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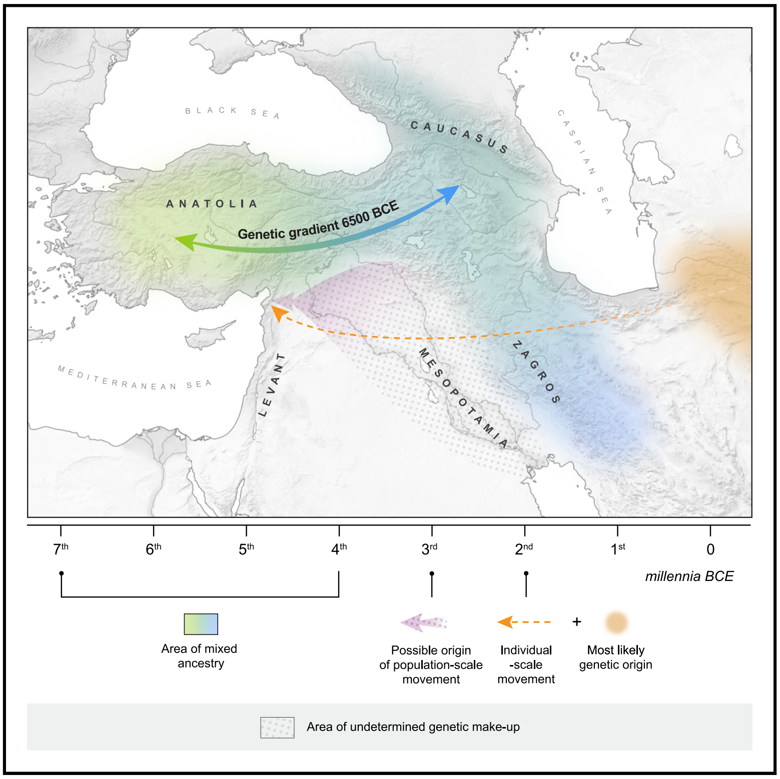
# Genomic History of Neolithic to Bronze Age Anatolia, Northern Levant, and Southern Caucasus

## Graphical Abstract




## Authors

Eirini Skourtanioti, Yilmaz S. Erdal, Marcella Frangipane, ..., Philipp W. Stockhammer, Wolfgang Haak, Johannes Krause

## Correspondence

warinner@fas.harvard.edu (C.W.), cwjeong@snu.ac.kr (C.J.), philipp.stockhammer@lmu.de (P.W.S.), haak@shh.mpg.de (W.H.), krause@shh.mpg.de (J.K.)

## In Brief

Reconstruction of genomic history of the Near East in a time transect spanning from the Neolithic through the globalization events of the Middle and Late Bronze Ages.

## Highlights

- Genome-wide analysis of 110 ancient individuals from the Near East
- Gene pools of Anatolia and Caucasus were biologically connected ~6500 BCE
- Gene flow from neighboring populations in Northern Levant during 3rd millennium BCE
- One individual of likely Central Asian origin in 2nd millennium BCE Northern Levant

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# Genomic History of Neolithic to Bronze Age Anatolia, Northern Levant, and Southern Caucasus

Eirini Skourtanioti,[1] Yilmaz S. Erdal,[2] Marcella Frangipane,[3] Francesca Balossi Restelli,[3] K. Aslıhan Yener,[4] Frances Pinnock,[3] Paolo Matthiae,[3] Rana Özbal,[5] Ulf-Dietrich Schoop,[6] Farhad Guliyev,[7] Tufan Akhundov,[7] Bertille Lyonnet,[8] Emily L. Hammer,[9] Selin E. Nugent,[10] Marta Burri,[1] Gunnar U. Neumann,[1] Sandra Penske,[1] Tara Ingman,[5] Murat Akar,[11] Rula Shafiq,[12] Giulio Palumbi,[13] Stefanie Eisenmann,[1] Marta D'Andrea,[3] Adam B. Rohrlach,[1,14] Christina Warinner,[1,15,*] Choongwon Jeong,[1,16,*] Philipp W. Stockhammer,[1,17,*] Wolfgang Haak,[1,*] and Johannes Krause[1,18,*]

[1]Department of Archaeogenetics, Max Planck Institute for the Science of Human History, Jena 07745, Germany
[2]Department of Anthropology, Hacettepe University, Ankara 06800, Turkey
[3]Department of Classics, Sapienza University of Rome, Rome 00185, Italy
[4]Institute for the Study of the Ancient World (ISAW), New York University, New York, NY 10028, USA
[5]Department of Archaeology and History of Art, Koç University, Istanbul 34450, Turkey
[6]School of History, Classics and Archaeology, University of Edinburgh, Edinburgh EH8 9AG, UK
[7]Institute of Archaeology and Ethnography, Azerbaijan National Academy of Sciences, Baku AZ1073, Azerbaijan
[8]PROCLAC/UMR Laboratory, French National Centre for Scientific Research, UMR 7192, Paris 75005, France
[9]Near Eastern Languages and Civilizations, University of Pennsylvania, Philadelphia, PA 19104, USA
[10]School of Anthropology and Museum Ethnography, University of Oxford, Oxford OX2 6PE, UK
[11]Department of Archaeology, Mustafa Kemal University, Alahan-Antakya, Hatay 31060, Turkey
[12]History Department, Ibn Haldun University, Istanbul 34494, Turkey
[13]Université Nice Sophia Antipolis, CEPAM (Cultures et Environnements. Préhistoire, Antiquité, Moyen Âge), CNRS-UMR 7264, Nice 06357, France
[14]ARC Centre of Excellence for the Mathematical and Statistical Frontiers, The University of Adelaide, Adelaide, SA 5005, Australia
[15]Department of Anthropology, Harvard University, Cambridge, MA 02138, USA
[16]School of Biological Sciences, Seoul National University, Seoul 08826, Republic of Korea
[17]Institute for Pre- and Protohistoric Archaeology and Archaeology of the Roman Provinces, Ludwig Maximilian University, Munich 80539, Germany
[18]Lead Contact
*Correspondence: warinner@fas.harvard.edu (C.W.), cwjeong@snu.ac.kr (C.J.), philipp.stockhammer@lmu.de (P.W.S.), haak@shh.mpg.de (W.H.), krause@shh.mpg.de (J.K.)
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## SUMMARY

**Here, we report genome-wide data analyses from 110 ancient Near Eastern individuals spanning the Late Neolithic to Late Bronze Age, a period characterized by intense interregional interactions for the Near East. We find that 6$^{th}$ millennium BCE populations of North/Central Anatolia and the Southern Caucasus shared mixed ancestry on a genetic cline that formed during the Neolithic between Western Anatolia and regions in today's Southern Caucasus/Zagros. During the Late Chalcolithic and/or the Early Bronze Age, more than half of the Northern Levantine gene pool was replaced, while in the rest of Anatolia and the Southern Caucasus, we document genetic continuity with only transient gene flow. Additionally, we reveal a genetically distinct individual within the Late Bronze Age Northern Levant. Overall, our study uncovers multiple scales of population dynamics through time, from extensive admixture during the Neolithic period to long-distance mobility within the globalized societies of the Late Bronze Age.**

## INTRODUCTION

Since the beginnings of agriculture, the Near East has been an influential region in the formation of complex and early state-level societies and has drawn considerable research interest in archaeology since the 19$^{th}$ century (Killebrew and Steiner, 2014; McMahon and Steadman, 2012). Developments in the field of ancient DNA (aDNA) over the last decade have shed light onto questions related to the process of Neolithization. Near Eastern farmers from South-Central Anatolia, the Southern Levant, and Northwestern Iran were descended from local foragers, and the transition from foraging to farming in these areas was shown to have been a biologically continuous process with only minor gene flow among them

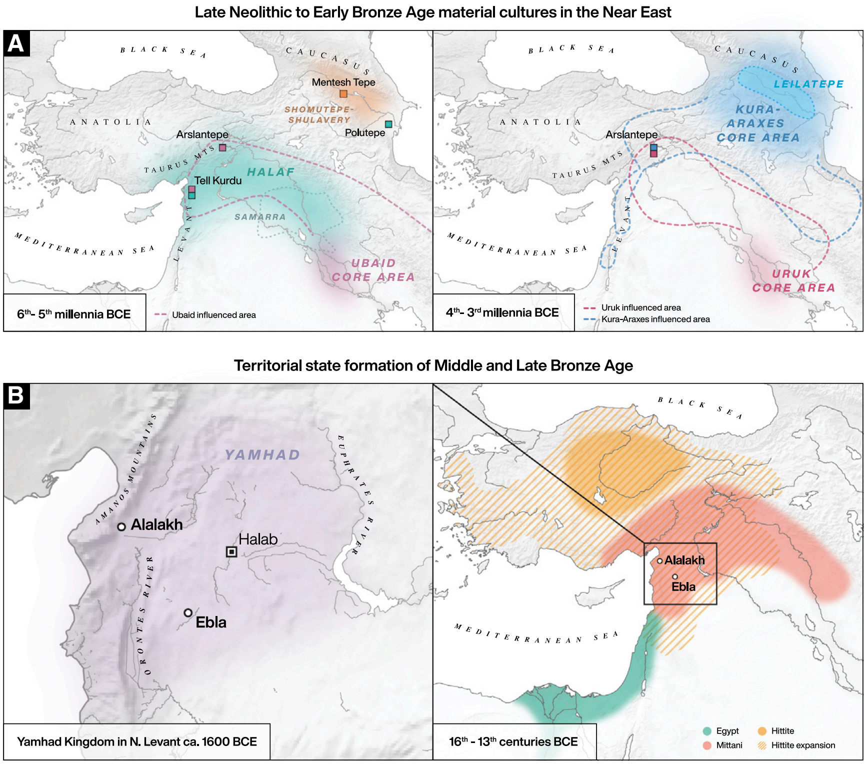



**Figure 1. Cultural Developments and Territorial State Formation in Western Asia (Near East) from the 6th to the 2nd Millennia BCE**

(A) Approximate areas where important material cultures mentioned in the text developed between the 6th and 3rd millennia BCE. Approximate expansion range of these cultures outside of their proposed original land is given (dashed lines). Archaeological sites related to our study that have been influenced by these cultures are plotted in corresponding colors.

(B) Territorial shifts between Bronze Age kingdoms from the 16th to the 13th centuries BCE and location of studied sites Alalakh and Ebla.

See also Figure S2.

(Broushaki et al., 2016; Feldman et al., 2019; Lazaridis et al., 2016).

Almost two millennia later, this situation had changed. In contrast to these Early Holocene populations, Chalcolithic/Eneolithic and Bronze Age populations from Western and Central Anatolia, the Southern Levant, Iran (Zagros), and the Caucasus show less genetic differentiation from each other, suggesting that these later periods were characterized by an extensive process of gene flow spanning a large area (Allentoft et al., 2015; de Barros Damgaard et al., 2018; Haber et al., 2017; Harney et al., 2018; Jones et al., 2015; Lazaridis et al., 2016, 2017; Wang et al., 2019). However, the spatiotemporal scope of this process is poorly understood because of the lack of ancient genomes from areas that bridge these distant regions (i.e., Central and Eastern Anatolia) that, in turn, requires denser sampling. To date, the spatial distribution of features attributed to the ''Neolithic package'' across Anatolia suggests a heterogeneous multiple-event process that correlates with broader geographical zones (Özdoğan, 2014). However, whether population movement played a prominent role in the formation of these zones within Anatolia remains an open question.

Throughout Western Asia, archaeological evidence for the movement of peoples, material, and/or ideas is well documented (Figure 1). In the Southern Caucasus, archaeological research indicates relations with Northern Mesopotamia during the Late Neolithic (Halaf and Samarra cultures) (Badalyan et al., 2010; Nishiaki et al., 2015), and in Eastern Anatolia, a network of cultural connections marked by several expansive events, mostly related to the Mesopotamian world, is attested. These include an early intrusion of the South Mesopotamian Ubaid culture into Upper Mesopotamia as far as the Taurus mountains of Southeastern Anatolia during the 5th millennium BCE (Frangipane, 2015a; Carter and Philip, 2010). It was followed, in the Southern Caucasus, by a strong influence at this time from Upper Mesopotamia during the late 5th–mid 4th millennium (Lyonnet, 2007; Lyonnet, 2012). From the middle to the end of the 4th millennium, another Southern Mesopotamian influence (the so-called ''Middle and Late Uruk expansion'') reached Upper Mesopotamia and the upper stretches of the Euphrates and Tigris river valleys in Eastern Anatolia (Allen and Rothman, 2004). At the same time, during the second half of the 4th millennium BCE, the Kura-Araxes culture, which is generally thought to originate in the Southern Caucasus, expanded outward around 3000–2900 BCE, spreading westward to Eastern Anatolia and the Northern and Southern Levant (Palumbi, 2017; Palumbi and Chataigner, 2014) and eastward to Iran (Rothman, 2011). Evidence of these events comes from numerous excavations and is especially apparent in the long and extensively excavated sequence of occupations at Arslantepe in the Malatya plain of Eastern Anatolia. In the Northern Levant, material connections with Northern Mesopotamia start appearing in the 4th millennium BCE and have been attributed to either extensive cultural contacts or population movements.

The major question is, therefore: what was moving? Was this a movement of populations, material culture, ideas, or some combination? These earlier developments lead to the increasing ''globalization'' in the Eastern Mediterranean basin from the Middle Bronze Age (MBA) onward, which is characterized by an intensification of resource exploitation and management through connected sea and land routes (Akar, 2013; Feldman, 2006; Hodos, 2017). However, the role of human mobility is unclear and a challenging question to address due to the scarcity of Middle and Late Bronze Age (LBA) burials. In this regard, the site of Alalakh in the Amuq Valley (Turkey), with more than 300 burials dated to that period, represents an exceptional case for the application of aDNA studies.

Understanding the nature of this movement was the primary motivation behind this study. Here, we present a large-scale analysis of genome-wide data from key sites of prehistoric Anatolia, the Northern Levant, and the Southern Caucasian lowlands. Our goal was to reconstruct the genomic history of this part of the Near East by systematically sampling across this transition from the Neolithic to the interconnected societies of the MBA and LBA. Our new ancient genome-wide dataset consists of 110 individuals and encompasses four regional time transects in Central/North Anatolia, East Anatolia, the Southern Caucasian lowlands, and the Northern Levant, each spanning 2,000 to 4,000 years of Near Eastern prehistory. We find that mid-6$^{th}$ millennium populations from North/Central Anatolia and the Southern Caucasian lowlands were closely connected; they formed a genetic gradient (cline) that runs from Western Anatolia to the Southern Caucasus and Zagros in today's Northern Iran. This cline formed after an admixture event that biologically connected these two regions ca. 6500 BCE. Chalcolithic and Bronze Age populations across Anatolia also mostly descended from this genetic gradient. In the Northern Levant, by contrast, we identified a major genetic shift between the Chalcolithic and Bronze Age periods. During this transition, Northern Levantine populations experienced gene flow from new groups harboring ancestries related to both Zagros/Caucasus and the Southern Levant. This suggests a shift in social orientation, perhaps in response to the rise of urban centers in Mesopotamia, which to date remain genetically unsampled.

## RESULTS

### Sample Corpus and Data Compilation

We report genome-wide data from a targeted set of ~1.24 million ancestry-informative SNPs for 110 individuals from Anatolia, the Northern Levant, and the Southern Caucasian lowlands spanning ~4,000 years of prehistory. Nine of these individuals date to Late Neolithic/Early Chalcolithic ("LN/EC"; 6$^{th}$ millennium BCE) and come from three different geographic sectors: the Central/Northern Anatolian Boğazköy-Büyükkaya, the Amuq Valley in Southern Anatolia/Northern Levant (Tell Kurdu), and the Southern Caucasian lowlands (Mentesh Tepe and Polutepe) (Figure 2A). The remaining 101 individuals date from the Late Chalcolithic to the Late Bronze Age ("LC-LBA"; 4$^{th}$–2$^{nd}$ millennia BCE) and were collected from the following archaeological sites: Alalakh (modern Tell Atchana), Alkhantepe, Arslantepe, Ebla (modern Tell Mardikh), Çamlıbel Tarlası, İkiztepe, and Titriş Höyük (Figure 2A).

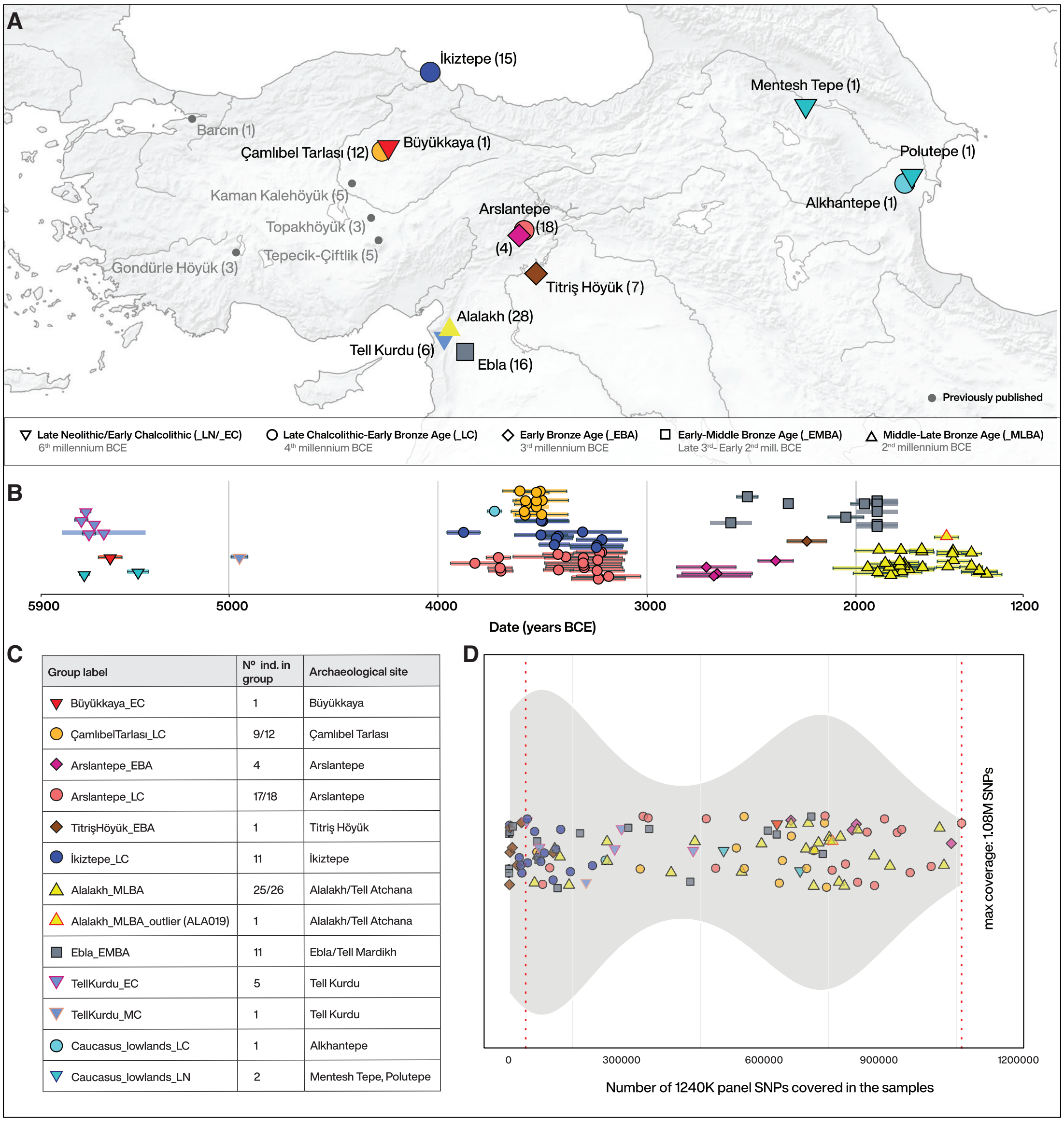
For in-depth population genetic analyses, we excluded a total of 16 individuals that did not meet quality requirements (e.g., SNP coverage, absence of damage patterns, contamination). All the remaining individuals showed damage patterns expected for ancient samples and had low contamination estimates ($\leq$5% for all but one, which has 10%). Overall, we performed genetic analyses on genome-wide data from 94 individuals, and 77 of these were accelerator mass spectrometry (AMS) radiocarbon dated (Figure 2B; Table S1). We grouped the individuals by archaeological site or area and archaeological period applying a nomenclature scheme that preserves this information (Figure 2C; STAR Methods). We also identified seven cases of 1$^{st}$ or 2$^{nd}$ degree relative pairs (Figure S1; Table S2) and restricted group-based genetic analyses for these groups (*f*-statistics, *qpWave*/*qpAdm*, and DATES) to 89 unrelated ($\geq$3$^{rd}$ degree) individuals (Figure 2C).

We merged our dataset with genetic data from ca. 800 previously published ancient individuals (Table S3; STAR Methods). Among these, 17 Anatolian individuals from the following archaeological sites overlap with our time transect and were co-analyzed with the Anatolian groups from our study: Tepecik-Çiftlik (Kılınç et al., 2016) ("Tepecik_N"), Barcın (Mathieson et al., 2015) ("Barcın_C"); Gondürle-Höyük (Lazaridis et al., 2017) ("GondürleHöyük_EBA"), Topakhöyük (de Barros Damgaard et al., 2018) ("Topakhöyük_EBA"), and Kaman-Kalehöyük (de Barros Damgaard et al., 2018) ("K.Kalehöyük_MLBA") (Figure 2A).

### The Late Neolithic/Early Chalcolithic Genetic Structure in Anatolia, Northern Levant, and Caucasian Lowlands

So far, our knowledge of the gene pool of Neolithic Anatolia has been limited to individuals from Barcın and Menteşe in Western Anatolia (abbreviated here as "Barcın_N") (Mathieson et al., 2015), Boncuklu from the Konya Plain in Central Anatolia (Feldman et al., 2019; Kılınç et al., 2016), and Tepecik-Çiftlik in Southern Anatolia (Kılınç et al., 2016). These individuals date from the 9$^{th}$ to the 7$^{th}$ millennium BCE and are succeeded by LN/EC individuals of this study. To overview the genetic structure in this Near Eastern region from the Neolithic to the Bronze Age, we first performed principal-component analysis (PCA) (Patterson et al., 2006; Price et al., 2006) of present-day West Eurasians populations and projected ancient individuals onto the top PCs (Figure 3A). Overall, LN/EC individuals are scattered along PC2 between Barcın_N and ancient individuals from Iran/Caucasus (Figure 3B). TellKurdu_EC are slightly shifted along PC1 toward Neolithic and Chalcolithic Levantine individuals. Büyükkaya_EC is positioned further away from any Neolithic Anatolian reported to date and toward the direction of Neolithic and Chalcolithic Iranian individuals. Caucasus_lowlands_LN (two individuals from Polutepe and Mentesh Tepe) are positioned upward along PC2, between Büyükkaya_EC and Chalcolithic Iran.

To formally test the qualitative differences observed in PCA, we compared the genetic affinity of LN/EC groups to earlier populations in Western Eurasia by computing $f_4$-statistics (Patterson et al., 2012) of the form $f_4$(*Mbuti*, *p2*; *p3*, *X*) (Figure 4). The statistic deviates from zero if a pair of Anatolian/Levantine/Caucasian groups (*p3* and *X*) differ from each other in their genetic affinities to Epipaleolithic and Neolithic populations (*p2*). We observe that Büyükkaya_EC and Caucasus_lowlands_LN differ from Barcın_N by sharing more alleles with Caucasus hunter-gatherers (CHG; Satsurblia and Kotias Klde caves) and Iran_N (Ganj Dareh site in Zagros mountains) than with Barcın_N (+2.2 to +5.5 SE), while sharing less alleles with hunter-gatherers from Western Europe (WHG) ($\leq -4.3$ SE), Early European Farmers (EEF) ($\leq -3.6$ SE), the Epipaleolithic Pınarbaşı individual from Anatolia ($\leq -6.8$ SE), and with the Neolithic/Epipaleolithic Levant ($-1.3$ to $-9.4$ SE). By summarizing the $f_4$-statistics using *qpAdm* (Haak et al., 2015), we can adequately model both Büyükkaya_EC and Caucasus_lowlands_LN as a two-way mixture of Barcın_N and Iran_N as source populations ($p \geq 0.083$; 24%–31% from Iran_N; Figure 4). Tepecik_N, which occupies an intermediate




| Group label | N° ind. in group | Archaeological site |
|---|---|---|
| Büyükkaya_EC | 1 | Büyükkaya |
| ÇamlıbelTarlası_LC | 9/12 | Çamlıbel Tarlası |
| Arslantepe_EBA | 4 | Arslantepe |
| Arslantepe_LC | 17/18 | Arslantepe |
| TitrişHöyük_EBA | 1 | Titriş Höyük |
| İkiztepe_LC | 11 | İkiztepe |
| Alalakh_MLBA | 25/26 | Alalakh/Tell Atchana |
| Alalakh_MLBA_outlier (ALA019) | 1 | Alalakh/Tell Atchana |
| Ebla_EMBA | 11 | Ebla/Tell Mardikh |
| TellKurdu_EC | 5 | Tell Kurdu |
| TellKurdu_MC | 1 | Tell Kurdu |
| Caucasus_lowlands_LC | 1 | Alkhantepe |
| Caucasus_lowlands_LN | 2 | Mentesh Tepe, Polutepe |

**Figure 2. Overview of Location, Ages, and Data Generation of Analyzed Individuals**

(A) Geographic location of archaeological sites with respective number of individuals with genetic data.

(B) Age of analyzed individuals in years BCE. Age is given as mean of the 2-sigma range of calibrated $^{14}$C date (black horizontal lines) or mean of their proposed archaeological range when direct $^{14}$C dates not available (colored thick lines).

(C) Grouping of individuals (after quality filtering) according to their location, time period and genetic profile. Number of individuals before and after removal of biological relatives is given when applicable.

(D) Distribution of SNP coverage across individuals. Only individuals within a certain coverage range (marked with red dotted lines) were included in downstream analyses.

See also Tables S1 and S2 and Figure S1.

position between Barcın_N and Büyükkaya_EC in the PCA, also fits the same model (p = 0.975; 22% from Iran_N). By replacing Iran_N with CHG, we still obtain a good model fit for Büyükkaya_EC (p $\geq$ 0.825; 24% from CHG), but not for Caucasus_lowlands_LN (p = 0.0001).

Consistent with their positions on the PCA plot, TellKurdu_EC does not fall on this cline of mixed Barcin_N-Iran_N ancestries but shows extra affinity with ancient Levantine populations. Accordingly, $f_4$-statistics of the form $f_4$(*Mbuti*, *Levant_N*; *X*, *TellKurdu_EC*) $\geq$3.3 SE, show that TellKurdu_EC has more affinity with the pre-pottery Neolithic Levantines ("Levant_N") than with any other Neolithic-Early Chalcolithic ("N-EC") Anatolian population including an almost 1,000-year younger individual from the same area (TellKurdu_MC). When compared to Barcın_N, TellKurdu_EC has significantly (<$-$4 SE) less affinity with Mesolithic hunter-gatherers from Western, Eastern, and Southeastern Europe

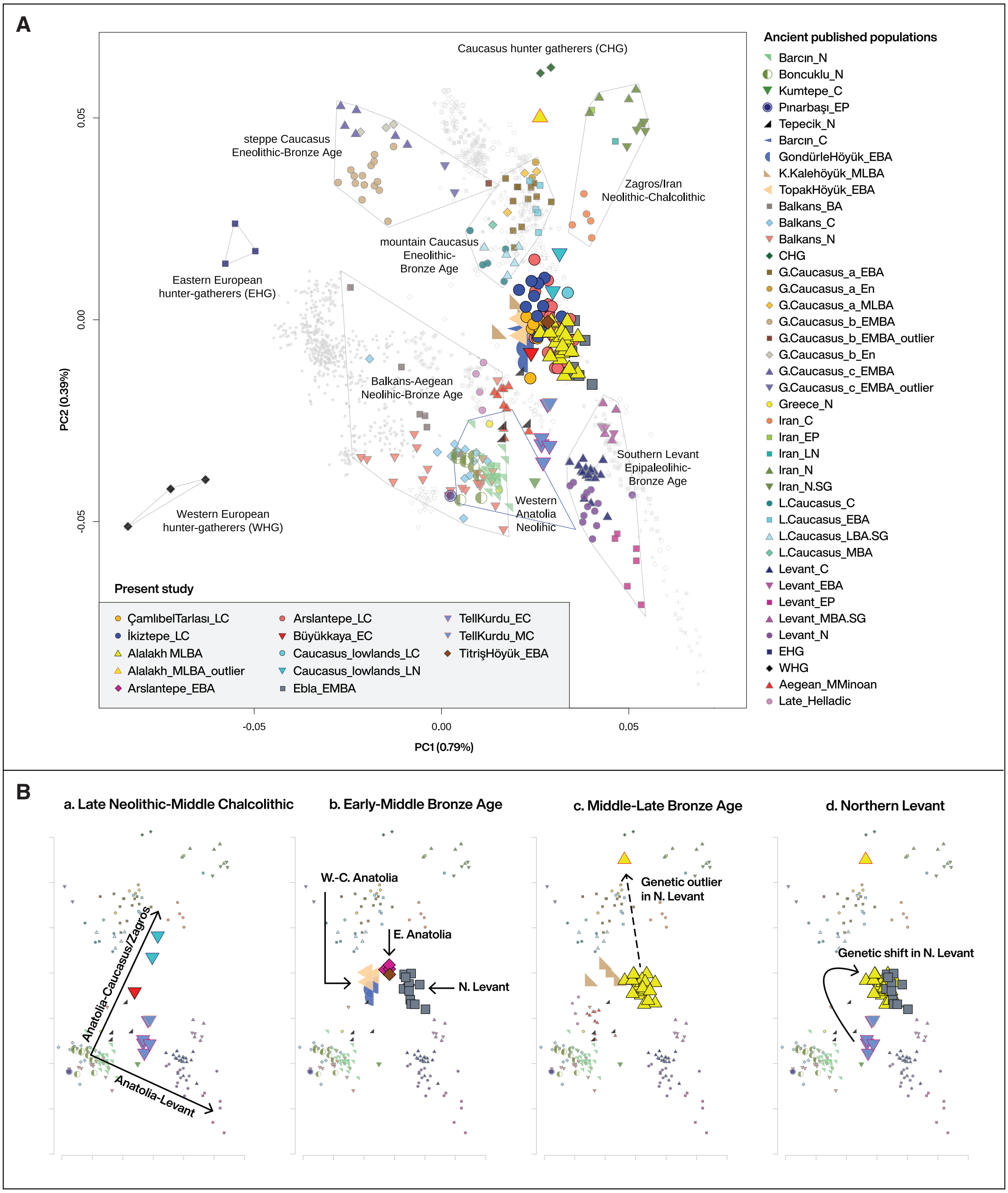



**Figure 3. Principal-Component Analysis**

Principal-component analysis (PCA) was computed on the Human Origins (HO) SNP panel data of present-day West Eurasian populations (gray symbols) and ancient individuals were projected on them.

(A) PC1 and PC2 for ancient individuals from the present study and selected from previous publications.

(B) PC1 and PC2 for individuals by archaeological time or geographic sector (a–d) with some of the important findings annotated.

(WHG, EHG, and Iron_Gates, respectively). The admixture model with Barcın_N+Iran_N/CHG used above is not supported for Tell-Kurdu_EC ($p < 1.47 \times 10^{-5}$). Instead, we can successfully model TellKurdu_EC as a three-way mixture of Barcın_N, Iran_N (or CHG), and Levant_N ($p = 0.298$; 15.5% ± 3.7% from Iran_N and 36.6% ± 7.1% from Levant_N; Figure 4).

## Neolithic Admixture and a Common Genetic Profile of Chalcolithic and Bronze Age Groups

In contrast to the LN/EC individuals, LC-LBA individuals form a dense cloud in the West Eurasian PCA, roughly falling mid-way along the LN-EC cline that is delimited by ancient groups from Iran, the Caucasus, the Levant and Western Anatolia. We

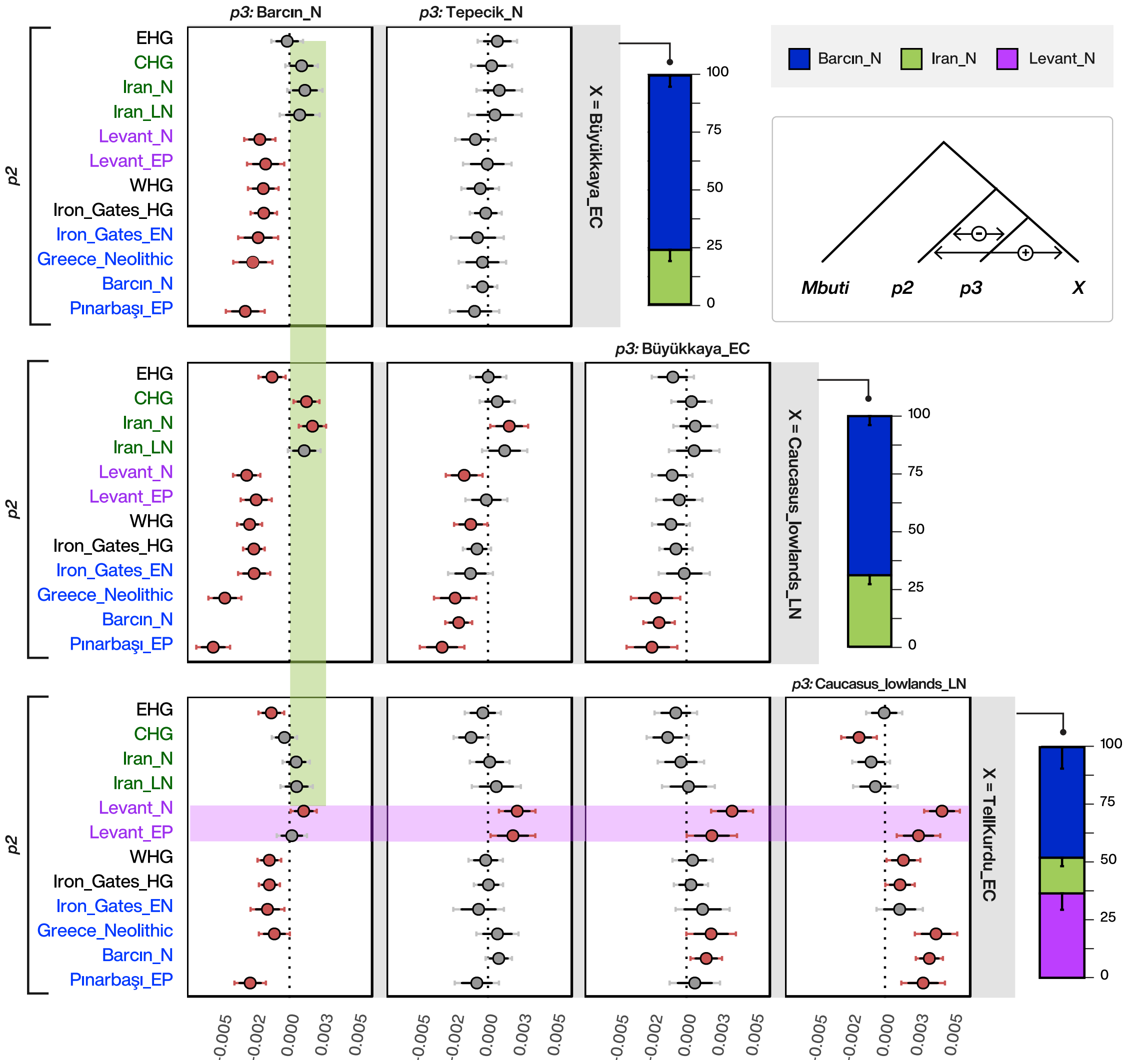



**Figure 4. Genetic Affinity of Late Neolithic/Early Chalcolithic Populations with Early Holocene Populations from Iran, Caucasus, and Levant Measured with $f_4$-Statistics and Quantified with *qpAdm***

$f_4$-statitstic tests whether either *p3* or *X* has excess affinity with *p2* and becomes negative or positive accordingly, as shown in the simplified tree. **S**E for $f_4$-statitstics are estimated by 5 cM block jackknifing and values that do not deviate from 0 in the ±3 SE are represented in gray color. All three groups have more affinity with Iran compared to Barcın_N (green bar), and TellKurdu_EC has the more Levantine affinity compared to all (purple bar). These affinities are reflected in the inferred *qpAdm* models on the right. Ancestry proportions are plotted with ±1 SE.

hypothesize that LC-LBA groups from Central/North and Eastern Anatolia may have descended from this older genetic structure and therefore share the same ancestry profile.

Consistent with PCA, outgroup-$f_3$ and $f_4$-statistics suggest a common genetic profile of the LC-LBA groups that is similar to that of the LN-EC cline. First, outgroup $f_3$(*Mbuti*; *LC-LBA*, *Test*), which measures the average shared genetic drift between LC-LBA and *Test* from their common outgroup Mbuti (Patterson et al., 2012), reached highest values when *Test* were Neolithic and Chalcolithic populations from Europe, Anatolia, and Northern Levant, such as Barcın_N, TellKurdu_EC, and Büyükkaya_EC (Table S4). Second, using Barcın_N and additionally TellKurdu_EC as local baselines, we computed $f_4$(*Mbuti*, *Test*; *Barcın_N/TellKurdu_EC*, *X*) to characterize the difference between Barcın_N or TellKurdu_EC and the LC-LBA groups (*X*) with respect to a set of ancient *Test* populations from West Eurasia (Table S5). Iran Neolithic and/or CHG consistently show excess affinity to LC-LBA when compared to TellKurdu_EC and Barcın_N. The Chalcolithic and Bronze Age populations from Iran (Iran_C from the Seh Gabi site) and the Caucasus (Allentoft et al., 2015; Lazaridis et al., 2016; Wang et al., 2019)—temporally closer to LC-LBA and located between Iran_N/CHG and LC-LBA in the PCA—also occasionally only share more alleles with some of the LC-LBA groups when compared to Barcın.

We further explored the temporal aspect of the shared admixed profile of LC-LBA groups by estimating their admixture dates using the recently developed method, DATES (M. Chintalapati, N. Patterson, N. Alex, and P. Moorjani, personal

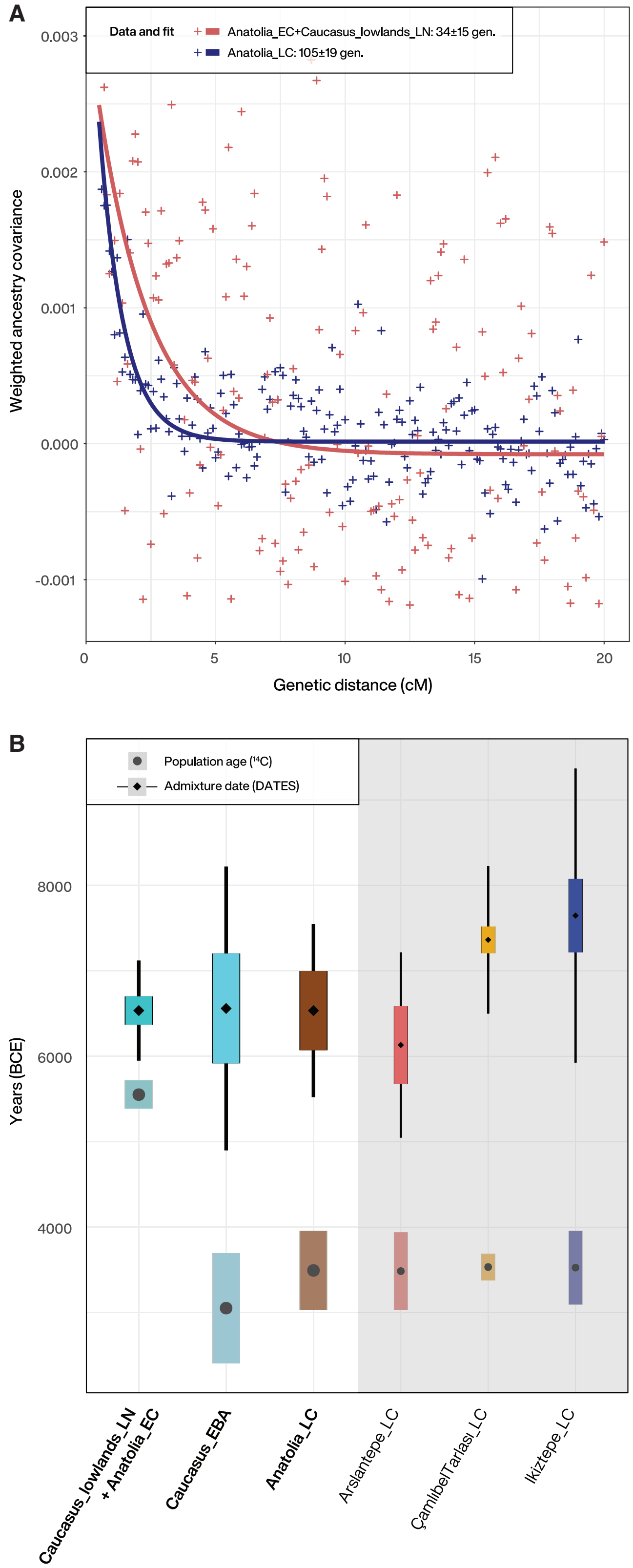



**Figure 5. Dating of Admixture in Anatolian and Caucasian Populations from the Late Neolithic to the Early Bronze Age**

(A) Decay of ancestry covariance estimated by DATES for Anatolia_EC (Büyükkaya_EC) and Caucasus_lowlands_LN grouped together and the three Late Chalcolithic populations Arslantepe_LC, ÇamlıbelTarslası_LC, and İkiztepe grouped as "Anatolia_LC."

(B) Conversion of admixture dates into calendar dates (upper part of plot) after including both the age range for each population calculated from direct $^{14}C$ dates (lower part of plot) and the ±1 SE from DATES. Average population and admixture dates are shown with black dot. Average admixture date for the three populations with grouped individuals (bold letters) is 6500 years BCE. Admixture dates for individual populations from Anatolian_LC span a wider time range.

communication) (STAR Methods). As we previously described, the LN-EC cline as varying proportions of Barcın_N and Iran_N/CHG ancestries, we selected both as source populations. However, given the small sample size of both Iran_N and CHG and the large number of missing SNPs in Iran_N, we also considered modern Caucasians (Armenians, Georgians, Azerbaijanis, Abkhazians, and Ingushians) as proxies of the second source population.

We focused on the three Late Chalcolithic groups with sufficiently large sample size and who are the earliest in time among the LC-LBA groups: ÇamlıbelTarlası_LC (n = 9), İkiztepe_LC (n = 11), and Arslantepe_LC (n = 17). Taking individual estimates from all these individuals together ("Anatolia_LC"), we obtain a robust admixture date estimate of 105 ± 19 generations ago when we use Barcın_N and modern Caucasians as proxies of the source gene pools (Figure 5A). Using a generation time of 28 years (Moorjani et al., 2016), this estimate equates to an admixture event ~3,000 years before the time of the LC-LBA individuals, corresponding to ~6500 years BCE (Figure 5B). We observe similar but noisier estimates from individual groups ÇamlıbelTarlası_LC, İkiztepe_LC, and Arslantepe_LC. Admixture dates estimated by two alternative methods, ALDER and rolloffp (STAR Methods), overall matched our estimates with DATES (Figure S2).

Encouraged by these results, we extended the analysis to other ancient populations that are on the Early Chalcolithic cline, including Caucasus_lowlands_LN and Büyükkaya_EC, published Early Bronze Age (EBA) individuals from the Caucasus (cluster a) (Wang et al., 2019; Lazaridis et al., 2016) (see Table S3 for group labels), as well as Iran_C. For the Caucasus EBA individuals ("Caucasus_a_EBA"), dated to ~3,100 years BCE, which is similar to the Late Chalcolithic Anatolian individuals, we obtain a similar admixture date of 121 ± 35 generations. Importantly, the earlier two Caucasus_lowlands_LN and the one Büyükkaya_EC individuals yielded more recent admixture dates of 34 ± 15 generations before the age of the individuals (~5600 years BCE) (Figure 5A). The converted calendar date of ~6500 years BCE matches the timing of the admixture event estimated from the Late Chalcolithic individuals (Figure 5B).

## Admixture Modeling of the Chalcolithic and Bronze Age Groups

Although we showed that it requires both Barcın_N and Iran_N-related ancestries to explain the ancestry composition of the LC-LBA groups, alternative combinations of ancient populations, which may be temporally and spatially more proximal to

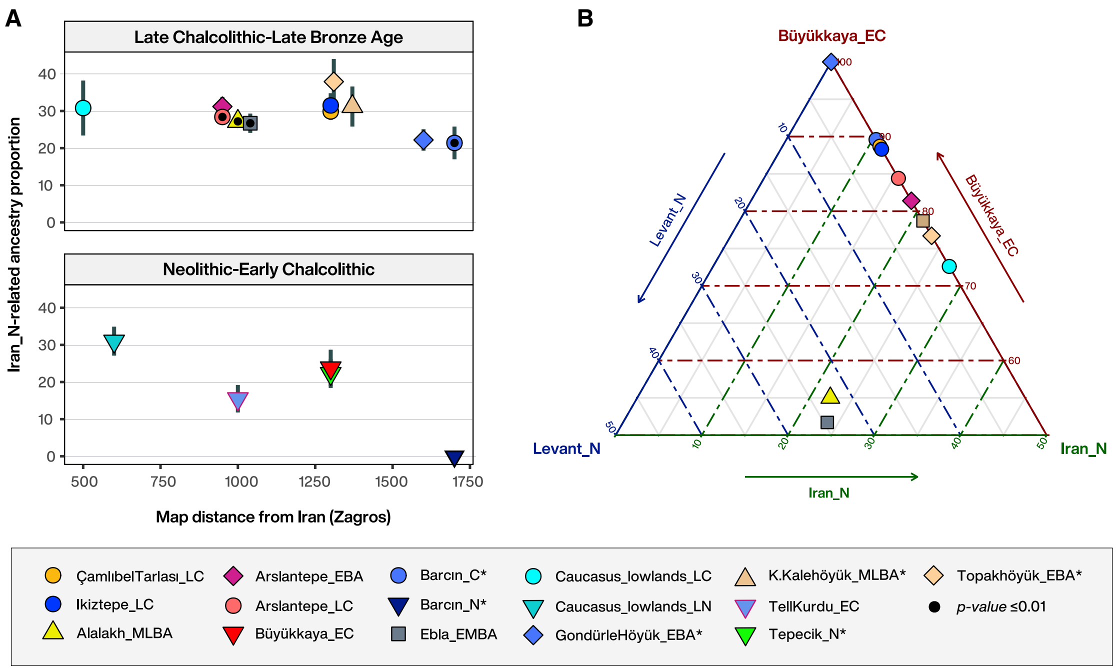



**Figure 6. *qpAdm* Modeling of Ancient Anatolian, Northern Levantine, and Southern Caucasian Populations from the Present and Previously Published (*) Studies**

(A) When we model the ancient populations as Western Anatolia (Barcın_N) and Zagros (Iran_N), LN/EC populations fall on a spatial gradient of Iran_N-like ancestry which is attenuated in the subsequent LC-LBA populations. Vertical bars represent ±1 SE estimated by 5 cM jackknifing.

(B) LC-LBA can be modeled as the geographically proximal source Büyükkaya_EC from Central Anatolia, with contribution from Iran_N that ranges from 0% in GonrdürleHöyük_EBA from Western Anatolia and ~30% in Caucasus_lowlands_LC. In order to model Ebla_EMBA and Alalakh_MLBA with Büyükkaya_EC and Iran_N extra contribution from a source like Levant_N is necessary.

See also Figure S3 and Tables S4, S5, S6, S7, and S8.

the LC-LBA groups, may also provide equally fitting models. To obtain a plausible admixture model that more likely reflects the true demographic history, it is crucial to precisely distinguish between closely related candidate source populations. We used *qpAdm* to model all LC-LBA groups as a mixture of two sources, one related to the Neolithic Anatolian ancestry and the other related to Iran and the Caucasus populations (Tables S6 and S7). For the former, we used three Neolithic or Early Chalcolithic groups (Barcın_N/TellKurdu_EC/Büyükkaya_EC). For the latter, we used Iran_N and CHG, as well as more recent Chalcolithic and Bronze Age populations from the same region (Allentoft et al., 2015; Lazaridis et al., 2016; Wang et al., 2019). Although the admixture signal in LC-LBA is older than these later populations, we nonetheless used them as a proxy because they might represent a gene pool that is not yet sampled but had contributed to LC-LBA individuals.

We find that Barcın_N+Iran_N adequately explain many LC-LBA groups, but it fails for Alalakh_MLBA, Ebla_EMBA, Arslantepe_LC, Barcın_C, and Caucasus_lowlands_LC ($p < 0.05$). Iran_N-related contribution varies from 21% ± 9% to 38% ± 6% (Figure 6A). The alternative model of Barcın_N+CHG provides slightly higher estimates for CHG-related contribution from 27% ± 13% to 41% ± 7%, although most groups (8/12) cannot be modeled with CHG. For the Chalcolithic and Bronze Age groups, Iran_C provides similar results with Iran_N but with a higher contribution (34%–53%; $p \geq 0.05$ for 8/12 groups). Iran_C itself can be modeled as a mixture of Iran_N and Barcın_N ($p = 0.365$; 37% ± 3% from Barcın_N), which corresponds well with the modeling results for LC-LBA. In contrast, those from the Caucasus, specifically the Eneolithic to Bronze Age (_En/BA) groups, mostly fail to fit LC-LBA.

We repeated our admixture modeling by replacing Barcın_N with TellKurdu_EC. Models with TellKurdu_EC in general provide a good fit to the LC-LBA groups, although we caution that it may be an artifact of reduced statistical power for detecting discrepancies between the model and the actual target groups, due to the much smaller sample size of TellKurdu_EC ($n = 5$) compared to Barcın_N ($n = 22$). While models with ancient Iranian populations fail for multiple LC-LBA groups ($p < 0.05$ for 5/12 with Iran_N and for 3/12 with Iran_C), TellKurdu_EC+CHG can model all LC-LBA groups with varying level of CHG contribution ranging from 13% ± 19% to 40% ± 9%, except for Barcın_C. Replacing CHG with a later Caucasus group ("G.Caucasus_a_En") provides the same pattern with a higher Caucasus-related contribution (40%–67%; $p \geq 0.05$, also with the exception of Barcın_C). When we repeated the analysis after adding Barcın_N to the outgroup set, most results remained similar. However, two LC-LBA groups from the same region with TellKurdu_EC (i.e., Ebla_EMBA and Alalakh_MLBA) became deviant from the model ($p < 0.03$), suggesting that TellKurdu_EC may not be a good local proxy in a simple two-way admixture model. Therefore, it seems to hold that ancient Iranian groups overall serve as a better proxy than the Caucasus groups, although higher resolution data are necessary to compare them further.

Büyükkaya_EC is the earliest individual in our dataset with a genetic profile similar to the LC-LBA groups within Anatolia. Therefore, we also tested a scenario in which the later LC-LBA groups had descended from the same gene pool without further external contribution. *f4*(*Mbuti*,*X*;*Büyükkaya_EC*,*LC-LBA*) suggests that Büyükkaya_EC shares more alleles with the European/Anatolian Farmers (e.g., Boncucklu, LBK, Barcın_N) than LC-LBA groups do (Table S5). Likewise, most LC-LBA groups cannot be modeled in *qpAdm* as a sister group with Büyükkaya_EC when Barcın_N is included in the outgroups ($p < 0.05$ for 1-way model for 11/12). Most LC-LBA groups are adequately modeled by adding the second ancestry of ancient Iran/Caucasus populations, while Alalakh_MLBA and Ebla_EMBA require a substantial contribution from ancient southern Levantine populations (Figure 6B).

Overall, the inference of the same admixture date drawn from both Late Neolithic and Late Chalcolithic populations combined with the *qpAdm* analyses suggest that the LC-LBA populations also derived from the Neolithic genetic cline but were substantially more homogenized than their predecessors (Figure 6A). Although the ancient groups from Iran are a better proxy for the eastern source than those from the Caucasus, we caution a naive literal interpretation of our results, as yet unsampled proxies from within Mesopotamia may represent true historical sources of this Iran/Caucasus-related ancestry.

### Genetic Turnover in the Bronze Age Northern Levant

The Northern Levant, represented by the sites Tell Kurdu, Ebla, and Alalakh, showcases the most noticeable genetic turnover among our four time transects. Within two millennia after the last Middle Chalcolithic Tell Kurdu individual (TellKurdu_MC), the genetic profile of the populations in and around the Amuq valley (Alalakh_MLBA and Ebla_EMBA) changed to largely resemble contemporaneous Anatolians. However, the *qpAdm* modeling with Büyükkaya_EC suggests that Alalakh_MLBA and Ebla_EMBA are still distinct from the other Anatolian groups with respect to their connection to the ancient Southern Levant. Their distinction is also captured by $f_4$-statistics whereby Ebla_EMBA and Alalakh_MLBA differ from the other LC-LBA groups with respect to their relation with older populations such as Barcin_N and Caucasian groups (Figure S3). In addition, Barcin_N/TellKurdu_EC and/or ancient Caucasian groups cannot successfully model Ebla_EMBA and Alalakh_MLBA in *qpAdm* (Tables S6 and S7), suggesting that these sources do not represent good proxies of their true ancestries. Alternative models with the predecessor TellKurdu_EC as a baseline ancestry and the geographically close Arslantepe_LC as a potential proximal source did not improve the fit either ($p \leq 1.3 \times 10^{-5}$; Table S8). However, admixture models become adequate by adding a southern Levantine population as the third source, with significant Levantine contributions: e.g., 27%–34% TellKurdu_EC + 36%–38% G.Caucasus_a_En + 28%–38% Levant_EBA ($p \geq 0.492$).

Consistent with the extra gene flow after the time of TellKurdu_EC, we obtain younger admixture dates in Alalakh_MLBA than the other LC-LBA groups when we use either Anatolian or Caucasian gene pools as sources: 78 ± 27 generations (3880 ± 746 years BCE) with Anatolia_LC and 44 ± 8 (3060 ± 224 years BCE) with Caucasus_a_EBA. No exponential decay could be fitted when we used either Anatolia_LC or Caucasus_a_EBA as one source and Levant_C as a second.

### Evidence for Individual Mobility in Alalakh

All genetic analyses of Alalakh_MLBA were conducted at the exclusion of one female (ALA019) because of her outlier position in the PCA (Figure 3B). Discovered at the bottom of a well, the archaeological and anthropological context suggest that the skeletal remains of this woman, C14-dated to 1568–1511 cal BCE (AMS; 2-sigma), represent an irregular burial with evidence of several healed skeletal traumata (Figure 7; STAR Methods). We have ruled out the possibility of modern-day contamination based on the characteristic aDNA damage profile, low mitochondrial contamination and reproduction of the PCA coordinates after discarding all sequence reads without damage (STAR Methods). In the Eurasian PCA (Figure S4), ALA019 falls genetically closer to Chalcolithic and Bronze Age individuals from ancient Iran and Turan (present-day area of Iran, Turkmenistan, Uzbekistan, and Afghanistan) (Narasimhan et al., 2019). These populations represent a west-east genetic cline with varying proportions of ancestries related to Barcın_N, Iran_N and WSHG (hunter gatherers from Western Siberia). We confirmed the genetic affinity of ALA019 observed in the PCA with an *outgroup*-$f_3$ test (Figure 7A). Other ancient populations from the Caucasus and the Western steppe also produced high affinity but $f_4$(*Mbuti*, *X*; $Turan_x$, *ALA019*) suggest that ALA019 differs from other Turan individuals by occasionally sharing more or less alleles with either Iran_N or WSHG (Figure 7B), which agrees with the presence of a genetic cline in this area. In the absence of ancient genomes from nearby regions such as Southern Mesopotamia, the most likely ancestral origin of this individual was somewhere in Eastern Iran or Central Asia.

## DISCUSSION

### Genetic Homogenization across Anatolia and the Southern Caucasus prior to the Bronze Age

Our study covers time transects of ~4,000 years of Syro-Anatolian and ~2,000 years of Southern Caucasian history, both starting from the 6th millennium BCE. In addition, our admixture date estimates allow us to infer a millennium further back in time to the Neolithic period. We describe a Late Neolithic/Early Chalcolithic (6th millennium BCE) genetic cline stretching from Western Anatolia (i.e., area around the Sea of Marmara) to the lowlands of the Southern Caucasus that was formed by an admixture process that started at the beginning of Late Neolithic (~6500 years BCE). The eastern end of this cline extends beyond the Zagros mountains with minute proportions of Anatolian (i.e., Western Anatolian-like) ancestry reaching as far as Chalcolithic and Bronze Age Central Asia (Narasimhan et al., 2019). To the south, Anatolian ancestry is present in the Southern Levantine Neolithic populations (Lazaridis et al., 2016), and to the north, in the Chalcolithic and Bronze Age populations from the Caucasus (mainly mountainous area) (Allentoft et al., 2015; Lazaridis

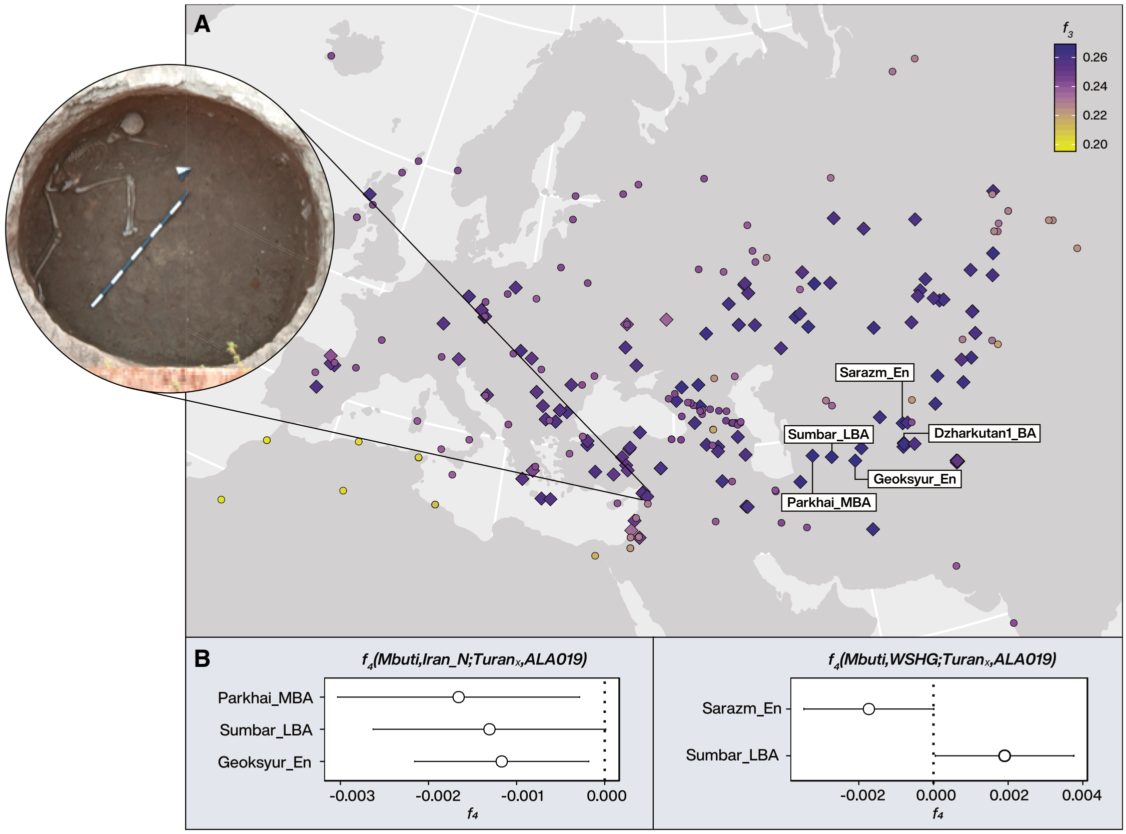



**Figure 7. Individual ALA019 from Alalakh Has High Genetic Affinity to the Ancient Contemporaneous Populations from Eastern Iran and Turan (Central Asia)**

(A) Shared genetic drift measured with outgroup $f_3$-statistics between ALA019 and ancient Eurasian (diamonds) and worldwide modern (circles) populations. The highest five values of the test are produced by populations from Turan which are labeled.

(B) Symmetry $f_4$-statistics show variable affinity to Iran_N and WSHG among Turan$_x$ and ALA019. Horizontal bars represent ±3 SE estimated by 5 cM jackknifing. Photo of "Well Lady" (ALA019): Murat Akar, Alalakh Excavations Archive.

See also Figure S4.

et al., 2016; Wang et al., 2019), most likely as a result of the Late Neolithic admixture.

Evidence for genetic homogenization across larger geographic distances also comes from the uniparentally inherited Y chromosome lineages (Table S9). We observe the most common male lineages J1a, J2a, J2b, and G2a in all spatio-temporal groups of the region. Alongside the less frequent lineages H2 and T1a, these all form part of the genetic legacy that dates to the Neolithic or was already present in the region during the Upper Paleolithic (Wang et al., 2019; Lazaridis et al., 2016; Jones et al., 2015; Feldman et al., 2019; Broushaki et al., 2016). A few notable exceptions provide rather anecdotal but nonetheless important evidence for long distance mobility and extended Y-haplogroup diversity. For example, individual ART038 carries Y-haplotype R1b-V1636 (R1b1a2), which is a rare clade related to other early R1b-lineages, such as R1b-V88 that was found in low frequency in Neolithic Europe (e.g., Haak et al., 2015) and R1b-Z2103—the main Y-lineage that is associated with the spread of "steppe ancestry" across West Eurasia during the early Bronze Age. However, R1b-V1636 and R1b-Z2103 lineages split long before (~17 kya) and therefore there is no direct evidence for an early incursion from the Pontic steppe during the main era of Arslantepe. Lineage L2-L595 found in ALA084 (Alalakh) has previously been reported in one individual from Chalcolithic Northern Iran (Narasimhan et al., 2019) and in three males from the Late Maykop phase in the North Caucasus (Wang et al., 2019). These three share ancestry from the common Anatolian/Iranian ancestry cline described here, which indicates a widespread distribution that also reached the southern margins of the steppe zone north of the Caucasus mountain range.

Dating the formation of the west-to-east cline during the 7$^{th}$ millennium BCE enables the contextualization of these genetic signals observed on both autosomal and uniparental markers with archaeological evidence of human mobility and changes in socio-cultural practices. The time around 6500–6400 years BCE marks a significant junction in the Anatolian Neolithic because it saw a sudden and massive expansion of sedentary communities into areas that had previously supported no or very few food-producing communities before (Brami, 2015; Düring, 2013). Subsequently, in the Southern Caucasus, the abrupt appearance of a Neolithic lifestyle and the introduction of exogenous domesticated animal and plant species ca. 6000 BCE suggests some type of interaction with, and eventually intrusion of Neolithic populations from the neighboring regions, among which Southeastern Anatolia—along with Zagros and the Caspian belt—could be one of the most suitable candidates (Chataigner et al., 2014). Related to these events, the genetic structure of domesticated caprine populations within the Near East began to break down, and by the Chalcolithic period, goat herds across the region were found to harbor ancestries both from eastern and western Neolithic populations (Daly et al., 2018; Kadowaki et al., 2017). Although the exact timing of this admixture is not known, the parallel between human and livestock genetic histories suggests that livestock moved not only through trade networks but also together with people, as well as their material culture, ideas, and practices. This is indicated, for instance, by the circular Neolithic architecture of the Southern Caucasus (Baudouin, 2019; Lyonnet et al., 2016), which is reminiscent of the Halaf traditions, that were developing during the early 6th millennium in North Mesopotamia and along the Anatolian stretches of the Tigris and Euphrates river valleys.

In the subsequent millennia and until the Late Bronze Age, genetic continuity persisted in North-Central and Eastern Anatolia, which is supported by the genetic similarity of these later populations and the absence of new ancestry sources after the Neolithic period. This contradicts prior hypotheses for population change based on archaeological evidence of intense cultural interactions during this period. For example, the site of İkiztepe on the Turkish Black Sea Coast contains a material culture with strong Balkan affinities, and this has been argued to signify direct contact with populations across the Black Sea (e.g., Thissen, 1993), but these contacts do not seem to be accompanied by gene flow.

The site of Arslantepe provides another representative example. At the beginning of EBA, archaeological evidence at the site strongly suggests the presence of a disruptive socio-political conflict that led to the occupation of Arslantepe by pastoral populations with a connection to the Caucasus. In PCA and $f_4$-statistics, two individuals dating to this period show excess affinity with populations from the Caucasus and the Pontic steppe compared to their peers, while later Arslantepe_EBA individuals do not share this Caucasian affinity (Table S10). This implies that the postulated demic interaction must have been transient and of small scale, although the small sample size from Arslantepe_EBA (n = 4) may not be sufficient to detect it. Subtle gene flow is consistent with recent findings from the site, suggesting that the EBA pastoralists occupying the site were more likely well-established local groups moving around the mountains rather than intrusive groups from the Caucasus (Frangipane, 2014).

The genetic landscape of Arslantepe also has important implications with respect to the interactions with the Mesopotamian world. Archaeological evidence indicates that in the 4th millennium BCE Mesopotamian populations established colonies in Southeastern Anatolia and Northern Syria (e.g., Habuba Kabira, Jebel Aruda, Hacinebi) during a period referred to as the Uruk Expansion (Algaze, 2005). However, the Uruk expansion was also a very complex and deep process of socio-cultural transformation that reoriented the economic, political, and cultural interests of indigenous elites toward Southern Mesopotamia. Artifacts in Arslantepe reflect this complexity, and the genetic continuity shown here supports the notion that indigenous populations adopted these broader Uruk features and ideas without the transmission of genes.

## Population and Territorial State Dynamics in the Northern Levant

In contrast to the rest of Anatolia, the Northern Levant stands out as a region of the Near East with traceable post-Neolithic changes in the genetic structure. We found that the gene pools at Ebla and Alalakh can only be explained by more complex models that require additional contributions both from the Caucasus and Southern Levant. The inclusion of a source related to the Caucasus in our proposed model raises the question whether this turnover could be linked to the expansion of the Transcaucasian Kura-Araxes material culture to the Levant. This expansion is recorded in the region of the Northern Levant ca. 2800 BCE and could be associated with the movement/migration of people from Eastern Anatolia and the Southern Caucasian highlands (Greenberg and Palumbi, 2015; Greenberg et al., 2014). However, our results do not support this scenario for a number of reasons: (1) we do not find any substantial increase of Caucasus-related ancestry in the populations of the primary expansion area of Kura-Araxes (e.g., Eastern Anatolia), (2) populations from the highlands of the Southern Caucasus—including individuals from a Kura-Araxes context ("L.Caucasus_EBA")—as secondary source populations also fail, and (3) so do models with Arslantepe from Eastern Anatolia, a population located mid-way along the proposed expansion route from the Southern Caucasus to the Northern Levant.

Consequently, these interpretative caveats call for consideration of alternative historical scenarios, including scenarios of multiple gene-flow events that could have taken place in the intervening two millennia between the Tell Kurdu population and those of Bronze Age Ebla and Alalakh. However, written sources, archaeological, and paleoclimatic evidence suggest that a narrower time period—the end of the EBA—had been very critical with respect to political tensions and population mobility. It was during this period, for example, that Ebla was destroyed twice and re-established at the beginning of MBA. There are extensive textual references from the end of the EBA through the LBA referring to groups of people arriving into the area of the Amuq Valley. Although these groups were named, likely based on designations (e.g., Amorites, Hurrians), the formative context of their (cultural) identity and their geographic origins remain debated. One recent hypothesis (Weiss, 2014, 2017; Akar and Kara, 2020) associates the arrival of these groups with climate-forced population movement during the "4.2k BP event," a Mega Drought that led to the abandonment of the entire Khabur river valley in Northern Mesopotamia and the search of nearby habitable areas.

Taking the above into consideration, we suggest that the ancestries we inferred for Alalakh and Ebla might best describe the genetic make-up of the EBA populations of unsampled Northern Mesopotamia. During the following MBA and LBA, we find no evidence of genetic disruption, even though shifts in territorial control dynamics between kingdoms/empires affected Ebla's and Alalakh's socio-cultural development (see STAR Methods).

Nevertheless, the case of the Alalakh individual with likely Central Asian origin is a finding that can be interpreted within the context of nascent internationalism of the Middle and Late Bronze Age Eastern Mediterranean societies. It calls for future research on the various societal features of this phenomenon and how these are reflected on the individual life histories.

## Conclusions

Overall, our large-scale genomic analysis reveals two major genetic events. First, during the Late Neolithic, gene pools across Anatolia and the Southern Caucasus mixed, resulting in an admixture cline. Second, during the Early Bronze Age, Northern Levant populations experienced gene flow in a process that likely involved yet to-be-sampled neighboring populations from Mesopotamia. Even though we could detect subtle and transient gene flow in Arslantepe, we acknowledge that disentangling questions related to local-scale population dynamics within the homogeneous Chalcolithic and Bronze Age Anatolian gene pool might be beyond the resolution of current analytical tools. Furthermore, while our sampling expands in number and geographic range on previous studies, the critical area of Mesopotamia remains unsampled; thus, although our picture of the genetic landscape of the Near East is highly suggestive, it remains incomplete. Nevertheless, the cumulative genetic dataset of Anatolia, the Southern Caucasus, and the Northern Levant between the Early and Late Bronze Age indicates that, following the genetic events of the Late Neolithic and Early Bronze Age, there was no intrusion of genetically distinct populations in this region. This conclusion is of great importance with respect to our understanding of the formation of complex Bronze Age socio-political entities.

## STAR★METHODS

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## SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cell.2020.04.044.

A video abstract is available at https://doi.org/10.1016/j.cell.2020.04.044#mmc7.

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## AUTHOR CONTRIBUTIONS

J.K., W.H., P.W.S., C.J., and C.W. conceived the study. C.J., W.H., and J.K. supervised the genetic work. Y.S.E., M.F., K.A.Y., F.P., P.M., R.Ö., F.G., T.A., B.L., E.L.H., S.E.N., and U.D.S. provided archaeological material. P.W.S., Y.S.E., M.F., F.B.R., K.A.Y., T.I., M.A., R.S., R.Ö., G.P., F.G., B.L., E.L.H., U.D.S., and S.E. advised on the archaeological background and interpretation. Y.S.E., M.F., F.B.R., K.A.Y., T.I., M.A., R.S., R.Ö., T.A., B.L., U.D.S., M.D'A., and E.S. wrote the archaeological and sample background section. E.S., M.B., G.N., and S.P. performed the laboratory work. E.S. performed the data analyses with C.J. and W.H. providing guidance. A.B.R. performed analyses on the Y chromosome markers and assignment of Y-haplogroups. E.S., C.J., and W.H. wrote the manuscript with input from all co-authors.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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# STAR★METHODS

## KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Biological Samples | | |
| Ancient skeletal element | This study | ALA001 |
| Ancient skeletal element | This study | ALA002 |
| Ancient skeletal element | This study | ALA004 |
| Ancient skeletal element | This study | ALA008 |
| Ancient skeletal element | This study | ALA009 |
| Ancient skeletal element | This study | ALA011 |
| Ancient skeletal element | This study | ALA013 |
| Ancient skeletal element | This study | ALA014 |
| Ancient skeletal element | This study | ALA015 |
| Ancient skeletal element | This study | ALA016 |
| Ancient skeletal element | This study | ALA017 |
| Ancient skeletal element | This study | ALA018 |
| Ancient skeletal element | This study | ALA019 |
| Ancient skeletal element | This study | ALA020 |
| Ancient skeletal element | This study | ALA023 |
| Ancient skeletal element | This study | ALA024 |
| Ancient skeletal element | This study | ALA025 |
| Ancient skeletal element | This study | ALA026 |
| Ancient skeletal element | This study | ALA028 |
| Ancient skeletal element | This study | ALA029 |
| Ancient skeletal element | This study | ALA030 |
| Ancient skeletal element | This study | ALA034 |
| Ancient skeletal element | This study | ALA035 |
| Ancient skeletal element | This study | ALA037 |
| Ancient skeletal element | This study | ALA038 |
| Ancient skeletal element | This study | ALA039 |
| Ancient skeletal element | This study | ALA084 |
| Ancient skeletal element | This study | ALA095 |
| Ancient skeletal element | This study | ALX002 |
| Ancient skeletal element | This study | ART001 |
| Ancient skeletal element | This study | ART004 |
| Ancient skeletal element | This study | ART005 |
| Ancient skeletal element | This study | ART009 |
| Ancient skeletal element | This study | ART010 |
| Ancient skeletal element | This study | ART011 |
| Ancient skeletal element | This study | ART012 |
| Ancient skeletal element | This study | ART014 |
| Ancient skeletal element | This study | ART015 |
| Ancient skeletal element | This study | ART017 |
| Ancient skeletal element | This study | ART018 |
| Ancient skeletal element | This study | ART019 |
| Ancient skeletal element | This study | ART020 |
| Ancient skeletal element | This study | ART022 |

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***Continued***

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Ancient skeletal element | This study | ART023 |
| Ancient skeletal element | This study | ART024 |
| Ancient skeletal element | This study | ART026 |
| Ancient skeletal element | This study | ART027 |
| Ancient skeletal element | This study | ART032 |
| Ancient skeletal element | This study | ART038 |
| Ancient skeletal element | This study | ART039 |
| Ancient skeletal element | This study | ART042 |
| Ancient skeletal element | This study | CBT001 |
| Ancient skeletal element | This study | CBT002 |
| Ancient skeletal element | This study | CBT003 |
| Ancient skeletal element | This study | CBT004 |
| Ancient skeletal element | This study | CBT005 |
| Ancient skeletal element | This study | CBT010 |
| Ancient skeletal element | This study | CBT011 |
| Ancient skeletal element | This study | CBT013 |
| Ancient skeletal element | This study | CBT014 |
| Ancient skeletal element | This study | CBT015 |
| Ancient skeletal element | This study | CBT016 |
| Ancient skeletal element | This study | CBT017 |
| Ancient skeletal element | This study | CBT018 |
| Ancient skeletal element | This study | ETM001 |
| Ancient skeletal element | This study | ETM003 |
| Ancient skeletal element | This study | ETM004 |
| Ancient skeletal element | This study | ETM005 |
| Ancient skeletal element | This study | ETM006 |
| Ancient skeletal element | This study | ETM010 |
| Ancient skeletal element | This study | ETM012 |
| Ancient skeletal element | This study | ETM014 |
| Ancient skeletal element | This study | ETM015 |
| Ancient skeletal element | This study | ETM016 |
| Ancient skeletal element | This study | ETM017 |
| Ancient skeletal element | This study | ETM018 |
| Ancient skeletal element | This study | ETM021 |
| Ancient skeletal element | This study | ETM023 |
| Ancient skeletal element | This study | ETM025 |
| Ancient skeletal element | This study | ETM026 |
| Ancient skeletal element | This study | IKI002 |
| Ancient skeletal element | This study | IKI006 |
| Ancient skeletal element | This study | IKI009 |
| Ancient skeletal element | This study | IKI012 |
| Ancient skeletal element | This study | IKI016 |
| Ancient skeletal element | This study | IKI017 |
| Ancient skeletal element | This study | IKI019 |
| Ancient skeletal element | This study | IKI020 |
| Ancient skeletal element | This study | IKI024 |
| Ancient skeletal element | This study | IKI030 |
| Ancient skeletal element | This study | IKI032 |

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| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Ancient skeletal element | This study | IKI034 |
| Ancient skeletal element | This study | IKI036 |
| Ancient skeletal element | This study | IKI037 |
| Ancient skeletal element | This study | IKI038 |
| Ancient skeletal element | This study | KRD001 |
| Ancient skeletal element | This study | KRD002 |
| Ancient skeletal element | This study | KRD003 |
| Ancient skeletal element | This study | KRD004 |
| Ancient skeletal element | This study | KRD005 |
| Ancient skeletal element | This study | KRD006 |
| Ancient skeletal element | This study | MTT001 |
| Ancient skeletal element | This study | POT002 |
| Ancient skeletal element | This study | TIT003 |
| Ancient skeletal element | This study | TIT012 |
| Ancient skeletal element | This study | TIT014 |
| Ancient skeletal element | This study | TIT015 |
| Ancient skeletal element | This study | TIT019 |
| Ancient skeletal element | This study | TIT021 |
| Ancient skeletal element | This study | TIT025 |
| Chemicals, Peptides, and Recombinant Proteins | | |
| 0.5 M EDTA pH 8.0 | Life Technologies | Cat# AM9261 |
| 1 M Tris-HCl pH 8.0 | Thermo Fisher Scientific | Cat# 15568025 |
| 10x Buffer Tango | Life Technologies | Cat# BY5 |
| 1x Tris-EDTA pH 8.0 | AppliChem | Cat# A8569,0500 |
| 20% SDS | Serva | Cat# 39575.01 |
| 3M Sodium Acetate (pH 5.2) | Sigma Aldrich | Cat# S7899 |
| 5M NaCl | Sigma Aldrich | Cat# S5150 |
| ATP 100 mM | Thermo Fisher Scientific | Cat# R0441 |
| BSA 20mg/mL | New England Biolabs | Cat# B9000 |
| Bst DNA Polymerase2.0, large frag. | New England Biolabs | Cat# M0537 |
| D1000 Reagents | Agilent Technologies | Cat# 5067-5583 |
| D1000 ScreenTapes | Agilent Technologies | Cat# 5067-5582 |
| Denhardt's solution | Sigma Aldrich | Cat# D9905 |
| dNTP Mix | Thermo Fisher Scientific | Cat# R1121 |
| Dynabeads MyOne Streptavidin T1 | Thermo Fisher Scientific | Cat# 65602 |
| Ethanol | Merck | Cat# 1009832511 |
| GeneAmp 10x PCR Gold Buffer | Thermo Fisher Scientific | Cat# 4379874 |
| GeneRuler Ultra Low Range DNA Ladder | Life Technologies | Cat# SM1211 |
| Guanidine hydrochloride | Sigma Aldrich | Cat# G3272 |
| Herculase II Fusion DNA Polymerase | Agilent Technologies | Cat# 600679 |
| Human Cot-I DNA | Thermo Fisher Scientific | Cat#15279011 |
| Isopropanol | Merck | Cat# 1070222511 |
| PEG-8000 | Promega | Cat# V3011 |
| PfuTurbo Cx Hotstart DNA Polymerase | Agilent Technologies | Cat# 600412 |
| Proteinase K | Sigma Aldrich | Cat# P2308 |
| Salmon sperm DNA | Thermo Fisher Scientific | Cat# 15632-011 |
| Sera-Mag Magnetic Speed-beads Carboxylate-Modified (1 mm, 3EDAC/PA5) | GE LifeScience | Cat# 65152105050250 |

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| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Sodiumhydroxide Pellets | Fisher Scientific | Cat# 10306200 |
| SSC Buffer (20x) | Thermo Fisher Scientific | Cat# AM9770 |
| T4 DNA Polymerase | New England Biolabs | Cat# M0203 |
| T4 Polynucleotide Kinase | New England Biolabs | Cat# M0201 |
| Tween-20 | Sigma Aldrich | Cat# P9416 |
| Uracil Glycosylase inhibitor (UGI) | New England Biolabs | Cat# M0281 |
| USER enzyme | New England Biolabs | Cat# M5505 |
| Water | Sigma Aldrich | Cat# 34877 |
| Critical Commercial Assays | | |
| High Pure Viral Nucleic Acid Large Volume Kit | Roche | Cat# 5114403001 |
| HiSeq 4000 SBS Kit (50/75 cycles) | Illumina | Cat# FC-410-1001/2 |
| DyNAmo Flash SYBR Green qPCR Kit | Thermo Fisher Scientific | Cat# F415L |
| MinElute PCR Purification Kit | QIAGEN | Cat# 28006 |
| NextSeq 500/550 High Output Kit v2 (150 cycles) | Illumina | Cat# FC-404-2002 |
| Oligo aCGH/Chip-on-Chip Hybridization Kit | Agilent Technologies | Cat# 5188-5220 |
| Quick Ligation Kit | New England Biolabs | Cat# M2200L |
| Deposited Data | | |
| Raw and analyzed data (European nucleotide archive) | This study | ENA: PRJEB37213 |
| Haploid genotype data for 1240K panel (Edmond Data Repository of the Max Planck Society) | This study | https://nam03.safelinks.protection.outlook.com/?url=https%3A%2F%2Fedmond.mpdl.mpg.de%2Fimeji%2Fcollection%2Fzdj1HseOUbd1OaEo&data=02%7C01%7Ctarpin%40cell.com%7C9eeeee0ef7c44fa29cf808d7f0cd4e15%7C9274ee3f94254109a27f9fb15c10675d%7C0%7C0%7C637242637306430495&sdata=sua73V0iRT5WUYnKdCdVszof7MzyI5bA3LkT%2FM6tQv0%3D&reserved=0 |
| Software and Algorithms | | |
| AdapterRemoval v2.2.0 | Schubert et al., 2016 | https://github.com/MikkelSchubert/adapterremoval |
| ADMIXTOOLS v5.1 | Patterson et al., 2012; Loh et al., 2013 | https://github.com/DReichLab/AdmixTools |
| ALDER v1.03 | Loh et al., 2013 | http://cb.csail.mit.edu/cb/alder/ |
| ANGSD v0.910 | Korneliussen et al., 2014 | http://www.popgen.dk/angsd/index.php/ANGSD |
| bamUtil v1.0.13 | https://github.com/statgen/bamUtil | https://github.com/statgen/bamUtil |
| BWA v0.7.12 | Li and Durbin, 2009 | http://bio-bwa.sourceforge.net/ |
| CircularMapper v1.93.5 | Peltzer et al., 2016 | https://github.com/apeltzer/CircularMapper |
| DATES | M. Chintalapati, N. Patterson, N. Alex, and P. Moorjani, personal communication | https://github.com/priyamoorjani/DATES |
| DeDup v0.12.2 | Peltzer et al., 2016 | https://github.com/apeltzer/DeDup |
| EIGENSOFT v6.0.1 | Patterson et al., 2006; Price et al., 2006 | https://github.com/DReichLab/EIG |

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| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
| Geneious | Kearse et al., 2012 | https://www.geneious.com |
| haplogrep | Kloss-Brandstätter et al., 2011 | https://haplogrep.i-med.ac.at |
| mapDamage v2.0.6 | Jónsson et al., 2013 | https://github.com/ginolhac/mapDamage |
| pileupCaller | https://github.com/stschiff/sequenceTools | https://github.com/stschiff/sequenceTools |
| PMDtools | Skoglund et al., 2014 | https://github.com/pontussk/PMDtools |
| preseq v2.0 | Daley and Smith, 2013 | https://github.com/smithlabcode/preseq |
| READ | Monroy Kuhn et al., 2018 | https://bitbucket.org/tguenther/read/src/default/ |
| Rsamtools | Morgan et al., 2019 | http://bioconductor.org/packages/release/bioc/html/Rsamtools.html |
| SAMtools v1.3 | Li et al., 2009 | http://www.htslib.org/doc/samtools.html |
| Schmutzi | Peltzer et al., 2016 | https://github.com/grenaud/schmutzi |

## RESOURCE AVAILABILITY

### Lead contact

Further information and requests for resources and reagents should be addressed to and will be fulfilled by the Lead Contact, Johannes Krause (krause@shh.mpg.de).

### Materials Availability

This study did not generate new unique reagents.

### Data and Code Availability

The accession number for the aligned suquence data (BAM format) reported in this paper is European Nucleotide Archive (ENA): PRJEB37213. Haploid genotype data for the 1240K panel is available in eigenstrat format via the Edmond Data Repository of the Max Planck Society (https://edmond.mpdl.mpg.de/imeji/collection/zdj1HseOUbd1OaEo).

## EXPERIMENTAL MODEL AND SUBJECT DETAILS

### Description of origin, archaeological and anthropological context of analyzed individuals

Alkhantepe, Azerbaijan

39.3607139°N, 48.4613556°E

Excavation: Mughan Neolithic-Eneolithic expedition of the Institute of Archaeology and Ethnography of Azerbaijan National Academy of Sciences, 2006-2017, directed by Tufan Isaak oglu Akhundov

The site of Alkhantepe is situated on a plain without visible water ways, 4 km north of the Uchtepe village, in the Jalilabad district of Azerbaijan. It is a narrow belt of the eastern part of the Mughan steppe limited by the spurs of Brovary Range from the west and the Caspian Sea from the east. Presently, the topography of the site is flat with its north-eastern part slightly refracting and lowering. The surface of the settlement has been surveyed for many years and samples of ceramic vessels and stone objects have been found. Test trenches and expanded excavations show that the area occupied by the ancient settlement was about 4 ha in size and the thickness of cultural layers is up to 3 m. Materials recovered from the surface surveys as well as the excavation of cultural layers are identical and give the opportunity to relate this settlement to the Leilatepe tradition.

The cultural layers below the modern-day surface of the site consisted of seven construction horizons which can be divided into two distinct units. As it became clear in the process of excavation, the upper 1.2 m. cultural layer was formed in ancient times due to an earthquake which resulted in a period of abandonment (at least of the excavated parts of the site). Settlement activity resumed shortly afterward. Judging from the material evidence, this new settlement equally represents a new stage in the history of the site with distinct features in architecture and building techniques.

In contrast to the preceding time when adobe was widely used, buildings of the younger settlement stage were light constructions of rectangular form made of reeds and poles covered with clay and with a hearth in the middle.

For the first stage of settlement, excavations revealed round and rectangular mud-huts with subsoil walls and walls constructed from adobe, altars, different household hearths and production furnaces, pits, and partition walls of adobe. The burials of the settlement's inhabitants were found on different levels among these constructions. The burials included individuals of all age groups, from new-borns and teenagers to adults. Only one exception was observed: babies were buried in ceramic vessels.

Survey and excavation uncovered a rich archaeological material consisting mainly of ceramics of Leilatepe tradition that is also represented by tools and objects of stone and bone. Additionally, metal objects, metallic slag and tools of metallic production were found (Akhundov, 2014, 2018).

One individual from Alkhantepe was analyzed for aDNA and is included in genetic analyses.

- ■ ALX002 (Alkhantepe Burial N2) is the individual from a burial that was revealed in a distance from the eastern wall in the south square of the excavated area at a depth of 1,48 m. The remains of this individual were buried in a shallow oval pit and they, as well as the pit, were poorly preserved. However, judging from the preserved remains, the deceased was put into the pit in a crouched position, lying on his/her left side with the head placed on a north-east orientation. A lead ring with unclosed ends, made of round wire, was found lying on the shin's bone. Dating of human tooth: 3776-3661 cal BCE (4950 ± 23 BP, MAMS-40330)

**Arslantepe, Turkey**

38.381944°N, 38.361111°E

Excavation: Sapienza University of Rome, 1961-present, directed by Marcella Frangipane

The site of Arslantepe is a 4.5 ha mound located in the highland fertile Malatya plain of Eastern Anatolia, 12 km from the western bank of the Euphrates river. From the point of view of Mesopotamian archaeology, the site is at a geographical and cultural border zone, in the northern highlands outside Mesopotamia proper and along pathways that potentially connect the alluvium of the Euphrates with different worlds, from the Caucasus to the Pontic regions and Central Anatolia. The uninterrupted and extensive excavation of the site since 1961 brought to light a four millennia long occupation starting around 4700 BCE, but possibly even earlier, as testified by the presence of Neolithic and Chalcolithic pottery on the surface of the mound. Among this are Ubaid ceramics and we know that the Malatya plain was directly involved by the expansion of Mesopotamian Ubaid culture, also by the Ubaid presence at the neighboring site of Değirmentepe. The finding of Halaf period ceramics suggests that this contact was strong in Neolithic phases too. During the fourth millennium, Arslantepe undergoes developments that structurally resemble those of Mesopotamia, even though it shows its own peculiarities, with a clear and steady growth in economic and social development, which brings the site to develop a primary state system toward the end of the millennium, parallel to that of Mesopotamia, but with features of its own (Frangipane, 2018). In the earlier phases of this period (Arslantepe Period VII, 3900-3400 BCE) contacts with Central Anatolia are also evidenced, but material culture shows that the strongest relations of the site are with the south-west toward the Amuq and Quoeiq (Balossi Restelli et al., 2012). The moment of proper state development (Arslantepe Period VI A, 3400-3200 BCE) is revealed by the foundation of a precocious palace complex with a sophisticated bureaucracy and control over the economy of the populations, which shows an increase in contacts with Mesopotamia proper, but also with other mountainous regions of North-Central and North-Eastern Anatolia and the Caucasus (Frangipane, 2012b). The contacts with the north-eastern regions further increase at the collapse of this early state system, when pastoral groups that were already living in the area and moving along the mountains with their flocks of sheep and goats briefly settle at the site, by building huts and fences for animals directly on the ruins of the palace (period VI B1, 3200-3100 BCE), giving rise to a period of profound instability characterized by meetings and clashes of various populations contending the site. In the course of their seasonal occupations, the pastoral groups of Period VIB1 also built more durable structures, among which a large mud-brick communal building, probably used a reception hall for meetings and feasting (Frangipane, 2012a, 2014, 2015b; Siracusano and Palumbi, 2014). This is a period of unrest and fast changes: Following the less permanent occupation of Period VI B1, an imposing fortification wall was built on the top of the mound, surrounding a large open area and with a series of rooms adjoining it on the interior (period VIB2, early phase). In this phase, only the remains of post-holes, probably belonging to temporary huts and fences, were found outside the wall, and the dates obtained from charcoals and seeds from the rooms adjoining the wall indicate an approximate date of about 3100 BCE. In a second phase of Period VIB2, a village of farmers was extensively brought to light along the slope, outside the fortification wall that was not in use anymore, and was dated between 3000 and 2850 BCE. The frequent overlapping of the C14 dates from all these periods, as well as the features of the archaeological evidence suggest that all the events occurred at Arslantepe from the destruction and collapse of the Palace to the establishment of the VIB2 village of farmers seem to have succeeded one another in a very fast and dramatic way, in the course of a short period of time.

Occupation at Arslantepe continues uninterruptedly throughout the whole 3$^{rd}$ millennium with an initial return to mobility (VI C, 2750-2500 BCE), followed by the presence of competing small policies in the whole plain, of which Arslantepe was probably one of the largest (VI D, 2500-2000 BCE) (Frangipane, 2012a; Conti and Persiani, 1993). This was a period of greater stability and an apparent decrease in external contacts, as material culture shows a remarkable continuity for several centuries.

During the 2$^{nd}$ millennium the site comes under Hittite influence (first with the Hittite reign and then the Empire) (Manuelli, 2013) and will eventually become capital of a Neo-Hittite reign at the collapse of the Empire. Arslantepe is eventually abandoned after the Assyrian king Sargon II conquers and destroys the site in 712 BCE.

Human remains at Arslantepe have been found both as burials and as scattered human remains within pits and fills of buildings. Period VII is the one with the most finds, predominantly formed by burials related to domestic occupation, thus dug under the floors of houses. Buried individuals are mostly infants and adult women (Erdal and Balossi Restelli, in press). Rarely sparse human bones are found, but are probably due to disturbances of burials that must have taken place already in antiquity. In the latest level of occupation in Period VII a burial ground has also been identified, outside a Temple structure, where possibly special burials were positioned: 2 infant jar burials were identified, one infant stone cist and ad adult inhumation.

The following VI A period is the period in which Arslantepe becomes the center of a primary state system, testified by a monumental palatial complex. No burials belonging to this phase have been found, but in one of the two temples of the complex (Temple A) a human skull was lying on the floor at the center of the building together with the skull of a wild pig. Both must have been part of a ritual practice, taking place in the room.

Yet different is the situation of human bones found in Period VI B1, when most remains are partial skeletons, found in pits or scattered within fills covering the collapsed palace ruins, thus not proper burials.

In the following VI B2 village of Early Bronze Age very interestingly the practice of burying infants under the house floors appears to have disappeared. An interesting group of human bones have been however found in a pit cut into the floor of the open space inside the fortification wall in the early phase of the period. These belong to a minimum number of 16 partial individuals not in anatomical connection, mostly male and adults, found in this pit together with some animal bones (Erdal, 2012b).

To a period in between the end of VI B1 and the beginning of VI B2 belongs the so-called 'royal tomb' (Frangipane et al., 2001), an imposing cist grave built at the bottom of a large pit, which was very atypical for the local culture. It was an extremely rich tomb containing an adult man with plenty of funerary gifts among which 65 metal objects, and with a complex funerary practice including the possible sacrifice of 4 adolescents (almost all female) on the stone slabs covering the cist (Palumbi, 2011; Frangipane et al., 2001). Ceramic materials in the tomb are perfectly in keeping with what was found in the early phase of Period VIB2, as well as in the communal building of Period VIB1, that is a mixture of local light-colored wares with Reserved Slip decoration in the Uruk tradition and Red-Black handmade ware of Caucasian and Anatolian inspiration.

The rest of the Early Bronze Age period sees rare human remains, and only one of a male burial from the vicinities of the domestic area has been included in this work.

Twenty-two individuals from Arslantepe produced genome-wide data and are included in genetic analyses.

- ART001 (H156 S138) is a female in pit burial from Period VI D2. Evidence of epicondylitis was observed on both humeri. The remains also exhibit evidence of severe osteoarthritis. Dating of human bone: 2470-2301 cal BCE (3908 ± 26 BP, MAMS-33533).
- ■ ART004 (H238 S156) is an old male in a pit dug under and sealed by the floor of a house. Period VII. Dating of human bone: 3758-3642 cal BCE (4906 ± 26 BP, MAMS-33534)
- ■ ART005 (H250 S169) is an old female buried in a domestic area of the settlement from Period VII. The relation with the overlying architecture is not preserved. A red slipped and burnished beaker were held in her hands and traces of red ochre were found on and next to the knees. Evidence for the following pathological conditions was present on the remains: osteoporosis, hyperostosis frontalis interna, severe osteoarthritis on joints, severe osteoarthritis on cervical and lumbar vertebra, dental diseases such as dental carries, periapical abscess, periodontitis, dental calculus, and linear enamel hypoplasia. Dating of human bone: 3770-3654 cal BCE (4934 ± 27 BP, MAMS-33535).
- ■ ART009 (H326) is an adult male represented by a skull and disarticulated bones found on the floor of a dwelling from Period VI B2, together with other bones from at least two individuals. No pathology was found on the preserved bones. Dating of human bone: 2834-2497 cal BCE (4069 ± 20 BP, MAMS-33536)
- ■ ART010 (H327 S220-2) is a ca. 7-year-old child represented by a skull and disarticulated long bones found on the floor of a dwelling from Period VI B2, together with other bones from at least two individuals. The cranium exhibits evidence of a possible perimortem trauma on left parietal bone and infectious lesions on the endocranial surface of the occipital. Linear enamel hypoplasia was observed on the permanent upper central incisors and the deciduous canines display evidence of non-alimentary use. Dating of human bone: 2857-2505 cal BCE (4095 ± 26 BP, MAMS-33537)
- ■ ART011 (S220-1) is a ca. 30-year-old female represented by a skull and disarticulated long bones found on the floor of a dwelling from Period VI B2, together with other bones from ART009 and ART010. No pathology was found on preserved cranial bones. Dating: 2839-2581 cal BCE (4103 ± 26 BP, MAMS-33538)
- ■ ART012 (H331) is a young adult female represented by a skull found on the floor of central room of Temple A (palatial complex of Period VI A) lying next to the skull of a wild pig. No pathology was found on this skull. Dating of human bone: 3338-3031 cal BCE (4479 ± 27 BP, MAMS-33539)

S216 is a simple pit containing a collective burial of human remains belonging to a minimum of 16 individuals. The pit is partly sealed by a VI B2 floor surface and cuts VI B1 levels of occupation of Arslantepe. There are also bone fragments of animals. This pit is not a burial type that is encountered in this period in Anatolia or neighboring areas. The human remains in this secondary burial consist of unarticulated cranial and post-cranial bones. Some small bones such as metacarpals, metatarsals and phalanges are also present but they are very few compared to the long bones and crania. Bioarchaeological studies of the human remains suggest that there are at least 13 adult crania. Moreover, three sub-adults are also present among the human remains. A total of eight out of the 13 adult crania have signs of perimortem blunt forced traumas (Erdal, 2012b). Petrous bones from the following eleven individuals were analyzed for DNA:

- ■ ART014 (S216 Cr2) is the cranium of a male individual. Dating of human bone: 3492-3119 cal BCE (4573 ± 27 BP, MAMS-33540)
- ■ ART015 (S216 Cr3) is the cranium of a male individual with a perimortem and two healed traumas. Dating of human bone: 3369-3110 cal BCE (4557 ± 25 BP, MAMS-33541)
- ■ ART017 (S216 Cr8) is the cranium of a male individual. No pathology was observed. Dating of human bone: 3351-3103 cal BCE (4516 ± 25 BP, MAMS-33542)
- ■ ART018 (S216 Cr9) is the cranium of a male individual. No pathology was observed. Dating of human bone: 3491-3122 cal BCE (4573 ± 25 BP, MAMS-33543)
- ■ ART019 (S216 Cr10) is the cranium of a male individual. No pathology was observed. Dating of human bone: 3499-3355 cal BCE (4623 ± 24 BP, MAMS-33544)
- ■ ART020 (S216 Cr11) is the cranium of an individual with one healed and one unhealed trauma on the left parietal bone. Dating of human bone: 3362-3105 cal BCE (4536 ± 25, BP MAMS-33545)
- ■ ART022 (S216 Cr13) is the cranium of an individual with one perimortem trauma on the right parieto-temporal region. Dental diseases were also detected. Dating of human bone: 3642-3137 cal BCE (4681 ± 75 BP, MAMS-33546)
- ■ ART023 (S216 Cr14) is the cranium of a male individual with one healed trauma on the right parietal and one perimortem trauma on the left parietal. Dating of human bone: 3486-3117 cal BCE (4563 ± 25 BP, MAMS-33547)
- ■ ART024 (S216 Temp1) is an isolated temporal bone of a male individual. Dating of human bone: 3497-3352 cal BCE (4614 ± 24 BP, MAMS-33548)
- ■ ART026 (S216 Temp3) is an isolated temporal bone of a female individual. Dating of human bone: 3340-3096 cal BCE (4491 ± 26 BP, MAMS-33549)
- ■ ART027 (S216 Temp4), temporal bones of a male individual. Dating of human bone: 3365-3108 cal BCE (4546 ± 25 BP, MAMS-33550)
- ■ ART032 (A1335 rP4 B) is represented by sparse human bones found under the floor of entrance of a communal building from Period VI B1. Dating of human bone: 3484-3124 cal BCE (4568 ± 21 BP, MAMS-34110)
- ■ ART038 [S150 (H221)] is a young female from Period VI B1/VI B2 lying on top of stone slabs closing the Royal tomb. Probably sacrificed. Dating of human bone: 3361-3105 cal BCE (4534 ± 27 BP, MAMS-34112)
- ■ ART039 [C7-D7 (H378)] is represented by a disturbed mandible stratigraphically contemporary to the burial ground of the end of Period VII. Dating of human tooth: 3762-3646 cal BCE (4916 ± 27 BP, MAMS-34116)
- ■ ART042 [S254 (H382)] is an infant in a jar burial from burial ground belonging to the end of Period VII. Dating of human bone: 3941-3708 cal BCE (5014 ± 29 BP, MAMS-34119)

### Boğazköy-Büyükkaya, Turkey

40.022056°N, 34.620611°E

Excavation: Boğazköy Expedition of the German Archaeological Institute (Istanbul Section), 1996-1998, directed by Jürgen Seeher

The settlement on the rock massif Büyükkaya (Çorum Province), within the boundaries of the later Hittite capital Hattuša, is, so far, the oldest known settlement in North-Central Turkey (Schoop, 2005, 2018). A small hamlet-sized village was situated on the uppermost plateau of Büyükkaya, high above the later city area, from where it overlooked the southern end of the Budaközü Valley. Although detailed information about the palaeo-environment of the area is lacking, this area must have been covered by forest in the past and offered few of the open spaces which are more typical for other parts of Anatolia.

Later use of the location is responsible for the fragmentary preservation of the site. Covering an area of ca. 300 sqm at the southern end of the plateau, a number of floors, hearths and storage pits were found which indicated the (probably short-lived) existence of a few small wooden structures above a fill consisting of burnt *pisé* material. At the western limit of the site, the segment of a narrow ditch was found. A single grave, belonging to a young child, was found beneath a strip of flooring, not far from one of the hearths.

Very few small finds were recovered, including a number of sickle blades made from local flint, a few heavy stone pounders and a series of fragments of polished marble bracelets. The pastoral economy relied predominantly on the exploitation of cattle, sheep and goats (von den Driesch and Nadja, 2004).

The pottery of this small settlement displays the dark-faced, burnished surfaces which are typical for the Anatolian north of this time. A small number of sherds are decorated in stab-and-drag technique or painted on a white slip. Although the assemblage is certainly representative of a discrete cultural entity which has not yet discovered elsewhere, there are clear morphological links toward contemporary Early Chalcolithic societies further to the west (Eskişehir area) and the south (Cappadocia/the Central Anatolian Plain).

Two radiocarbon dates, taken from human bone (see below) and from charcoal recovered from one of the pits, indicate a chronological position of the settlement within the second quarter of the 6th millennium BC (Schoop et al., 2012).

The single individual from Boğazköy-Büyükkaya produced genome-wide data and is included in genetic analyses.

- ■ CBT018 (Grave 347/410-315) is an infant aged 6-12 months (Thomas, 2012; Schoop et al., 2012) buried in a pit grave without any goods. The skeleton was found in contracted body position. In all probability, this grave represents an intramural burial below a house floor. Dating of human bone: 5626-5515 cal BCE (6635 ± 30 BP, SUERC-36800 [GU25423]).

### Çamlıbel Tarlası, Turkey

40.019745°N, 34.586129°E

Excavation: Boğazköy Expedition of the German Archaeological Institute (Istanbul Section) / University of Edinburgh, 2007-2009, directed by Ulf-Dietrich Schoop

Çamlıbel Tarlası is a small settlement situated on a low plateau within a narrow lateral valley branching off the southern end of the main Budaközü Valley (Çorum Province), approximately 2.5 km west of the earlier site on Büyükkaya (Schoop, 2015). The site was the location of a small hamlet which never comprised more than three to five contemporary houses. There are three distinctive and relatively short periods of permanent human presence at Çamlıbel Tarlası. In between these habitation phases, the site continued to be visited on a seasonal bases, probably by the same community, as shown by the remnants of continued agricultural and other activities during these times.

One attracting factor of the location appears to have been the presence of copper ore outcrops further into the valley. Within the settlement, fragments of copper ore, slag and crucibles show metallurgical as well as other pyrotechnical activities such as the production of enstatite (artificial steatite), quicklime and charcoal-burning. Beginning environmental degradation in the surroundings may have been a consequence of these fuel-intensive activities (Marsh, 2010).

Houses had walls constructed from stamped *pisé* on stone bases. Many had domed bread ovens in their interiors, standing on floors made from stamped earth or lime plaster. One ÇBT III building (S3 "Burnt House") clearly had a special, probably ritualistic purpose. Notable finds include a casting mold for ring-shaped figurines, enstatite micro-beads, Cappadocian obsidian and blades made from exotic flint. The pastoral economy showed an emphasis on cattle and pig-raising, with evidence of secondary product use for cattle and caprines (Bartosiewicz and Gillis, 2011). The plant-based economy suggests the working of small, intensively tended agricultural plots, with a high importance of legumes (Papadopoulou and Bogaard, 2012).

A total of 17 graves were retrieved during excavations. The majority belonged to infants and children (Thomas, 2011, 2017). Most of the stratigraphically attributable graves belong to ÇBT II and a small number to ÇBT III. Two adults seem to have been buried at times when the site was uninhabited. Babies and younger children (up to two years) were found in large pottery containers, within which their bones were not usually encountered in articulated arrangement. Elder children and adults, by contrast, were buried in narrow pits, as intact skeletons in contracted body position. With the possible exception of Graves 4 and 13, none of the burials contained any grave goods. Most children were encountered in exterior spaces, in close proximity to the house walls. Deviating from this scheme, three graves (2,16 and 17) were found below the floors of two separate structures. Remarkably, DNA analysis has shown these three individuals to be siblings (see Figure S1). Human remains and a large set of animal bones were subjected to stable-isotope analysis (Pickard et al., 2016, 2017).

Radiocarbon analysis conducted on plant seeds and human bone show a short chronological span of the whole sequence of 70 to 140 years toward the middle of the 4$^{th}$ millennium BCE (3676/3535 to 3634/3508 cal BCE cal; 17 samples) (Schoop et al., 2009). Çamlıbel Tarlası and the nearby site of Yarıkkaya constitute a variant of a larger cultural entity whose best-known representative is the Late Chalcolithic settlement at the base of Alişar Höyük (Schoop, 2011).

Twelve individuals from Çamlıbel Tarlası produced genome-wide genetic data and are included in genetic analyses.

- ■ CBT001 (Grave 1, ÇBT 204-1103) is a 9-15 months-old infant in a jar burial in juxtaposition to the west wall of building S9 (ÇBT II), under a strip of external flooring. Dating of human bone: 3632-3378 cal BCE (4725 ± 20 BP, MAMS-41627).
- ■ CBT002 (Grave 2, ÇBT 327-921) is a 9-15 months-old infant in an intramural jar burial within one of two immediately juxtaposed pits under ÇBT II building S11. The outlines of the neighboring empty pit were marked and visible on the surface of the floor. Traces of red ochre were found on some of the bones. This grave also contained a few bones of a second individuum, a second trimester fetus. Dating of human bone: 3652-3525 cal BCE (4809 ± 30 BP, MAMS-41630).
- ■ CBT003 (Grave 3, ÇBT 80-1086) is a 2-4 years-old infant, probably buried in contracted body position. The burial was fragmentary and came from a disturbed ÇBT II-III context but is possibly associated with the "Burnt House" S3 (ÇBT III). No grave goods were found.
- ■ CBT004 (Grave 4, ÇBT 406-3224) is a 8-10 years-old infant buried in a pit grave from a ÇBT II/III context. The skeleton was recovered in an extremely contracted body position. Copper staining on the upward-facing mandible and disturbance of vertebrae suggest that the grave was re-opened and that a metallic artifact was recovered at some point after the burial. Dating of human bone: 3636-3521 cal BCE (4765 ± 20 BP, MAMS-41628).
- ■ CBT005 (Grave 5, ÇBT 464-4072) is a 6-8 years-old child in a pit grave with the skeleton in contracted body position. This grave was found close to a major ÇBT IV building (S6), dug into virgin soil and covered by topsoil (context ÇBT I-IV). Dating of human bone: 3630- 3377 cal BCE (4713 ± 21 BP, MAMS-41629).
- ■ CBT010 (Grave 10, ÇBT 923-5423) is a 2$^{nd}$-3$^{rd}$ trimester fetus in a jar burial cut into bedrock, associated with a fragmentary ÇBT III building above.
- ■ CBT011 (Grave 11, ÇBT 970-6074) is a 7-9 years-old child buried in a pit grave with the skeleton in contracted body position. The grave was in an external area, in juxtaposition to the southeast wall of building S21 (ÇBT II).

- ■ CBT013 (Grave 13, ÇBT 950-6118) is a 6-8 years-old child buried in a pit grave with the skeleton in contracted body position. The burial was found under an auxiliary structure to the building S21 (ÇBT II). A bent copper perforator was found underneath the skull bones. Dating of human bone: 3643-3526 cal BCE (4796 ± 23 BP, MAMS-41631).
- ■ CBT014 (Grave 14, ÇBT 971-6144) is a 4-5 years-old child buried in a pit grave with the skeleton in contracted body position. The burial was found in an external area close to the building S29 (ÇBT II). Dating of human bone: 3640-3385 cal BCE (4767 ± 28 BP, MAMS-41632).
- ■ CBT015 (Grave 15, ÇBT 978-6140) is a fetus - 3 months-old infant in a jar burial below the building S21 (ÇBT II). Dating of human bone: 3643-3522 cal BCE (4787 ± 28 BP, MAMS-41633).
- CBT016 (Grave 16, ÇBT 894-5819) is a 1.5-2.5 years-old infant in a jar burial below the east room of the building S25 (ÇBT II). The location of the grave was marked by a circle of stones set in the floor. This grave also contained a rib from a second individuum, a fetus. Dating of human bone: 3692-3527 cal BCE (4828 ± 29 BP, MAMS-41634).
- ■ CBT017 (Grave 17, ÇBT 1010-5876) is a 12-15 months-old infant whose skeletal remains were poorly preserved. The burial was possibly a pit grave found under a strip of flooring under the west room of building S25 (ÇBT II).

### İkiztepe, Turkey

41.6136944°N, 35.8711361°E

Excavation: Istanbul University, from 1974 to 2012, directed by late U. Bahadır Alkım and Önder Bilgi

İkiztepe is a prehistoric site in the Black Sea Region in Anatolia, Turkey. The site is located 7 km west of modern town of Bafra in Samsun province, on a hilly area, 9 km north of actual seashore of Black Sea (Bilgi, 2004; Özdemir and Erdal, 2012). İkiztepe means twin mounds in Turkish, however it actually consists of four mounds (I-IV). All these mounds were settled from the Early Chalcolithic period up to the Early Hittite period. A total of 700 simple pit graves, dated to the Late Chalcolithic period and belonging to the dwellers of Mound III, were excavated in the extramural graveyard in Mound I (Bilgi, 2004). Human remains, which are extremely well preserved in terms of bone and collagen contents, are housed in the Hacettepe University Skeletal Biology Laboratory (Husbio-L).

İkiztepe is surrounded by modern Bafra plain formed by the alluvial deposits of Kızılırmak and some lagoons on the sea shore (Alkım et al., 1988). It is suggested that the settlement was located on the edge of the Black Sea during the time it was settled (Bilgi, 2000). Kızılırmak, 7 km to the east of the site at the present time, was running close to the settlement. The lifestyle of İkiztepe people was dependent on agriculture. However, the studies on animal remains and human mobility suggest that pastoral lifestyle might have also been important for these people (Welton, 2010). Dietary habits of the people were mainly based on the terrestrial C3 food sources (Irvine, 2017). Sulfur and nitrogen isotopes do not support a nutrition model that is composed of seafood and freshwater food sources.

Almost all the individuals at İkiztepe were excavated in simple pit burials without a standard tendency concerning the direction of the bodies. Except for the other Anatolian Late Chalcolithic and Early Bronze Age settlements, İkiztepe individuals were buried in supine position with the arms parallel to the body. Plenty of metal objects such as spearhead, dagger, harpoon, hook, spiral, ring and bracelet were found together with burials (Bilgi, 2004). Metal objects were produced by arsenical copper alloy. However, golden and silver rings, earrings, amulets, and pendants were also found. The number of grave goods tends to increase with the age of individuals. Moreover, there are some important differences between genders: males were buried mostly with weapons such as spearheads and quadruple spirals, on the other hand, females were buried with jewelleries, pottery and daggers.

A total of eleven individuals from İkiztepe produced genome-wide data and are included in genetic analyses.

- ■ IKI002 (IT SK528) is a 50 to 60-year-old female in a primary simple pit burial. The individual was buried in supine position with the legs extended and the arms parallel to the body. The skeleton was well preserved except from some missing long bones (right and left ulna and tibia, right radius). Grave goods include a stone necklace and a spearhead. The remains displayed evidence of a possible dermoid cist on the skull, a healed fracture on a rib, moderate osteoporosis, moderate osteoarthritis on the vertebra and caries on upper third molar. Small amount of dental calculus and mild were also observed. Dating of human tooth: 3338-3095 cal BCE (4488 ± 22 BP, MAMS-40673)
- ■ IKI009 (IT SK552) is a 18 to 28-year-old female in a primary simple pit burial. The individual was buried in supine position, extending southeast to northwest with the legs extended, the arms parallel to the body, and the skull facing left. The left arm, the pelvis and both femur bones are missing. Among the grave goods three spearheads were found. The remains display evidence of infection on the maxillary sinus (sinusitis), mild porotic hyperostosis, small amount of calculus and enamel hypoplasia on the anterior teeth. Dating of human tooth: 3366-3115 cal BCE (4552 ± 22 BP, MAMS-40674)
- ■ IKI012 (IT SK567) is a 25 to 46-year-old female in supine position, extending east to west with the legs extended, the right arm on the abdominal cavity, the left arm on the chest, and the skull facing right. The preservation of the skeleton was very good. Grave goods included a spearhead. The remains exhibit presence of two healed depression traumas on the skull, mild osteoarthritis on thoracic vertebra. Small amount of calculus and enamel hypoplasia on anterior teeth were also observed. Dating of human tooth: 3368-3118 cal BCE (4557 ± 22 BP, MAMS-40675)

- ■ IKI016 (IT SK581) is a 45 to 70-year-old female in supine position, extending west to east with the legs extended, the arms parallel to the body, and the skull facing left. All bones are present. Grave goods include two daggers, a spearhead, a bowl, two gold earrings, a frit necklace and a lead pendant. The remains exhibit presence of an unhealed fracture on a rib, mild osteoarthritis on joints and vertebra, Schmorl's nodes on thoracic and lumbar vertebra, and small amount calculus. Dating of human tooth: 3518-3371 cal BCE (4671 ± 22 BP, MAMS-40676)
- ■ IKI017 (IT SK593) is a 63 to 70-year-old female in supine position, extending southeast to northwest with the legs extended and the arms parallel to the body. The skeleton is well preserved except from some missing long bones (right forearm, right tibia). A spearhead and earrings are among the grave goods. The remains exhibit presence of moderate osteoarthritis on the joints and the lumbar vertebra, caries on the upper second molar, small amount of calculus, enamel hypoplasia on both anterior and posterior dentition and moderate periodontitis. Dating of human tooth: 3494-3124 cal BCE (4580 ± 26 BP, MAMS-40677)
- ■ IKI024 (IT SK635) is a 25 to 35-year-old male, in supine position. All bones are complete and well preserved. The remains of this individual exhibit a number of pathologies: a healed fracture on left radius, a healed fracture on fifth metacarpal, periostitis on anterior surfaces of tibia and fibula, moderately developed porotic hyperostosis, severe osteoarthritis on the distal end of left ulna possibly because of the fracture on left radius, mild osteoarthritis on thoracic and lumbar vertebra, three dental caries on both upper and lower posterior dentition, small amount of calculus, linear enamel hypoplasia on the upper anterior dentition, periapical abscess on the lower third molar and mild periodontitis. Dating of human tooth: 3958-3799 cal BCE (5080 ± 27 BP, MAMS-40678)
- ■ IKI030 (IT SK652) is a 45 to 60-year-old female, in supine position. The skeleton is complete and well preserved. The remains of this individual exhibit a number of pathologies: a healing fracture on a rib, infection on the internal surface of a rib, severe osteoporosis, mildly developed osteoarthritis on thoracic and lumbar vertebra, antemortem loss of upper second molar, 4 dental caries on posterior dentition, moderate calculus, periapical abscess on upper first molars and severe periodontitis. Dating of human tooth: 3512-3357 cal BCE (4536 ± 26 BP, MAMS-40679)
- ■ IKI034 (IT SK665) is a 14 to 15-year-old child in supine position, extending west to east. The state of the skeleton's preservation was fair. No grave goods were found. The remains exhibit evidence of a healed depression trauma on skull, small amount of dental calculus on the anterior dentition and linear enamel hypoplasia on both anterior and posterior dentitions. Dating of human tooth: 3500-3352 cal BCE (4623 ± 26 BP, MAMS-40680)
- ■ IKI036 (IT SK668) is a 30 to 40-year-old female in supine position, extending west to east with the skull facing right. The skeleton was well preserved except from distal ends of tibia and feet which were missing. Grave goods consist of a frit necklace and a ring. The remains exhibit the following pathologies: a healed depression trauma on skull, mildly developed osteoarthritis on lumbar vertebra, nine dental caries on both upper and lower posterior dentitions, small amount of dental calculus and linear enamel hypoplasia on all teeth. Dating of human tooth: 3627-3374 cal BCE (4700 ± 26 BP, MAMS-40681)
- ■ IKI037 (IT SK675) is a 35 to 40-year-old male, extending south to north, scattered. The skeleton was found complete. Grave goods include a spearhead and a frit necklace. The following pathologies were detected on the remains: three healed depression traumas on skull, both healed and unhealed fractures on carpals and phalanges, healed green stick fractures on three ribs, small sized auditory exostoses on both ear holes, mild osteoarthritis on carpals and metacarpals, Schmorl's nodes on thoracic and lumbar vertebra, two dental caries on upper posterior dentition, small amount of calculus, linear enamel hypoplasia on both upper and lower anterior teeth. Dating of human tooth: 3635-3382 cal BCE (4748 ± 29 BP, MAMS-40682)
- ■ IKI038 (IT SK677) is a 45 to 50-year-old female in supine position, extending south to north. The preservation state of the remains was very good. No grave goods were found. The remains exhibit multiple healed and unhealed fractures on ribs, a small sized button osteoma on frontal, mildly developed osteoarthritis on joints, thoracic and lumbar vertebra. Dating of human tooth: 3633-3381 cal BCE (4738 ± 26 BP, MAMS-40683)

### Mentesh Tepe, Azerbaijan

40.9418889°N, 45.8327778°E

Excavation: French Ministry of Foreign Affairs, CNRS and French-German ANR, 2008-2015, directed by Bertille Lyonnet and Farhad Guliyev

The small mound of Mentesh Tepe on the lower fan of the Zeyem Chaj – an affluent of the left bank of the Kura River, originally probably covered 0.5 ha but had been totally destroyed recently or lays beneath modern houses. Remains of its lower/main occupations were preserved under the surface. Three main periods interrupted by gaps of several centuries have been identified. The earliest (period I) is related to the Late Neolithic Shomu-Shulaveri Culture (SSC) with circular architecture both above ground and partly dug into it, and is dated by radiocarbon dates between ca. 5770-5600 BCE (Lyonnet et al., 2016). However, being on the most eastern edge of the SSC, it also presents some specific features, and relations with areas further east in the Mil'-Karabagh Steppe have been underlined (Lyonnet, 2017). This period provided several infant burials and an exceptional collective grave most probably dug into an abandoned circular house with 30 individuals of mixed ages and sexes in primary position, with no evidence of trauma, enamel hypoplasia or other pathology indicating a violent episode or starvation (Pecqueur and Jovenet, 2017). After a long abandonment, a very light reoccupation probably by mobile groups is dated to ca. 4600 BCE (period II). It was followed ca. 4350-4100 BCE by an important settlement (period III) with a totally new rectangular, and possibly tripartite, architecture. This with several other features in the material culture point at relations with the eastern areas of the Mugan Steppe and with Northern Mesopotamia (Lyonnet, 2012). Copper-based metallurgy shows a quick development (Courcier et al., 2016). This period at Mentesh clearly announces the further development and tighter relations between Southern Caucasus (Leilatepe culture) and Northern Mesopotamia (LC2-3) in the first half of the 4$^{th}$ millennium BCE (Akhundov, 2007; Lyonnet, 2007). Not very far from Mentesh, on the right bank of the Kura River, the same team excavated kurgans at Soyuq Bulaq dating to this first half of the 4$^{th}$ millennium, with one rather richly furnished with a copper knife, a stone scepter, lapis, gold and silver-copper beads. These kurgans are clearly related on the one hand to those of Sé Girdan on the south of Lake Urmia and on the other to those of the Maykop culture (Lyonnet et al., 2008), as well as to the Leilatepe culture.

Mentesh Tepe was abandoned during all this period and later only used for burials (period IV). A first kurgan was built for collective/successive inhumations (at least 39 individuals) and used during the early phase of the Kura-Araxes culture in the second half of the 3$^{rd}$ millennium BC. The kurgan was put to fire at the end, leaving the human bones in a very bad state of preservation (Lyonnet, 2014; Poulmarc'h et al., 2014). The site was possibly short-term occupied after that, until a second kurgan was built ca. 2500-2400 BCE, containing three individuals and a four-wheel cart. Its rather rich material – gold and carnelian beads and ring, an imported shell ring, spirals of tin-bronze, a silver small casket and a good amount of pottery – relate it to the Martkopi phase of the so-called Early Kurgan Culture (Pecqueur et al., 2017), a period when long distance connections develop (Lyonnet, 2016).

Extensive genetic characterization of the Late Neolithic population of Mentesh Tepe is being conducted by CNRS UMR 7206/MNHN USM 104. Here, we analyzed one individual from the Late Neolithic collective burial of Mentesh Tepe which produced genome-wide data and was included in the genetic analyses.

- ■ MTT001 (Grave 342 20 7,12; Individual 1) is an immature individual aged between 10 and 14 years buried in the Late Neolithic collective grave. The skeleton, the last to be buried of a group of 30 individuals, was found lying face down with the legs twisted. In this collective grave, the imbrication of some of the skeletons tend to point at simultaneous inhumations, while a layer of sediment covers others indicating a possible lapse of time between them. The good bone preservation and their excavation by a group of anthropologists provided many details. They show a not natural distribution of sexes (more women than men) and ages (no infant less than one year, many immatures (65%)). For more details see Pecqueur and Jovenet (2017). Dating of human bone: 7010 ± 45 BP (Sac A 41508/Gif-13016); dating of human tooth: 5717-5670 cal BCE (6802 ± 23 BP, MAMS-40333)

### Polutepe, Azerbaijan

39.5186111°N, 48.6500000°E

Excavation: Mughan Neolitic-Eneolitic expedition of the Institute of Archaeology and Ethnography of Azerbaijan National Academy of Sciences, 2006-2017, directed by Tufan Isaak oglu Akhundov

The site of Polutepe is situated on the south coast of Injachay river, on the territory of Uchtepe village, in the Jalilabad district of Azerbaijan. It is a narrow belt (zone) of the eastern part of the Mughan steppe limited by the spurs of Brovary Range to the west and the Caspian Sea to the east. Presently, the settlement is represented by a 6-ha ashy hill of up to 6 m high. Its central part is occupied by the modern cemetery of Uchtepe village. Extensive excavations have revealed cultural layers of 7 m thick. The upper layer of the site's deposits is 1 m thick and is represented by the remains of a Medieval settlement related to the IX-XI centuries CE. It is saturated with a large number of simple and glazed ceramics characteristic of the above-mentioned time.

The lower 6 m layer of cultural deposits of the settlement belongs to the Neolithic period. It contains various remains of Neolithic material culture characteristic of other Neolithic settlements of this region and which were defined by us as "Mughan Neolithic" culture. A large number of remains of ceramic utensils, bone and stone tools and other objects, burials of Neolithic inhabitants of this settlement, remains of different constructions from adobe and kilns for baking of ceramics were revealed in the different construction horizons of this layer. The greatest part of the excavated area represents a productive sector of the settlement and the revealed constructions are mainly represented by the remains of different round-planned, oval and rectangular barriers.

The unearthed burials of the settlement's inhabitants included individuals of mixed sex and all age groups, from babies to old adults aged several dozen years. The burial rituals had been performed in shallow pits on different plots among the constructions. The deceased were placed in crouched position of different degrees. Often, they were covered by red ochre and were decorated with beads that were furnished by ceramic bowl. The lower horizons of the cultural layers revealed a cult hearth and more than two dozen small stylised female clay figures.

In the stretch between the Medieval and Neolithic layers ruins and separate findings of ceramics belonging to Kura-Araxes culture and different stages of the Middle Bronze Age have been revealed as well (Akhundov, 2011; Akhundov et al., 2017).

One individual from Polutepe was analyzed for aDNA and is included in genetic analyses.

- ■ POT002 (Polutepe Burial N2) is an infant buried in a pit in a crouched position and the head orientated to the north-west. The burial was unearthed at 2.4 m depth from the Neolithic layer (approximately 10 m below the earth). The remains of the infant were very poorly preserved. Dating of human tooth: 5508-5376 cal BCE (6491 ± 26 BP, MAMS-40331)

**Tell Atchana (Alalakh), Turkey**

36.23778°N, 36.38472°E

Excavation: Trustees of the British Museum, 1937-1939 and 1946-1949, directed by Sir Leonard Woolley; Turkish Ministry of Culture and Tourism, 2003-present, directed by Kutlu Aslıhan Yener

Tell Atchana is located at the southward bend of the Orontes River in the Amuq Valley in the modern state of Hatay, Turkey (Yener, 2005, 2010). The latest chronology (see Yener, 2013a; Yener et al. 2019) puts the foundation of the site in the terminal Early Bronze Age or the earliest Middle Bronze Age (ca. 2200-2000 BCE) and the abandonment of the city in the Late Bronze Age at ca. 1300 BCE, with an Iron Age re-occupation constituting Level O (ca. 1190-750 BCE). Three hundred and forty-two burials have been documented to date, although 151 of these were excavated in the initial excavations in the 1930s and 1940s, conducted by Sir Leonard Woolley (Woolley, 1955), and the skeletal remains were not preserved. The remaining 180 graves have been discovered since 2003 as part of the renewed excavations directed by K. Aslıhan Yener. Of these, 134 were found in an extramural cemetery just outside the city fortification wall in Area 3 on the northeast slope of the mound (Akar, 2017a; Ingman, 2017; Yener and Yazıcıoğlu, 2010), while the remaining 57 were within the city in various locations, e.g., in abandoned buildings, in courtyards, etc., 26 of which were found in 2015-2019 in Area 4 in what seems to be a designated cemetery area. The overwhelming majority of the graves are single, simple pit burials, although multiple burials, cist graves, pot burials, secondary burials, and cremations have also been found in smaller numbers, as well as two constructed tombs, the Plastered Tomb in the extramural cemetery and the Shaft Grave in the Level VII (Middle Bronze II) palace (Woolley, 1939, 1955). The preservation of the burials varies widely, with those in the extramural cemetery often badly preserved and heavily disturbed, due to proximity to topsoil, slope wash, and other post-depositional processes (Akar, 2017a; Ingman, 2017) and those which are within the city walls typically much better preserved. Types and numbers of grave goods also varies with burial context, with grave goods being much rarer in the extramural cemetery, typically consisting of one or two ceramic vessels and perhaps a single piece of jewelry (typically either a metal pin or a beaded bracelet/necklace) (Ingman, 2017). In the burials within the city, though, grave goods generally are much more numerous and varied (Ingman, 2020).

Little is known about the city's early history, given the very small areas exposed to date, but he material culture recovered belongs largely to the Northwest Syrian so-called Amorite horizon, including especially Syro-Cilician Ware ceramics (Bulu, 2016, 2017; Heinz, 1992; Woolley, 1955). Sometime during this period, Alalakh and Mukish became subservient to the Amorite kingdom of Yamhad, based in Aleppo, and the kings of Alalakh had close familial ties to the kings of Yamhad (Klengel, 1992; Lauinger, 2015). Most of our understanding of Middle Bronze Age Alalakh comes from the end of the period, in Period 7, where a large palace with an archive and an attached temple, as well as a tripartite city gate, the city's fortification wall, and another potential temple have been found (Woolley, 1955; Yener, 2015a, 2015b). This period marks the first real evidence of a nascent internationalism at Alalakh (Akar, 2017a), and it ends with a large-scale fire that burned the Royal Precinct (Klengel, 1992; Woolley, 1955), often attributed to the Hittite king Hattušili I in the course of his campaigns into Syria against Yamhad (Bryce, 2005). Although the precise date of the Period 7 destruction has not yet been fixed, it marks a shift in material culture and is therefore taken as the end of the Middle Bronze age at the site, ca. 1650 BCE.

The succeeding Late Bronze I, consisting of Periods 6-4 at Tell Atchana, can generally be described as having a Hurrian/Mitannian character. This period is unclear not only at Tell Atchana, but also across Syria more generally: the destruction of Aleppo and the kingdom of Yamhad by the Hittites, accomplished shortly after the destruction of Alalakh, was followed by their destruction of Babylon (Bryce, 2005; Klengel, 1992), ending the Amorite kingdoms and apparently causing no small amount of chaos in the region (Akkermans and Schwartz, 2003). By the early fifteenth century BCE, however, the kingdom of Mitanni, based at Washukanni in the Upper Khabur (identified as Tell el Fekheriye) (Bartl and Bonatz, 2013) had emerged from the territories once controlled by Yamhad (Akkermans and Schwartz, 2003), and Alalakh became a vassal to this new regional power. This period is most well-documented in Period 4 at the site, which is characterized by a palace with archives documenting a Hurrian-style class system and many Hurrian names (von Dassow, 2008), a temple, and other administrative buildings, such as Woolley's Level IV Castle (Woolley, 1955). The material culture of Late Bronze I shows affinities with the Hurrian world to the east, such as Nuzi Ware (Woolley, 1955; Yener et al., 2019), as well as strong contacts with other, more far-flung regions, such as Cyprus (Woolley, 1955; Yener et al., 2019). This period, like Period 7, ends with a site-wide burning ca. 1400 BCE that may be associated with Tudhaliya II (Akar, 2019).

Late Bronze II, Periods 3-1, represents the last stages of Mitanni vassalhood (Period 3) and the take-over of the city by the Hittites and its incorporation into their empire (Periods 2-1) (Yener, 2013a; Yener et al., 2019). The major construction in this period were the Northern and Southern Fortresses in Period 2 (Akar, 2013, 2019), which blend characteristics of Egyptian and Hittite defensive architecture. The scale of the construction projects, the unusual building techniques, and the hints of possible Hittite administration from this period, in the form of grain distribution tablets from probable late Period 3/early Period 2 contexts (von Dassow, 2005), all suggest that Hittite Great King Suppiluliuma I took over the site, installing a vassal to rule as governor [perhaps the Tudhaliya depicted on the basalt orthostat found by Woolley in the Level Ib temple; (Woolley, 1955) and that either the king or his governor initiated the Fortresses' construction (Yener et al., 2019). The arrival of the Hittites is also visible in the material culture of the site at this time, with the introduction of several types of North Central Anatolian (NCA) ceramics, typical of the Hittite homeland (Akar, 2017b; Horowitz, 2015, 2019), as well as Hittite seals and sealings (Woolley, 1955), and a Hittite-style shaft hole axe (Yener, 2011). Contacts with the Aegean world apparently increased, judging from the large quantities of Mycenaean wares found in these periods, and the Mitannian Nuzi Ware developed into a local style termed Atchana Ware which also continues to be found in great numbers (Yener et al., 2019). The Late Bronze II occupation ends ca. 1300 BCE, when the city was abandoned, except for the temple and perhaps several buildings around it, which continued in use into the mid-13th century BCE (Yener, 2013a; Yener et al., 2019). Early Iron Age ceramics date partial architectural remains to the mid-twelfth century BCE, testifying to a small-scale re-settlement in this period (Montesanto, 2020; Pucci, 2020; Yener, 2013a). Another structure dating to Iron II has also recently been identified above the Northern Fortress, demonstrating that small-scale occupation continued, at least sporadically, at Tell Atchana, even while the main settlement moved to Tell Tayinat, the Iron Age capital of the area, only 713 m away (Yener, 2013a).

A total of 26 individuals from Alalakh produced genome-wide data and are included in genetic analyses.

- ■ ALA001 (Square 45.71, Locus 03-3017, Pail 257, Skeleton 04-9), Burial 4 in the Plastered Tomb (Yener, 2013b) in the Area 3 extramural cemetery, is the adult man (auricular age estimation of 40-45 years old) (Haas et al., 1994) in the bottom layer of this tomb. The remains exhibit the presence of Diffuse Idiopathic Skeletal Hyperostosis (DISH), a joint disease characterized by the formation of new bone in the shape of flowing melted wax found on the right side of thoracic vertebrae 4-10. DISH etiology is unclear, but it is believed to be related to obesity and diabetes (Waldron, 2001). Several of the joints and vertebrae exhibit signs of degenerative joint disease in the form of marginal osteophytes and enthesophytes (Waldron, 2001). Examination of the dentition exhibited two episodes of dental enamel hypoplasia correlating to the ages of 1.9/2.1 years and 4.5/4.7 years old, thus indicating two health disturbances that occurred during childhood growth periods (Hillson, 2014). A piece of plaster had been inserted into his mouth. His head was propped up with an s-curve jar, and in the area of his torso and pelvis were found seven bronze pins and a silver toggle pin. Eight gold appliques stamped with rosettes were around his head and chest, and a gold foil was to the left of his head. A Cypriot Base Ring I jug was along the southeast wall of the tomb and another was near his right forearm; two spindle bottles (one Red Lustrous Wheelmade Ware and one locally made in Red Burnished Ware) were found, one placed in the south corner of the tomb and one at his left elbow; a Syrian Brown-Grey Burnished Ware cylindrical cup was in crook of his right arm and another was found just above his left elbow; and, a Red Slipped narrow-necked jug was along the southwest wall of the tomb. An amber pendant was found on his legs, along with a bone spindle whorl, several pieces of chert, and beads of carnelian, bone, faience, and glass were also discovered with the body. Two haunches of beef had been placed near his left arm and left femur, and a caprid molar was also found with his remains, indicating that food had been deposited with him. This is the single richest assemblage of grave goods ever found with an individual at Tell Atchana. Dating of human bone: 1496-1325 cal BCE (3151 ± 24 BP, MAMS-33675).
- ■ ALA002 (Square 45.71, Locus 03-3017, Pail 246, Skeleton 04-8), Burial 2 in the Plastered Tomb (Yener, 2013b) in the Area 3 extramural cemetery, is the young adult male (age estimation of 19-21 years based on the different degrees of epiphyseal plates fusion) (Schaefer et al., 2009) in the top layer of this tomb. The orbital bones exhibit *cribra orbitalia*, along with porotic hyperostosis on both parietal bones located medially along the coronal suture, indicating the body's response to a pathological condition (Rothschild, 2002). Both humeri have the non-metric trait of Septal Aperture (Barnes, 2012). A vertical bone had been placed inside his mouth. Six bronze pins were found around his torso, along with a bone needle. Several gold appliques stamped with rosettes (one with red pigment preserved on the stamped side) were found near his head, and he was wearing an *in situ* necklace of alternating gold, carnelian, and vitreous white beads. Additional beads of the same materials were also found with this individual. A gold ring was found *in situ* on his left thumb. Several clay pellets and pieces of chert, as well as two lumps of vitrified material (one placed under his chin), were also found with this individual. Dating of human bone: 1496-1401 cal BCE (3158 ± 22 BP, MAMS-33676).
- ■ ALA004 (Square 45.72, Locus 03-3002, Pail 40, Skeleton 04-25) is an adult male (age estimated as 40-45 years old) (Haas et al., 1994) found in a bone scatter that likely represents a disturbed primary burial in the Area 3 extramural cemetery. The remains are half complete and mixed with other individuals' remains. Both fibulae and the right tibia all exhibit well-healed Periostitis (indicating an episode of infection or trauma) along the medial shafts (Mann and Hunt, 2005). Marginal osteophytes and enthesopathy are found on the pelvis and left shoulder (Waldron, 2001), a condition that is typical of old age. The skull exhibits a well-healed trauma located on the left side of the frontal bone (Byers, 2011). No grave goods were recovered. Dating of human bone: 1895-1752 cal BCE (3507 ± 23 BP, MAMS-33677).
- ■ ALA008 (Square 45.44, Locus 133, AT 17652) is represented by an adult skull (with features indicating a male, age estimation of 25-35 years) (Haas et al., 1994) and several finger bones, although the simple pit grave continued into the east baulk, in the Area 3 extramural cemetery. No grave goods were found. Dating of human bone: 1881-1700 cal BCE (3473 ± 23 BP, MAMS-33678).
- ■ ALA011 (Square 45.44, Locus 146, AT 18960) is a child (3.5-4 years old) (Schaefer et al., 2009) buried in a simple pit grave inside a casemate within the Area 3 fortification wall (Ingman, 2017; unpublished data). Only the legs and feet were within the square, as the grave extended into the north baulk. A Simple Fine Ware shoulder goblet was found in the baulk near the child's pelvis. Dating of human bone: 1741-1624 cal BCE (3382 ± 23 BP, MAMS-33680).
- ■ ALA013 (Square 45.44, Locus 152, AT 19260) is an infant (dental age of 1.5-2 years old) (Schaefer et al., 2009) found in the Area 3 extramural cemetery. Age estimation based on skeletal long bone growth gave an age of 6-8 months (Schaefer et al., 2009), thus indicating that the child had stunted growth of around 1 year. The upper first molars exhibit the dental morphology feature of Carabelli's cusp (Scott and Irish, 2017). A bronze ring and a silver ring, two beaded necklaces, a Simple Ware biconical cup (at the left elbow), a Simple Ware globular juglet (at the left side of the pelvis), a Simple Ware short-neck jar

(at the left elbow), and a piece of lead wire were found. Dating of human bone: 1878-1693 cal BCE (3457 ± 24 BP, MAMS-33681).

- ■ ALA014 (Square 45.45, Loci 8 and 9, AT 8836) is an adult (age estimation of 35-55 years) (Haas et al., 1994) found in a simple pit grave in the Area 3 extramural cemetery. There were no grave goods. Dating of human bone: 1743-1630 cal BCE (3392 ± 23 BP, MAMS-33682).
- ■ ALA015 (Square 45.45, Loci 18 and 19, AT 15741) is an adult found in the Area 3 extramural cemetery in a simple pit grave. A shell pendant was found in the grave. Dating of human bone: 2014-1781 BCE (3566 ± 26 BP, MAMS-33683).
- ■ ALA016 (Square 32.54, Locus 85, AT 17541) is an adult female (age estimation of 65-75 years old) (Haas et al., 1994) buried in a simple pit grave in a temporarily abandoned building in the Royal Precinct below a subsequent floor. The skeletal remains exhibit evidence of degenerative joint disease (osteoarthritis - OA) found on the majority of the joints, such as knees and hand phalanges, with eburnation (Waldron, 2001). Vertebrae joints exhibited fusion, in addition to OA, with the cervical 7 and thoracic 1-4 all fused. There is the rare presence of adventitious bursa on lumbar 4 and 5 (Kwong et al., 2011). The frontal bone exhibited *hyperostosis frontalis interna* on the ventral surface (Roberts and Manchester, 1995). Examination of the dentition showed two episodes of dental enamel hypoplasia correlating to the ages of 2.8/3.1 years and 4.2/4.9 years old (Hillson, 2014), thus indicating two health disturbances that had occurred during childhood growth periods. A bronze pin was next to the skull, and several bone and vitreous beads were in the area of the neck. Dating of human bone: 1617-1506 cal BCE (3566 ± 26 BP, MAMS-33683).
- ■ ALA017 (Square 32.57, Loci 160 and 164, AT 10070) is a young adult female (dental age of 17-25 years old) (Brothwell, 1981) buried in a simple pit burial dug into a street in the Royal Precinct. Only the top of the skull was found within the excavation area, as the rest of the burial extended into the east baulk. The nuchal crest is score 4, as a male (Haas et al., 1994), thus indicating the use of the neck muscles for caring heavy material, possibly on the head. The upper first molars exhibit the dental morphology feature of Carabelli's cusp (Scott and Irish, 2017). The skull and the deposit above it were both burnt, likely as a result of a post-deposition burning episode unrelated to the burial. Three Grey Burnished Ware vessels (a narrow-necked jug, a long-necked globular juglet, and an omphalos bowl) were grouped above the head, and a conch shell pendant was also recovered from the burial. Dating of human bone: 1614-1466 cal BCE (3264 ± 23 BP, MAMS-33685).
- ■ ALA018 (Square 42.29, Locus 44, AT 19127) is a child (dental aged at 4.5-5.5 years) buried in a simple pit grave in an accumulation fill not far outside the Royal Precinct. Skeletal growth gave the age estimation of 3.5-4 years (Schaefer et al., 2009), thus indicating a stunted growth by around 1 year. Examination of the dentition exhibited two episodes of dental enamel hypoplasia correlating to the ages of 1.5/1.7 years and 2.0/2.3 years old (Hillson, 2014), thus indicating two health disturbances during childhood growth periods. A string of vitreous beads was around the neck, a Nuzi Ware goblet was behind the feet, and an astragalus was also found in the grave. Dating of human bone: 1497-1326 cal BCE (3154 ± 26 BP, MAMS-33686).
- ■ ALA019 (Square 32.57, Locus 247, AT 15878) is an adult female aged 40-45 years old (Haas et al., 1994) found at the bottom of a very deep well [hence, dubbed "the Well Lady"; (Shafiq, 2020)]. The remains exhibit presence of osteoarthritis with eburnation (OA) on the cervical vertebrae between C1 and C2 (Waldron, 2001), along with the rare presence of adventitious bursa (Kwong et al., 2011) on lumbar 3 and 4. The individual shows evidence of healed trauma on the frontal bone of the skull (Byers, 2011) and two healed fractured ribs (Shafiq, 2020). Enthesophytes were found on both calcaneal bones (Waldron, 2001). The upper lateral incisors exhibit the dental morphology feature of shoveling, score 5 (Scott and Irish, 2017). Her dentition exhibited multiple episodes of dental enamel hypoplasia, starting from 1.3 years old up to 4.6 years old, with a total of twelve childhood growth disturbances (correlating to the ages of 1.3/1.5, 1.7/1.8, 1.9/2.0, 2.0/2.3, 2.6/2.8, 2.7/3.0, 2.8/3.1, 3.1/3.4, 3.5/3.7, 3.7/4.2, and 4.0/4.4-4.6 years old) (Hillson, 2014). She was discovered facedown with her limbs splayed, indicating that she had been carelessly thrown into the well while it was still in use (probably for domestic/craft purposes or for animals). As this individual's deposition was the result of misadventure, rather than deliberate burial, there are no accompanying grave goods. Dating of human bone: 1625-1511 BCE (3298 ± 23 BP, MAMS-33687).
- ■ ALA020 (Square 44.86, Loci 18 and 22, AT 15460) is a young adult female (age estimation of 25-35 years old) (Haas et al., 1994) buried in a simple pit grave dug into a debris layer in Area 2, although bones of another individual, a male, based on the pelvic features, were mixed into the debris. The frontal bones exhibit *cribra orbitalia*, indicating a stressful health condition at the time of death (Rothschild, 2002). The dentition exhibits dental enamel hypoplasia occurred at the ages of 1.7/1.8 and 2.2/2.4-2.7 (Hillson, 2014). No grave goods were found. Dating of human bone: 1502-1395 BCE (3167 ± 29 BP, MAMS-33688).
- ■ ALA023 (Square 45.44, Locus 65, AT 6029) is a child (dental age of 6.5-7 years) (Schaefer et al., 2009) in a simple pit grave -part of a cluster of three burials in the Area 3 extramural cemetery (with ALA025 and Locus 67)- whose skull was placed directly over that of ALA025. The skull exhibits the non-metric feature of Apical Bone on the occipital bone (Barnes, 2012). A lead ring was found in the fill above the remains. Dating of human bone: 1921-1763 BCE (3520 ± 25 BP, MAMS-38610).
- ■ ALA024 (Square 45.44, Locus 68, AT 6572) is a child (2-3 years old) (Schaefer et al., 2009) in a simple pit grave in the Area 3 extramural cemetery. A Simple Ware short-neck jar was found above her head. Dating of human bone: 2111-1779 BCE (3586 ± 39 BP, MAMS-33690).
- ■ ALA025 (Square 45.44, Locus 66, AT 6032) is an adolescent female aged 13-14 years old in a simple pit grave directly under ALA023 in the Area 3 extramural cemetery. The skeletal growth of long bones gives an age of 11 years old (Schaefer et al., 2009), indicating stunted growth of two years. The frontal bones exhibit *cribra orbitalia* (Rothschild, 2002) in the healing process

at the time of death. Dentition exhibit two health disturbances, with dental enamel hypoplasia at the ages of 3.3/3.4 and 4.3/4.8 years (Hillson, 2014). A Simple Fine Ware short-neck jar was placed on her crossed arms. Dating of human bone: 1877-1686 BCE (3443 ± 25 BP, MAMS-33691).

- ■ ALA026 (Square 45.44, Locus 70, AT 6931) is a child aged 3.5-4 years in a simple pit burial in the Area 3 extramural cemetery. However, the skeletal age gives 2.5 years (Schaefer et al., 2009), indicating in stunted growth of 1 year. A Syrian Brown-Grey Burnished Ware piriform juglet was placed near the mandible. Dating of human bone: 1744-1628 BCE (3390 ± 25 BP, MAMS-33692).
- ■ ALA028 (Square 45.44, Locus 73, AT 7395) is an adult female aged 30-40 years old (Haas et al., 1994) represented by disarticulated remains in simple pit grave in the Area 3 extramural cemetery. This grave was directly above the pit grave of ALA029, with the pelvis of ALA028 resting on the skull of ALA029. This burial likely represents a primary burial that was disturbed; the disturbed remains were collected and then reburied. No grave goods were found. Dating of human bone: 1877-1666 BCE (3440 ± 26 BP, MAMS-33693).
- ■ ALA029 (Square 45.44, Locus 79, AT 7695) is an adult female aged 20-30 years old (Haas et al., 1994) represented by the skull in a simple pit grave directly below ALA028. The skull was partially crushed by the pelvis of ALA028, which rested directly on top of it. Although the majority of the bones were in anatomical position, the grave was clearly reopened/disturbed in antiquity, as both femurs had been turned upside-down. This may have occurred at the same time as ALA028's burial. A Simple Ware short-neck jar was under her chin, a Syrian Brown-Grey Burnished Ware piriform juglet was behind her skull, and a toggle pin was found during screening. Dating of human bone: 1880-1695 BCE (3465 ± 26 BP, MAMS-33694).
- ■ ALA030 (Square 45.44, Locus 105, AT 10669) is an adult female, aged 30-35 years old (Haas et al., 1994), who seems to have been killed during the destruction of the building next to the fortification wall in Area 3. The remains indicate a rather small-sized female, with a collapsed vertebra body of L1 (Waldron, 2001) on the left side of the vertebral body, a possible case of carrying heavy weights, along with bone growth on lower thoracic T11 and T12. The left shoulder exhibit a condition of *osteochondritis dissecanus*, a joint pathology (Waldron, 2001). Both humeri exhibit the non-metric trait of Septal Aperture (Barnes, 2012). The upper incisors show the dental morphology feature of shoveling (Scott and Irish, 2017). Evidence of six health disturbances during the growth period are visible as dental enamel hypoplasia at the ages of 1.3/1.5, 1.7/2.0, 1.9/2.1, 2.6/2.8, 2.8/3.1, and 3.2/3.3 years (Hillson, 2014). Found in a burnt room context, she was discovered on her back with her arms pulled up to her chin and her legs disappearing into the west baulk. Because this individual met with her death, and was subsequently buried, by misadventure, there were no grave goods. Dating of human bone: 1612-1457 BCE (3256 ± 25 BP, MAMS-33695).
- ■ ALA034 (Square 45.45, Locus 6, AT 8830) is an adult female aged between 25-35 years old (Haas et al., 1994) whose simple pit grave in the Area 3 extramural cemetery remains mostly within the west baulk. No grave goods were found. Dating of human bone: 1874-1666 BCE (3436 ± 24 BP, MAMS-33696).
- ■ ALA035 (Square 45.45, Locus 7, AT 7940) is an adult male aged between 25-35 years old (Haas et al., 1994) whose remains were found in the Area 3 extramural cemetery in a simple pit containing the dense and highly disarticulated remains of three other adults (two males and one female). ALA035 appears to have been a primary burial, and the remains of the three other adults were likely redeposited with this individual after having been disturbed. The lower limbs, femur, and tibia exhibit *periostitis* along the shafts (Mann and Hunt, 2005), and joint disease of the scapula was also identified (Waldron, 2001). There is one line of dental enamel hypoplasia at the age of 1.9/2.1 years old (Hillson, 2014). No grave goods were found. Dating of human bone: 1948-1774 BCE (3542 ± 24 BP, MAMS-33697).
- ■ ALA037 (Square 45.45, Loci 30 and 31, AT 11452) is a concentration of bones containing the disturbed remains of multiple individuals in the Area 3 extramural cemetery. The long bones are oriented northeast-southwest, parallel to the slope of the mound in this area, which may be the result of post-depositional slope wash or deliberate secondary repositioning. Given the high degree of disturbance in this area generally due to post-depositional processes (Ingman, 2017), the former is perhaps more likely. No grave goods were found. Dating of human bone: 1882-1701 BCE (3477 ± 24 BP, MAMS-33698).
- ■ ALA038 (Square 45.71, Locus 03-3017, Pail 236, Skeleton 09-07), Burial 1 in the Plastered Tomb (Yener, 2013b) in the Area 3 extramural cemetery is an adult female (aged 35-45 years old) (Haas et al., 1994) in the top layer of this grave and the final individual deposited in the tomb. Both humeri exhibit the non-metric trait of Septal Aperture (Barnes, 2012). Although, this burial was disturbed, probably due to its proximity to the topsoil, in the area of her head and torso were found several bronze pins, as well as beads made of gold, metal, amber, and stone. Two Simple Ware bottle jugs were placed with her, one atop her torso and one along her left femur, and two Simple Ware globular pitchers were found, one near her skull and one at her right hip. A Simple Ware lamp was under the right side of her pelvis. A cattle humerus and a sheep haunch were above the right side of her pelvis, indicating that food offerings were deposited with this individual. Dating of human bone: 1613-1461 cal BCE (3260 ± 24 BP, MAMS-33699).
- ■ ALA039 (Square 44.85, Locus 15, AT 14466) is represented by a skull of an adult female aged 50-60 years old (Haas et al., 1994) and was placed upright with a human pelvis (presumably belonging to the same individual, but this is uncertain) next to it. These remains were found in a simple pit dug into an accumulation layer with *tandırs* and trash pits in Area 2. The skull shows evidence of blunt trauma located on the right parietal bone in a circular shape, with the bones fractured ventrally. There are no radiating fracture lines and no signs of healing, termed *perimortem.* The fracture size measures 16.2 × 15.3 mm with a depth inside the bone of 2.5 mm, suggesting that this was most probably the cause of death, indicating a violent death (Byers, 2011).

Under the skull was a chunk of iron oxide. This is likely a secondary burial, given the iron oxide and the non-random positioning of the skull, but it could also have been disturbed from an unpreserved (or as-yet-undiscovered) grave. Dating of human bone: 1448-1303 BCE (3125 ± 24 BP, MAMS-33700).

- ■ ALA084 (Square 45.72, Locus 03-3065, Skeleton 04-19) is an adult female aged 25-30 years (Haas et al., 1994), buried in a simple pit grave in the Area 3 extramural cemetery. The ventral surface of the occipital, parietal, and frontal bones all exhibit meningeal reaction, indicating a case of infection or trauma (Schultz, 2003), and porotic hyperostosis was also observed (Rothschild, 2002). No grave goods were found. Dating of human tooth: 2006-1777 BCE (3556 ± 25 BP, MAMS-41108).
- ■ ALA095 (45.72, L03-3013/3016, pail 54) is represented by a tooth that was part of a heap of bones and teeth from a minimum of three individuals (2 mature and 1 immature) lying on top of a single pit grave of an adult male from the Area 3 extramural cemetery. No grave goods were found. Dating of human tooth: 1913-1756 BCE (3516 ± 25 BP, MAMS-41109)

### Tell Mardikh (Ebla), Syria

35.798°N, 36.798°E

Excavation: Italian Expedition of the Sapienza University of Rome (Missione Archeologica Italiana in Siria - MAIS), 1964-2010, directed by Paolo Matthiae

Tell Mardikh, ancient Ebla is an archaeological site located in the Idlib Governorate, 56 km southwest of Aleppo, on the limestone plateau of Northern Syria. The excavations revealed a long occupation sequence, spanning from at least Early Bronze Age III until the Iron Age, with later occupation or frequentation in the Hellenistic/Roman, Byzantine, and Crusader Periods (for an overview, see Matthiae, 2010).

Although stray archaeological materials dating from the Chalcolithic period were found at Ebla, the earliest settlement uncovered thus far at Tell Mardikh dates from Early Bronze III (ca. 2750/2700-2550 BCE) and is represented by the remains of non-residential structures with facilities for crop storage uncovered on the Acropolis Italian Expedition of the Sapienza University of Rome (Matthiae, 1993b; Mazzoni, 1991; Vacca, 2015). This evidence documents a formative phase of urbanisation that puts the developmental trajectory of Ebla in line with the development of other archaeological site in western inland Syria, such as Hama and Qatna, and with neighboring regional areas, such as the Middle Euphrates Valley and the Jazirah (Vacca, 2015).

The process toward increasing social, economic, and political complexity continued during the initial stage of Early Bronze IVA (ca. 2550-2450 BC) (Vacca, 2014–2015, 2015). It culminated, in the developed phase of the Early Bronze IVA (ca. 2450-2300 BCE), in the formation of an archaic state ruled by Ebla (Matthiae, 2013b), documented by the archives of cuneiform tablets discovered in the destruction layer of the Royal Palace B dating from this period. It is estimated that the territory controlled by Ebla extended from around Hama, to the south, to Karkemish, to the north. At this time, Ebla had diplomatic and commercial relationships with equivalent kingdoms located along the Euphrates River Valley, in Upper Syria and in Upper Mesopotamia, as well as with Byblos and with Egypt. A fierce destruction put an end to this flourishing phase (Matthiae, 2009a), which is placed in the interval between 2367 and 2297 cal BCE by the average weight of available radiometric determinations (Calcagnile et al., 2013).

After this dramatic event, during Early Bronze IVB (ca. 2300-2000 BCE) Ebla lived a stage of initial crisis and following reorganization during the initial and central stages of the period, respectively, followed by a phase of new growth, represented by the reappearance of public, monumental architecture at the site, during the late phase of the period, during the 21th century BCE (D'Andrea, 2014–2015; Matthiae, 2006, 2007, 2009b). At this time, Ebla had commercial relations with the Ur III Dynasty in southern Mesopotamia. Another destruction put an end to this phase of the settlement (Matthiae, 2009a, 2020) followed by a short squatters' reoccupation (Matthiae, 2020; D'Andrea, 2014–2015, 2018) and by a substantial reconstruction of the city of the Middle Bronze Age at the onset of the 2$^{nd}$ millennium BCE, when an Amorite dynasty seized power.

It seems more and more possible that some of the cultural developments of the Middle Bronze Age (ca. 2000-1600 BCE) started earlier, during Early Bronze IVB and elements of continuity between Early Bronze IV and the Middle Bronze Age have been noticed in material culture, architecture, iconography, and royal ideology (D'Andrea, 2019; Matthiae, 2002, 2013a; Pinnock, 2009). However, the reconstruction of the Middle Bronze Age city was marked by substantial changes in the urban layout. The new 2$^{nd}$ millennium BCE city comprised the massive earthen rampart fortifications with four city-gates and several forts and fortresses; a Royal Citadel with a royal palace and dynastic temple on the Acropolis (Matthiae, 2011), encircled by an inner fortification; and a belt of temples, sanctuaries, and palaces around the Acropolis uncovered on the north, west and south sides.

Epigraphic data allowed determining that the new Middle Bronze Age city was the seat of Amorite leaders since the beginning. From circa 1800 BCE, Ebla was subjugated by the kingdom of Yamhad, centered on Aleppo, but remained a major regional center, with a flourishing and sophisticated urban culture, as testified, for example, by the jewelry and metalwork found in the Royal Hypogea or the bone and ivory Egyptianizing inlays discovered in the Northern Palace (Scandone Matthiae, 2002), as well as with far-reaching interregional relations. A third, final, destruction brought also the Middle Bronze Age settlement of Ebla to an end; from a bi-lingual Hittite-Hurrian text called Song of Release, it seems that the site was destroyed by a coalition of Hittites and Hurrians led by an otherwise unknown personage called Pizikarra of Nineveh (Matthiae, 2009a).

After this major destruction, the site never recovered as a regional center, although it was continuously occupied during the Late Bronze Age (ca. 1600-1200 BCE), as demonstrated by the archaeological investigations on the Acropolis (Matthiae, 2011). The site was occupied by a rural village during Iron Age I-III (ca. 1200-535 BCE), and was the seat of a palace during the Persian/Hellenistic

Period (ca. 535-55 BCE). Subsequently, it was occupied by a monastic community during the Roman/Byzantine Period (ca. 55 BCE-AD 600), and, after this, it was never permanently settled again; at the time of the First Crusade, at the end of the 11th century AD, the troops of Godfrey of Bouillon shortly stopped at the site on their way to Jerusalem (Matthiae, 2010).

A total of eleven individuals from Ebla produced genome-wide data and were including in genetic analyses.

- ■ ETM001 (individual from TM.82/79.G.400, Dep K (A+B) or Tomb D1) (Baffi Guardata, 1988) is a 5 to 7-year-old child represented by a fragmentary skull and a few fragmentary skeletal remains in a multiple pit burial. The pit was cut through the layers associated with the EB IVA Palace G and is dated to the Middle Bronze I (ca. 2000-1800 BCE). Funerary goods included 19 pottery vessels, a bronze bracelet, and animal bones (Baffi Guardata, 1988).
- ■ ETM004 (TM.98.V.538, D.7417, Skull A) is a child aged between 6 and 12 years whose remains were identified by a skull in a pit burial with multiple mixed disarticulated inhumations (e.g., ETM005 and ETM006). The burial is dated to the Middle Bronze Age I (ca. 2000-1800 BCE). Funerary goods were represented by 16 pottery vessels, either complete or almost complete.
- ■ ETM005 (TM.98.V.538, D.7417, Skull B; same burial as ETM004) is an adult aged between 30 and 40 years identified by the skull. Dental pathologies were observed.
- ■ ETM006 (TM.98.V.538, D.7417, Skull C; same burial as ETM004) is an adult aged between 30 and 40 years identified by the skull. Dental pathologies were observed.
- ■ ETM010 (TM.98.CC.113, D.7278) is a macroscopically possible male individual, aged between 30 and 40 years in a pit grave from the Early Bronze III Period (ca. 2700-2500 BCE). The skeletal remains were fragmentary and disarticulated. Dental pathologies and osteological conditions at the lower limbs were observed.
- ■ ETM012 (TM.91.P.853/2) is an infant aged 6-12 months, possibly buried in a jar. The skeletal remains were found in room L.5021 of Building P4 (for the archaeological context and pottery assemblage of the building) (see Matthiae, 1993a, 2013; Marchetti and Nigro, 1995–1996), a workshop area, lying on the floor of the room, along with a large amount of pottery sherds, suggesting that this might have originally been a jar burial. In spite the fragmented condition of the burial, almost the complete skeleton of the infant was recovered. No evidence of pathologies was present and no associated funerary goods were found. Dating of human bone: 2572-2470 cal BCE (3997 ± 25 BP, MAMS-41114)
- ■ ETM014 (TM.95.V.491, D.6371) is an individual aged between 30 and 35 years in a poorly preserved pit burial (Baffi Guardata, 2000). The skeletal remains were also very fragmentary. Caries were observed on one of the preserved teeth. The tomb was identified in the area of the Middle Bronze Age I (ca. 2000-1800 BCE) rampart; funerary goods were represented by a single combed jar (Baffi Guardata, 2000).
- ■ ETM016 (TM.95.V.497, D.6384) is a male individual aged 20-30 years, buried in a crouched position in a pit that dates to the Late or terminal Middle Bronze IB (ca. 1850 BCE). The pit burial was possibly originally lined with mud bricks. The complete skeleton was preserved (Baffi Guardata, 2000) and did not display any evidence of pathologies. Funerary goods included five pottery vessels: a miniature cup in Cooking Ware fabric, a cooking pot, a combed jar, a miniature trefoil-mouthed juglet, and a carinated bowl (Baffi Guardata, 2000). Dating of human bone: 2026-1896 cal BCE (3605 ± 25 BP, MAMS-41116)
- ■ ETM018 (TM.98.AA.310, D.7363) is a macroscopically possible male individual, older than 45 years who was identified by an incomplete skull. He was buried with at least two more individuals in a pit burial that was covered by mud bricks and was dated to the Middle Bronze I (ca. 2000-1800 BCE). His dental condition is consistent with the age at death. Funerary goods included a fragmentary clay figurine, a shell, and eight pottery vessels: a jar, two collared jars/bowls, a piriform jar, an ovoid jar, and three carinated bowls. Presence of animal bones was associated with the burial. Dating of human tooth: (2135-1964 cal BCE, 3667 ± 26 BP, MAMS-41635)
- ■ ETM023 (TM.82.G.438, D. μ TM.83.G.438) is an individual aged 15-18 years that was found in pit seemingly intruding into the Early Bronze IVA layers of Palace G. The skeletal remains of this individual were incomplete and exhibited visible signs of burning. The skull was recovered complete. The chronology is not determined, although the anthropological report refers to an EB IVA date for the bones (ca. 2350/2300 BCE).
- ■ ETM026 (TM.83.G, D.3620 or D.22 in Baffi Guardata [2000]) is a male individual aged 25-30 years, in a primary crouched burial. The pit burial is dated to the Middle Bronze I (2000-1800 BCE), possibly to its earliest phase (Nigro, 2002). The skeletal remains were well preserved, though incomplete and fragmentary. The dentition displayed evidence of tartar and enamel hypoplasia. Funerary goods include a jar with double-everted rim and a cooking pot (Baffi Guardata, 1988) and the skull of an ovine was associated with the human bones (Baffi Guardata, 1988)

### Tell Kurdu, Turkey

36.329405°N, 36.444255°E

Excavation: University of Chicago, Oriental Institute, 1995-2001, directed by Kutlu Aslıhan Yener. The site of Tell Kurdu is located in the Amuq Plain in the Turkish province of Hatay in southern Turkey (Özbal et al., 2004). The roughly triangularly shaped Amuq Plain measures about 35 × 40 km and is covered with fertile agricultural soils. The plain is surrounded on all sides by upland ranges including the Amanus Mountains, Kurt Dağ, Jebel Zahwiye and Jebel al-Aqra and is fed by three rivers: the Kara Su, the Afrin and the Orontes. The mound of Tell Kurdu, located centrally in the plain, was occupied in the 6th and the 5th millennia BCE and is the largest prehistoric site known in the valley. The 6th millennium levels at the site correspond to the Amuq C Phase contemporaneous with the North Mesopotamian Halaf Period, while the 5th millennium levels correspond to the Amuq E Phase, which based on the Northern Mesopotamian chronological periods equates with the Ubaid Period. All of the six burials from Tell Kurdu analyzed for this project come from the 2001 excavations which were concentrated on the north of the mound (Özbal, 2006). Excavations here yielded a neighborhood of densely packed small structures separated by streets and alleys that date to the Amuq C Phase of the 6th millennium BCE. Based on stratigraphy, one of the burials analyzed (KRD001) was securely dated within the architectural phase while most of the other burials in this study including KRD003, KRD004, KRD005, KRD006 were stratigraphically unclear and were assumed to date to just after the architecture had been abandoned. However, the radiocarbon dates suggest that they fall squarely within the main architectural phase or were buried very briefly following abandonment. Even though it essentially came from the same area, KRD002 dates to about a millennium later when this part of the mound functioned as a cemetery during the Amuq E Phase. The main occupation in this phase was concentrated on the southern parts of the mound. The age descriptions and sex designations for the burials described below come from an unpublished study by Lorentz and supersede those published in (Özbal et al., 2004).

A total of six individuals from Tell Kurdu produced genome-wide data and are included in the genetic analyses.

- ■ KRD001 (TK_12:81) is an adolescent aged 10-12 years. The burial was securely dated to the Amuq C Phase related to the main architectural phase. No burial gifts were found associated with the skeleton which was discovered in a tightly flexed position. The inhumation was found cut into the lowest excavated floor of Room R06 and sealed by an overlying floor. Dating of human bone: 5710-5662 cal BCE (6783 ± 23 BP, MAMS-40663).
- ■ KRD002 (TK_24:3) is a relatively well-preserved mature adult. The burial included one small Amuq E Phase painted cup which was placed not far from the individual's head. Unlike other burials which are typically found in simple pits, this one was placed in a rectangular mudbrick box of which the bottom row of bricks was preserved. Dating of human bone: 4991-4911 cal BCE (6044 ± 22 BP, MAMS-40664).
- ■ KRD003 (TK_22:2) is a mature adult placed in a simple pit in a tightly flexed position. The burial included a small painted necked-jar placed near the head as well as a Dark Faced Burnished globular jar discovered by the feet. Dating of human bone: 5661-5630 cal BCE (6739 ± 23 BP, MAMS-40665).
- ■ KRD004 (TK_25:80) is an adult male placed in a pit in a tightly flexed position. A small Dark Faced Burnished necked-jar was discovered by the head. A partial cattle mandible had been left just over the neck of the jar. Dating of human bone: 5703-5639 cal BCE (6766 ± 25 BP, MAMS-40666).
- ■ KRD005 (TK_25:89) is an infant buried in a flexed position. A small unpainted vessel was directly by the infant's head. The burial's stratigraphic relationship to the architecture is not clear but it was placed in room R45 either when the room was in use or shortly after abandonment. Dating of human bone 5739-5676 cal BCE (6738 ± 24 BP, MAMS-40667).
- ■ KRD006 (TK_26:12) is an infant placed in a large bowl. Near the infant and possibly associated with the burial, excavations yielded a small painted miniature vessel, which based on decoration and style must be considered Amuq C in date. Given the location of the burial inside room R54 and the motifs on the nearby vessel, we expect this burial to be contemporaneous with the others analyzed here (with the exception of KRD002) and that it dates to approximately 5700 cal BCE.

### Titriş Höyük, Turkey

37.4759306°N, 38.6783333°E

Excavation: University of California San Diego 1991-1999, directed by Guillermo Algaze

Titriş Höyük, situated in the lower Euphrates basin, is located 45 km north of Şanlıurfa, Turkey (Matney and Algaze, 1995). On the basis of C14 dating, three culture levels were identified at the site; Early EBA (ca. 2900–2600 BCE), Mid EBA (ca 2600/2500–2400/2300 BCE) and Late EBA (ca. 2300–2200/2100 BCE) (Algaze et al., 1995, 1996, 2001; Matney et al., 1997, 1999). Spread over a 43-hectare area, Titriş Höyük has an acropolis in the center, the Lower Town surrounding the acropolis, and the Outer Town which consists of sparsely scattered suburban areas (Matney and Algaze, 1995).

The settlement expanded from the acropolis to the Lower Town during the Early EBA. In the Mid EBA, the Lower Town developed further and spread toward the Outer Town. There is an extramural cemetery dating to this period 400 m. west of the settlement. The settlement had undergone significant changes with the Late EBA; the houses in Outer Town were abandoned and the city was surrounded by a large fortification wall. Titriş Höyük people who started to live behind this wall in the Late EBA stopped using the extramural cemetery and began to bury their dead in housing areas, beneath the floors of rooms or courtyards (Laneri, 2007).

Since the excavations in the Early EBA level were limited to a small area, only one cist grave could be unearthed. On the other hand, there are 50 and 67 graves dating to Mid and Late EBA respectively. These graves consist of simple pits, stone cists and pithoi. Multiple burials were found in both Mid and Late EBA graves. While some individuals were articulated, some others completely lost their articulation. The skeletal remains which have no articulation, are represented only by skull and a few postcranial bones. It is stated that all the bones except skulls were removed to make room for the last deceased (Laneri, 2007; Matney et al., 2012). For this reason, the preservation condition of Titriş Höyük skeletal remains is not good and the individuals are represented only by fragments. Pots in various forms, bronze pins, bronze/silver earrings and rings, necklaces of stone beads are among the grave goods of both Mid and Late EBA graves. However, unlike Mid EBA graves, daggers and spearheads were found in Late EBA graves (Laneri, 2007).

The most remarkable burial among Titriş Höyük graves is the burial made on a plaster basin. Chemical analyses carried out with the samples taken from these plastered platforms found in most of the Late EBA houses demonstrate that these platforms might have been used in wine processing. The circular and slightly concave plastered platform, 140 cm in diameter, consist of a floor where small and medium-sized limestone is combined with muddy plaster at the bottom, pebbles in the middle and a thick limestone powder which was also used for the floor of the houses at the top (Laneri, 2002; Matney and Algaze, 1995). Skeletal remains belonging to minimum 19 individuals were found on one of these platforms during the 1998 excavation season (three subadults, three adult females, 13 adult males). At this unique burial, while postcranial bones were piled up at the center of the plaster basin, the crania were placed on the top of the postcranial bones at the edges without a unity of direction. 13 of the 16 adult individuals have perimortem traumas caused by an axe, dagger and spearhead on their skulls. Based on the presence of skeletal remains of each age and sex groups in this grave and the high frequency of perimortem traumata on the skulls, it was concluded that these individuals were victims of a possible massacre (Erdal, 2012a).

One individual from Titriş Höyük produced genome-wide data and is included in genetic analyses.

- ■ TIT021 (TH80084) is one of the 16 skulls on the plaster basin. Since it is a secondary burial, its relationship with scattered postcranial bones could not be established. Considering the morphological structure of the skull, the individual was estimated to be male. According to the ectocranial suture closure, it is estimated that the individual is a middle adult aged 35-40 years. There are two healed depressed traumas on the skull. In addition, two perimortem traumas were identified, one caused by a penetrating or a sharp object and the other by a sharp object. Due to the lack of healing marks around these penetrating and sharp force traumas on the left side of the skull, it was determined that the individual died as a result of these traumas. Dating of human tooth: 2331-2143 cal BCE (3799 ± 25 BP, MAMS-40684)

### Abbreviations

E = Early, M = Middle, L = Late, EP = Epipaleolithic, N = Neolithic, C = Chalcolithic, BA = Bronze Age, Eneolithic = En.

### Grouping of individuals and nomenclature

For the purpose of this study, we mainly used as group designation the name of the archaeological site and the archaeological period (Eisenmann et al., 2018). We caution here that period-based cultural divisions such as "Chalcolithic" and "Neolithic" vary from region to region and must be considered artificial boundaries instead of absolute chronological markers. For example, 6$^{th}$ millennium BCE is considered Early Chalcolithic in Anatolia and Late Neolithic in Southern Caucasus. Tell Kurdu, albeit located in Northern Levant, is a site that displays a mixture of both Anatolian and North Mesopotamian elements with regards to its architecture and material culture. Therefore, its 6$^{th}$ millennium BCE levels are more usually referred to as Early Chalcolithic based on the Anatolian chronological designations.

Sites for which samples covered more than one archaeological period were Arslantepe and Tell Kurdu. Given the temporal distribution of the samples at Arslantepe (Figure 2B), we grouped together all individuals from the Late Chalcolithic and the very beginning of Early Bronze Age as "Arslantepe_LC" and those from Early Bronze age as "Arslantepe_EBA."

Genetic information (PCA-based) was also taken into consideration for outlying individuals (i.e., Alalakh_MLBA_outlier). Also, in order to maintain information about intragroup variability, we measured with $f_4$-statistics whether any individuals systematically shared more alleles with other populations compared to other individuals from the group.

Exception to the archaeological site-period nomenclature were the two Neolithic sites in the Southern Caucasian lowlands (Mentesh Tepe and Polutepe), each represented by only one individual (MTT001 and POT002 respectively). We grouped these two individuals as Caucasus_lowlands_LN (in agreement with *f4*-statistics suggesting no breaks in their cladality). For consistency, we refer to the Chalcolithic site of Alkhantepe (ALX002) as Caucasus_lowlands_LC. Accordingly, published individuals/groups from Anatolia were renamed applying the same scheme, i.e., name of archaeological site "underscore" archaeological period.

For other ancient groups relevant to our study we applied a nomenclature system of area and archaeological time period (ex Levant_EBA) provided that this does not contradict genetic evidence. Especially, for the area of Caucasus where genetic characterization has been carried on a big number of ancient individuals (Allentoft et al., 2015; Lazaridis et al., 2016; Wang et al., 2019), we used a combined nomenclature of ecogeographical area, archaeological time and genetic clustering. All new group labels are given in Table S3.

## METHOD DETAILS

### Direct AMS radiocarbon dating

All individuals with newly-reported genetic data and without direct dating previously performed on them were dated at the radiocarbon dating facility of the Klaus-Tschira-Archäometrie-Zentrum at the CEZ Archaeometry gGmbH, Mannheim, Germany using a MICADAS-AMS and ~1gr of bone material. With a few exceptions, we dated a sample from the same skeletal element that was sampled for the DNA extraction. Collagen was extracted from the bone samples, purified by ultrafiltration (fraction > 30kD) and freeze-dried. Collagen was combusted to $CO_2$ in an Elemental Analyzer (EA) and $CO_2$ was converted catalytically to graphite. $^{14}C$

ages were normalized to $\delta^{13}C = -25‰$ and were given in BP (before present) meaning years before 1950. The calibration was done using the dataset INTCAL13 (Reimer et al., 2013) and the software SwissCal 1.0 (L. Wacker, ETH-Zürich).

### Preparation of aDNA

We extracted DNA and prepared next generation sequencing libraries from 174 samples in a dedicated aDNA facility in Jena following established protocols for DNA extraction and library preparation.

Prior to sampling of petrous bones, we carefully wiped the bone surface with 10% bleach and water and then UV-irradiated the surface for 30 min. Sampling targeted the inner-ear portion of the petrous bone (Pinhasi et al., 2015), but the method varied based on the preservation conditions of the sample and/or the destructive constraints as follows:

a. Well preserved samples without constraints in destructive sampling: a bone wedge was cut out around the region of the cochlea using an electric saw (K-POWERgrip EWL 4941), removed the surface and ground it to fine bone powder.
b. Poorly preserved samples: cutting in the middle with a jeweler's saw and drilling bone powder (K-POWERgrip EWL 4941) from one side directly at the osseous labyrinth.
c. Minimally invasive method: removal of surface layer and drilling from outside targeting the area of the inner ear.

After UV-irradiation step (30 min) teeth were cut at the cemento-enamel junction and then sampled by drilling from the inner pulp chamber of the crown. Whenever this sampling method could not yield a minimum of 50 mg of bone powder, we complemented with bone powder drilled from the pulp of the root.

We used 50-100 mg of bone powder for the DNA extraction. First, we incubated the bone powder in a lysis buffer containing 0.45 M EDTA, pH 8.0 and 0.25 mg/ml Proteinase K with overnight rotation at 37°C. After centrifugation, we transferred the supernatant to a new 15ml tube containing 10.4 mL of binding buffer of 5 M Guanidine hydrochloride (Sigma-Aldrich), 40% Isopropanol (Merck) and 400 µL of 3 M Sodium Acetate pH 5.2 (Sigma-Aldrich). We spun the mix through a silica column (High Pure Viral Nucleic Acid Large Volume Kit; Roche) at 1,500 rpm for 8 min. We dry-spun the column with centrifugation at 14,000 rpm for 2 min and washed the DNA bound to the column twice with 450 µL of wash buffer (High Pure Viral Nucleic Acid Large Volume Kit; Roche) and spinning at 8,000 *rcf.* for 1 min. After two dry-spin steps of 30 s, we incubated the columns for 3 min with 50 µL Tris-EDTA elution buffer (High Pure Viral Nucleic Acid Large Volume Kit; Roche) containing 0.05% of Tween 20% (Sigma- Aldrich) and spun for 2 min at 14,000 rpm. We repeated this elution step, and collected the 100 µL of eluted DNA in a LoBind collection tube (Eppendorf). All DNA extracts were stored at −20°C. At every extraction experiment we included one blank control (extraction buffer) and bone powder of cave bear as a positive control.

We prepared double-stranded libraries from 25 µL of DNA extract using the partial Uracil-DNA-glycosylase (UDG) protocol, which removes most of the deaminated cytosines – aDNA damage occurring post-mortem – but maintains some molecules with terminal damage (Rohland et al., 2015). We performed the partial UDG-treatment by adding 25 µL of mastermix consisting of 0.07 USER enzyme, 0.2 mg/ml BSA, 1.2 mM ATP (all NEB), 0.1 mM dNTP mix (Thermo Fisher Scientific), 1.2X Buffer Tango (Life Technologies), and finally incubating for 30 min at 37°C and 1 min at 12°C. We then added 0.13 U UGI (Uracil Glycosylase inhibitor) and repeated the incubation step. For the blunt-end repair of the double-stranded molecules we added 0.5 U T4 Polynucleotide Kinase, 0.08 U T4 DNA Polymerase (both NEB), and incubated for 20 min at 25°C for 20 min and then 10 min at 10°C. We purified the product with a standard MinElute PCR purification Kit (QIAGEN) eluting in 18 µL of EB containing 0.05% of Tween (EBT). The ligation of Illumina adaptors was carried out with 1X Quick Ligase Buffer (NEB) and (0.25 µM adaptor mix) in a total reaction volume of 40 µL and 1 µL of 0.125 U Quick Ligase followed by an incubation at 22°C for 10 min and another MinElute purification step. The fill-in of the ligated adaptors included 1X isothermal buffer, 0.4 U/µl Bst-polymerase (NEB), 0.125 mM dNTP mix and an incubation at 37°C for 30 min followed by 10 min at 80°C. A negative library control ($H_2O$) was taken along at every experiment.

We evaluated the success of library preparation by quantifying the number of unique molecules in an aliquot from each library with qPCR performed on a LightCycler 96 (Roche) installed outside the clean room and using IS7/IS8 primers and the DyNAmo SYBP Green qPCR kit (Thermo Fisher Scientific). We assigned unique combinations of two 8bp-long indices at every library and attached them with an amplification reaction using *Pfu-Turbo Cx Hotstart DNA Polymerase* (Agilent Technologies) and 10 cycles of 30 s at 58°C and 1 min at 72°C followed by an elongation step at 72°C for 10 min. We purified the amplified product with a MinElute kit (QIAGEN) and then eluted in 50 µL EBT. We re-quantified an aliquot from every indexed library with qPCR using IS5/IS6 primers and we reamplified to $10^{13}$ copies with Herculase II Fusion Polymerase following the manufacturer's protocol. After another purification step with final elution at 50 µL of EBT, we measured an aliquot at an Agilent 4200 TapeStation in order to check fragment length and concentration.

### Human genome enrichment, sequencing and haploid genotype sampling

We pooled libraries equimolarly to 10nm and submit them for sequencing in one of the in-house sequencing platforms HiSeq 4000 or NextSeq500 using a paired-end (PE 2x50) or a single-read (SR 75) kit. After initial shotgun sequencing of 5-10 million reads (or 10-20 for PE sequencing) and demultiplexing, all libraries were processed through EAGER (Peltzer et al., 2016), a modular pipeline that streamlines the raw sequence data from FastQC and quality filtering to mapping and duplicate removal and outputs important quality information such as complexity of libraries, percentage of endogenous DNA damage, and fragment length. Sequencing adapters were clipped with AdapterRemoval (*v2.2.0*) (Schubert et al., 2016) and merged (paired-end sequencing) while all fragments shorter than 30 bp were discarded. Mapping was performed with BWA (*v0.7.12)* (Li and Durbin, 2009) with a quality filter of q30 against the hs37d5 sequence reference. For the removal of PCR duplicates we used dedup (*v0.12.2*) (Peltzer et al., 2016), which considers both beginning and end of the merged reads with the same orientation. C to T and G to A mis-incorporations were evaluated with the tool mapdamage (*v2.0.6*) (Jónsson et al., 2013). Libraries that passed the thresholds of quality control (> 0.1% of endogenous DNA, > ~5% C to T mis-incorporation at terminal 5′ base) were subjected to an in-solution hybridization enrichment that targets at 1,233,3013 genome-wide and ancestry-informative SNPs ("1240K SNP capture") (Mathieson et al., 2015). Libraries were not pooled prior to this enrichment experiment. Whenever the mitochondrial reads from either the shotgun sequencing or the 1240K capture were not sufficient for the reconstruction of the whole mitochondrial genome, the call of mitochondrial haplotypes and the estimation of mitochondrial contamination, we carried out another in-solution enrichment which targets at the whole mitochondrial DNA ("mito capture") (Fu et al., 2015). Captured libraries were sequenced at the order of 20 million reads (or 40 million for PE) and were streamlined through EAGER with the same parameters as for shotgun sequencing data. We ran preseq (*v2.0*) (Daley and Smith, 2013) on 1240K data, a tool that uses a histogram of targeted sites and the number of unique and duplicated reads in order to compute an extrapolation of the library complexity for bigger sequencing experiments. Subsequently, we deeper-sequenced the captured libraries to maximize the use of each library's complexity. We merged bam files across libraries from the same individual and rerun dedup. We generated masked versions of the bam files in which we masked the ends of the reads until the nucleotide with misincorporation frequency ≤ 1% using trimBam (https://genome.sph.umich.edu/wiki/BamUtil:_trimBam). To minimize the reference bias in low-coverage data, after generating the pileup (with -q30 and -Q30 filters), we extracted haploid genotypes with the tool pileupCaller (https://github.com/stschiff/sequenceTools/tree/master/src/SequenceTools), which randomly chooses a single read at every SNP position and generates pseudo-diploid genotypes. We performed the random calling both on the original and the masked bam files of each library. For the final genotypes we kept the transitions from the masked and the transversions from the original bam files.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Quality control and test of kinship

We only included individuals with ≥ 40,000 SNPs of the potential 1240K SNPs covered for downstream population genetics analysis. We estimated contamination on these individuals based on the mitochondrial heterozygosity (Renaud et al., 2015) and on the heterozygosity at the polymorphic sites on the X chromosome on the males with ANGSD (Korneliussen et al., 2014).

Samples from same individual or samples from genetically related individuals are relatively common cases when working with bone material from archaeological sites. To test for biological kinship, we estimated the pairwise mismatch rate (pmr) (Kennett et al., 2017) among all possible pairs of individuals from within an archaeological site by counting the number of SNPs for which the two individuals had a mismatch on genotype (0-2 or 2-0) and dividing with the total number of overlapping SNPs (SNPs without missing data in either individual).

It is known that two genomic libraries produced from the same individual or two identical twins (coefficient of relatedness $r = 1$) will exhibit a pmr which should be half of that of a pair of unrelated individuals ($r = 0$) and the pmr will be a linear function of $r$ (Jeong et al., 2018). Assuming no inbreeding within the population, the pmr of unrelated individuals (UI) can be empirically estimated by the distribution of pmr of multiple individuals. When we detected pairs with IT pmr, we cross-checked with the archaeological context whether these can be attributed to cases of samples from the same individual and, subsequently we merged the data under the name of one individual. For pairs with IT < pmr < UI we calculated the coefficient of relatedness $r$ as (UI-pmr)/IT. For statistically robust estimates of the coefficient we used READ (Monroy Kuhn et al., 2018) which computes pmr in non-overlapping windows of 1 Mbps and also calculates standard errors.

### PMDtools

We used PMDtools (Skoglund et al., 2014), a statistical framework for the evaluation and isolation of aDNA reads based on their damage profile, on the one genetic outlier individual from Alalakh. To reduce reference bias, we provided a reference masked for 1240K SNP positions.

### Dataset

We merged our final dataset with publicly available datasets of ancient and modern individuals (de Barros Damgaard et al., 2018; Feldman et al., 2019; Fu et al., 2016; Gamba et al., 2014; González-Fortes et al., 2017; Günther et al., 2015; Haber et al., 2017; Harney et al., 2018; Hofmanová et al., 2016; Jeong et al., 2019; Jones et al., 2015; Lazaridis et al., 2014, 2016, 2017; Lipson et al., 2017; Martiniano et al., 2017; Mathieson et al., 2018; McColl et al., 2018; Meyer et al., 2012; Mittnik et al., 2018; Mondal et al., 2016; Olalde et al., 2015, 2018, 2019; Pickrell et al., 2012; Prüfer et al., 2017; Raghavan et al., 2014; Rasmussen et al., 2014; Seguin-Orlando et al., 2014; Skoglund et al., 2016, 2017; Vyas et al., 2017; Narasimhan et al., 2019) (see Table S3). We also merged with datasets of worldwide modern populations genotyped on the Human Origins array by keeping the intersection of SNPs. Both 1240K and HO datasets were restricted to the autosomal portion.

### Sex determination and uniparental haplotypes

We used "samtools depth" from the samtools (*v1.3*) (Li et al., 2009) providing the bed file with the 1240K SNPs to calculate the coverage on X, Y and autosomal chromosomes. We normalized X and Y coverage by the autosomal coverage (X-rate and Y-rate respectively). For females without contamination we expect X-rate $\approx 1$ and Y-rate $\approx 0$. Accordingly, for uncontaminated males we expect both X-rate and Y-rate to be $\approx 0.5$.

In order to determine the Y haplogroups of the male individuals, we first used pileups from the bam files Rsamtools package (Morgan et al., 2019) and called the Y chromosome SNPs from reads with mapping and base qualities $\geq$ 30. We manually assigned Y chromosome haplogroups by manually inspecting the derived SNPs in the pileups included in the ISOGG SNP index (*v.14.07*) (last downloaded 7 January 2019) (Table S9).

The mitochondrial consensus sequences were inferred from the mito-capture data using Schmutzi (Renaud et al., 2015) and mapping with CircularMapper (Peltzer et al., 2016) against the rCRS with mapping quality filter of *q30* and consensus quality score *Q30*. The mitochondrial haplotypes of the consensus sequences ($\geq$5X coverage) were assigned by Haplogrep (Kloss-Brandstätter et al., 2011) after visual inspection of bam pileup in Geneious (*v11.0.4*) (Kearse et al., 2012) (Table S9).

### Principal component analysis

We performed principal component analysis on two subsets of the Human Origins Dataset: (a) 171 West Eurasian populations (2,343 individuals), and (b) 85 West Asian and East Mediterranean populations (1,221 individuals) using the smartpca program of EIGENSOFT (*v6.01*) (Patterson et al., 2006; Price et al., 2006) with default parameters and the options lsqproject: YES, numoutlieriter: 0, to project ancient individuals onto the first two components.

### f-statistics

We computed outgroup $f_3$-statistics using the program qp3Pop from the package ADMIXTOOLS (*v5.1*) (Patterson et al., 2012) and looked for evidence of maximized shared drift. We also computed $f_4$-statistics using qpDstat from the same package that provide evidence of gene flow based on allele frequency sharing. We applied default parameters and the options f4mode: YES.

### Modeling of ancestry proportions

We used the programs *qpWave* and *qpAdm* (version 810) from ADMIXTOOLS to model the studied populations (targets) as a combination of ancestry proportions from putative selected source populations (references). This method does not require explicit knowledge about the phylogeny of the populations but harnesses the fact that if the target is related to a set of right populations (outgroups) through the references (left populations) and the references relate asymmetrically to the outgroup populations, then the target can be modeled as a combination of the references and the admixture proportions can be estimated by solving a matrix of $f_4$-statistics (Haak et al., 2015). Therefore, the choice of outgroups and references is of major importance. We used a set of outgroups that represents past and modern global genetic variation (Mbuti.DG, Ami.DG, Mixe.DG, Kostenki14, EHG, Villabruna, Levant_EP) and provides a good resolution for distinguishing populations from Iran, Levant Caucasus and Anatolia. Prior to the ancestry modeling we used *qpWave* to test whether our outgroup choice can distinguish the tested references.

### Test of recent admixture

We tested for signal of recent admixture events applying the recently developed method DATES (https://github.com/priyamoorjani/DATES) (M. Chintalapati, N. Patterson, N. Alex, and P. Moorjani, personal communication) with the following parameters: binsize = 0.001, and fit of decay curve from 0.0045 (lovalfit) to 1 (maxdist) distance bins (all in Morgan units). DATES is based on the algorithm of the roloffp program, which is specifically designed to test admixture in low-coverage ancient genome data where genotypes are typically haploid and missing rate is high (Narasimhan et al., 2019). For each individual in the admixed target population, it first estimates the global admixture proportion by simply fitting the genotype vector of the target individual as a linear combination of the allele frequency vectors of the two source populations. Then it calculates the genotype residual by subtracting the expected genotype value, a weighted mean of source allele frequency and the corresponding global admixture proportion, from the target genotype. Finally, it multiplies the allele frequency difference between the two sources to the genotype residual to correct for the arbitrariness of the allele coding as zero or one. The weighted genotype residual performs a crude estimate of local ancestry (i.e., whether a genomic segment descends from the first or the second source), and thus the correlation between a pair of SNPs within a single individual is expected to exponentially decay as a function of the genetic distance between SNPs and the number of generations since admixture. For each genetic distance bin, DATES calculates a correlation of the weighted genotype residual across all SNP pairs within that bin and estimates admixture date in a single individual by fitting the exponential decay curve against the genetic distance. It can also easily accumulate information across target individuals without information loss, by simply using all SNP pairs from all individuals to calculate the correlation coefficient in each distance bin. Estimated times are given in generations assuming 28 years per generation (Moorjani et al., 2016). Compared to admixture LD methods such as ALDER (Loh et al., 2013) and *Rolloff* (Moorjani et al., 2011; Patterson et al., 2012), which require a minimum number of samples and coverage of the target population in order to estimate LD with precision, DATES can perform on a single sample from the admixed population. We further tested results where DATES detected a signal of admixture by computing two-reference weighted LD and decay fit with ALDER (*v1.03*) and roloffp (https://github.com/DReichLab/AdmixTools/blob/master/src/rolloffp.c) from ADMIXTOOLS. Since ALDER allows only a small fraction of missingness for a SNP position across the individuals of the target population, grouping individuals with variable coverage decreases the resolution of the analysis. Therefore, we performed ALDER on all possible pairs of individuals within the target population, excluding individuals with less than ~10% coverage and parameters binsize = 0.0005, mindist = 0.005 (all in Morgan units), mincount = 2, checkmap = NO and use_naive_algo = NO. For rolloffp we used parameter binsize = 0.0005, fitted the exponential curve using data between 0.005 and 0.5 distance bins (all in Morgan units). The exponential fit was performed using the nls function in R. Standard errors were calculated using a leave-one-chromosome-out approach.

### Visualizations

We produced all graphs in Rstudio (*v1.1.383*) and Adobe Illustrator CC 2020 (24.0.2). Maps were created in QGIS using the Natural Earth dataset. We produced all graphs in Rstudio (*v1.1.383*) and Adobe Illustrator CC 2020 (24.0.2). Maps were created in QGIS using the Natural Earth dataset. We consulted Breniquet (1996); Greenberg and Palumbi (2015); Roaf (1998); Sagona (2017), Carter and Philip (2010) and Wittke (2010) for the creation of maps in Figure 1.

# Supplemental Figures

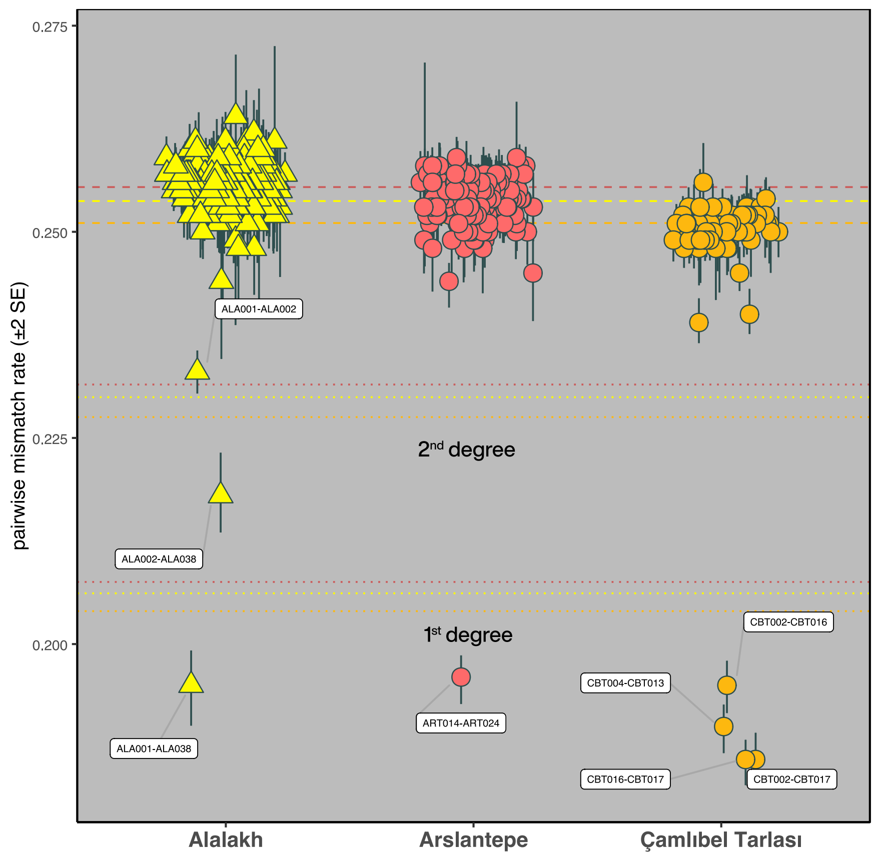


**Figure S1. Pairwise Mismatch Rate for the Three Sites with First- and Second-Degree Related Individuals, Related to Figure 2**

Pairwise SNP mismatch rates (pmr; the proportion of mismatching SNPs out of the total number of pairwise-overlapping SNPs) and their associated standard errors were estimated with READ (Monroy Kuhn et al., 2018). The baseline of unrelatedness (≥third degree) in pmr was estimated as the mean of all pairwise comparisons within every site. The relatedness classification cut-offs were estimated by multiplying the baselines by 0.90625 (≥third degree, dashed lines), 0.8125 and 0.625 for second and first degree, respectively (dotted lines).

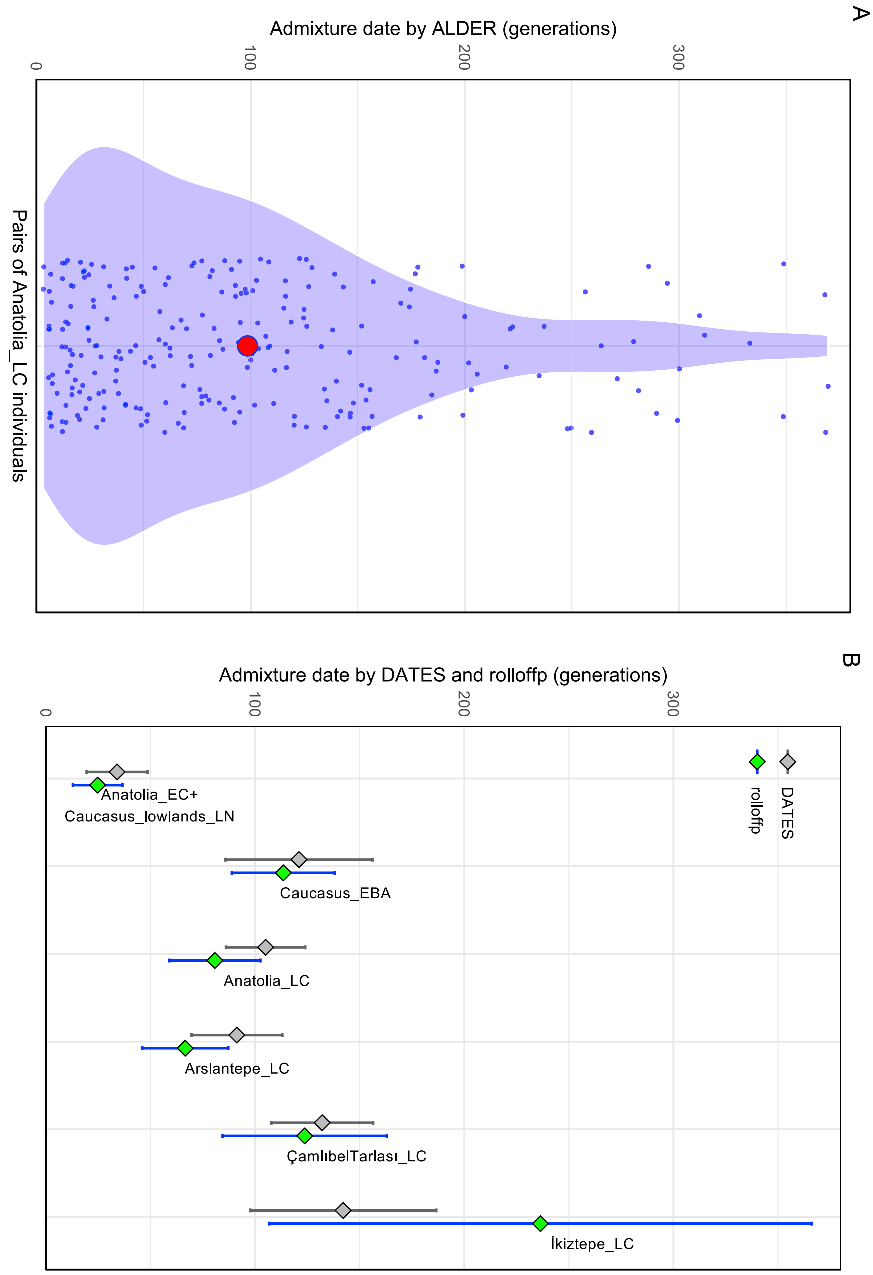


**Figure S2. Summary of Admixture Dates Estimated with Alder and Rolloffp, Related to STAR Methods (Test of Recent Admixture)**

(A) Alder admixture dates on all pair combinations from 27 Anatolia_LC individuals. Pairs include individuals from the Arslantepe_LC and ÇamlıbelTarlası_LC groups. Estimates for which computation of SE failed are not plotted. The average admixture date from the 241 independent tests (red dot) is very close to the estimation from DATES on Anatolia_LC (~100 generations).

(B) rolloffp estimates of admixture dates overlap with DATES within ±1 SE.

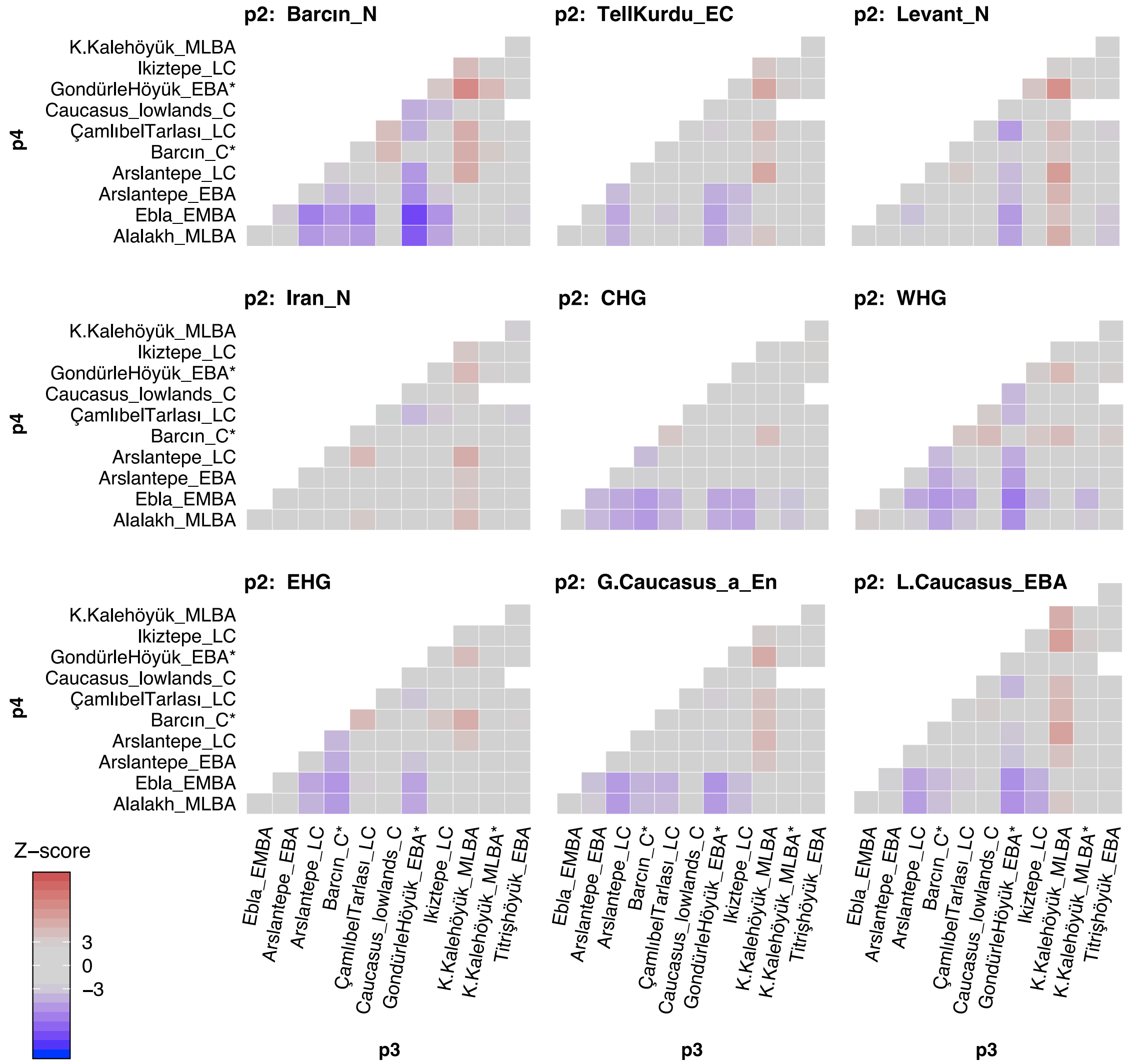


**Figure S3. Genetic Differences among Analyzed Chalcolithic and Bronze Age Groups, Related to Figure 6**

Heatmap of $f_4$-statistics of the form $f_4$*(Mbuti, p2; p3,p4),* where *p3* and *p4* are all possible pairs of LC-LBA groups from the present study and published contemporaneous (*), and *p2* a selection of ancient populations from West Eurasia. $f_4$-statistics that do not deviate significantly from 0 (i.e., |Z-score| $\leq$ 3) are represented with gray-colored tiles. Significant $f_4$-statistics are colored in red and blue scale according to the direction of allele sharing. $f_4$-statistics estimated on less than 50,000 SNPs are not plotted resulting in some missing tiles from the heatmaps.

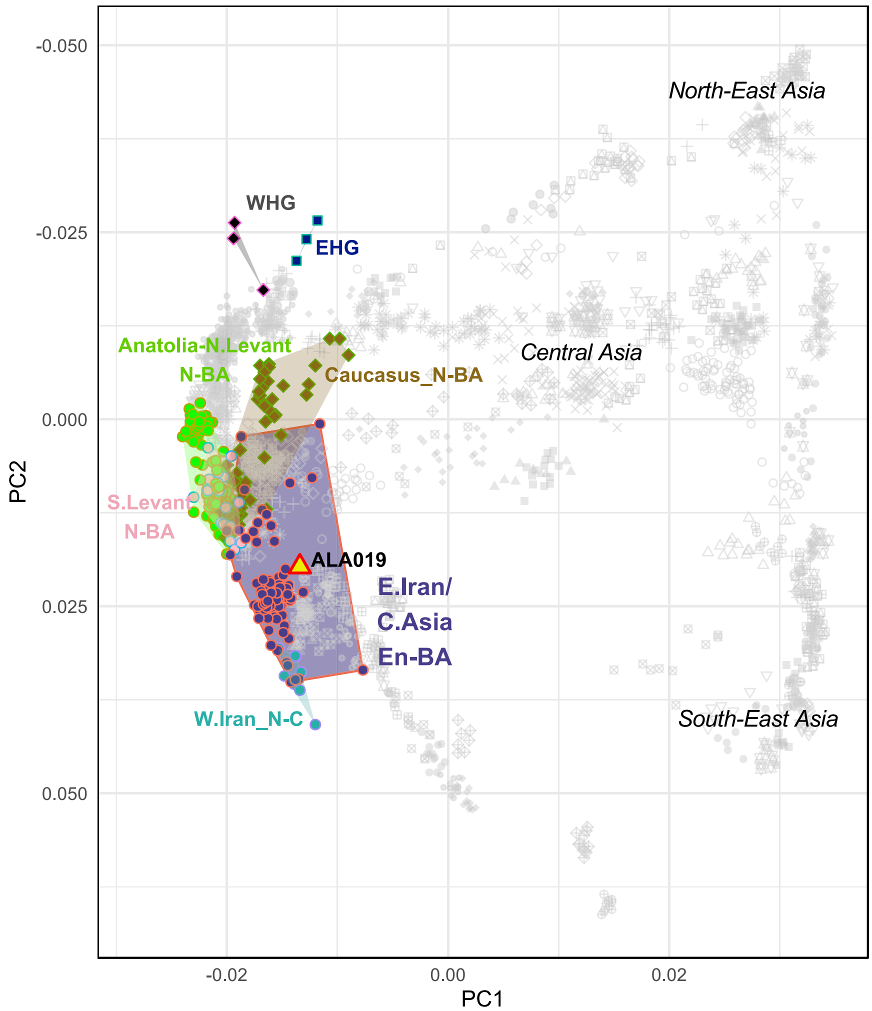


**Figure S4. Eurasian PCA with Neolithic to Bronze Age Individuals from Iran and Turan and the Genetic Outlier Individual from Alalakh (ALA019), Related to Figure 7**

Scatter plot of PC1 and PC2 from PCA computed on modern-day Eurasian populations (gray points) shows that the Alalakh_MLBA_outlier (ALA019) is genetically closer to individuals from Chalcolithic and Bronze Age Iran/Turan. Colored labels and points refer to ancient populations and black labels to modern-day populations.