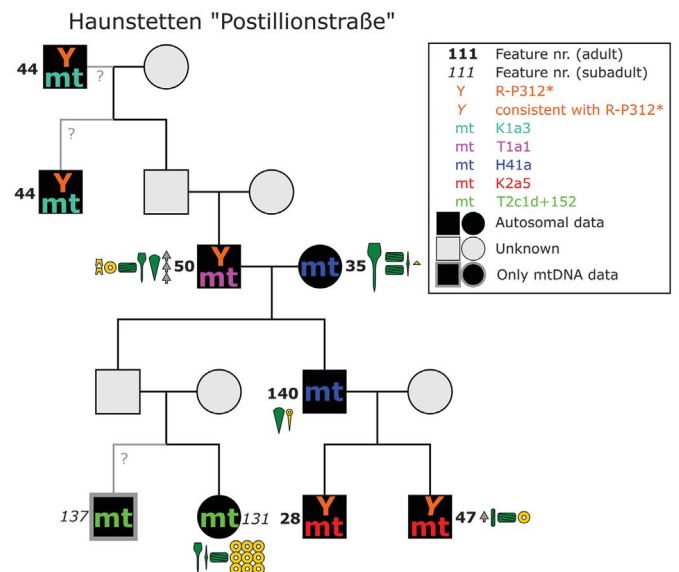
close spatial proximity (OBKR is an exception), highlighting their social cohesion (figs. S1 to S4). At POST, high status by grave goods is underlined by the construction of burial mounds (POST_50, POST_137) and marking of graves with alignments of wooden posts (POST_44, POST_50, and POST_137) (fig. 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). The first of these was the group of nonlocal females with high strontium isotope values who arrived in the Lech valley from beyond the pre-Alpine lowlands (figs. S10 to S25) (10). These females are not part of any pedigree, but almost all of them were well furnished with burial goods (for example, POST_32 and OBKR_50) (fig. S25). Second, some individuals (such as AITI_50 and UNTA85_1412) are not related to any other individual and poorly furnished in the grave. We found 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 ^{14}C ages in all individuals

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 with bold lettering, and subadult individuals are denoted with italics. Kinship connections with a question mark are proposed on the basis of mtDNA haplotype sharing but not confirmed with nuclear DNA (feature 137) or represent several different possibilities to resolve the pedigree (feature 44). Grave goods associated with the individuals are shown alongside the position in the family tree.



from an average 2σ error of 154 years with conventional calibration to 105 years on average, which is an improvement of ~30% on average, confining the dating range of the entire family from 233 years to 169 years within the 2σ range (fig. S30).

The examination of ancient family structures and social inequality are key aspects of understanding the 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 populations (6, 23). Here, we show a different kind of social inequality in prehistory: complex households that consisted of (i) a higher-status core family, passing on wealth and status to descendants; (ii) unrelated, wealthy, and high-status nonlocal women; and (iii) local, low-status individuals. On the basis of comparisons of grave goods, several of the high-status nonlocal females could have come from areas inhabited by the Únětice culture (6)—that is, from a distance of at least 350 km. Because the EBA evidence from most of Southern Germany is very similar to the Lech valley, we suggest that social structures comparable with our microregion

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 intrahousehold inequality has become visible.

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SUPPLEMENTARY MATERIALS

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Material and Methods
Supplementary Text
Figs. S1 to S31
Tables S1 to S14
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Ancient DNA informs on past cultures

Archaeology has used analysis of the artifacts and remains of people to uncover their past behaviors and to infer their cultural practices. However, establishing genetic relationships has only recently become possible. Mitnik *et al.* examined the kinship and inheritance of the remains of people from the German Lech River Valley over a time period spanning the Late Neolithic Corded Ware Culture, the Bell Beaker Complex, the Early Bronze Age, and the Middle Bronze Age (see the Perspective by Feinman and Neitzel). From genetic and archaeological analyses, it was revealed that the Early Bronze Age household's burials over multiple generations consisted of a high-status core family and unrelated low-status individuals. Furthermore, women were not related to the men within the household, suggesting that men stayed within their birth communities in this society, but women did not.

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