



Supplementary Materials for

The genetic history of the Southern Arc: A bridge between West Asia and Europe

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The PDF file includes:

Materials and Methods
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Tables S1 to S34
References

Other Supplementary Material for this manuscript includes the following:

Data S1 to S5
MDAR Reproducibility Checklist

Materials and Methods

The materials and methods described here are for the combined study of the population history of the Southern Arc and pertain to the present study (which describe the entire dataset and analytically focuses on the Chalcolithic and Bronze Age periods), and two studies on Neolithic populations and the more recent history of the Southern Arc which employ the same analysis dataset and methods.(6, 11)

Sampling of ancient individuals

The archaeological and anthropological context of sampled ancient individuals is described in Supplementary Text S1. All human remains newly analyzed in this study are either stewarded by co-authors who participated in their archaeological analysis, or are accessioned in museum collections. Information on the current housing of the human remains and how to access them for further analysis can be obtained from Data S1. Column C, “Skeletal code,” provides museum accession codes as well as information such as grave and burial number. Column G, “Co-authors associated with this individual,” lists the names of co-authors who should be contacted for questions about remains not accessioned in museums.

Ancient DNA data generation

We obtained powder from petrous bones, other bones, teeth, and ossicles(55) which we prepared in dedicated ancient DNA clean rooms except for the case of intact skulls where we sampled petrous bones through a small hole we drilled in the cranial based to minimize morphological damage(56). We extracted DNA using a method designed to retain short molecules(57-59), and then created double-stranded(60, 61) and single-stranded libraries(62) the great majority of which we treated with the enzyme Uracil DNA Glycosylase (UDG) to minimize characteristic errors associated with ancient DNA(63). We enriched for both mitochondrial DNA and about 1.2 million single nucleotide polymorphisms(64, 65), and after two rounds of enrichment sequenced the enriched molecules on Illumina NextSeq 500 or HiSeq X Ten instruments.

Bioinformatic processing of ancient DNA data

We demultiplexed the sequences based on library-specific barcode pairs (for double-stranded libraries) and index pairs (for all libraries), and merged paired-end sequences with at least 15 base pairs of overlap allowing up to one mismatch of base quality ≥ 20 or up to three mismatches of lower base quality. We aligned the resulting single-ended sequences to the mitochondrial genome (RSRS)(66) and human genome reference sequence (hg19)(67) using *samse* from the BWA software suite (*bwa-v.0.6.1*)(68). We removed duplicated molecules with the same start and stop positions and orientation (and for double-stranded libraries also required matching to the barcode pairs). For analysis, we restricted to sequences of at least 30 base pairs, trimming 2 base pairs from both ends for UDG-treated libraries and 5 base pairs for non-UDG-treated libraries to remove deamination artifacts. We merged data from all libraries for the same individual. Mitochondrial haplogroups were determined using (Haplogrep v2.1.1)(69) for sequences aligning to the mitochondrial genome (RSRS) from the data aligning to the mitochondrial genome RSRS. We represented each targeted SNP on chromosomes 1-22 and X by a single randomly sampled sequence for those SNPs (with a mapping quality threshold of 10, and base quality threshold of 20). For chromosome Y, we analyzed not only targeted SNPs but

also off-target SNPs, and determined allelic status by majority rule as discussed in detail in Supplementary Text S5.

Determination of ancient DNA authenticity

We assessed whether each individual had a rate of damage cytosine-to-uracil deamination consistent with authentic ancient DNA based on the rate of cytosine-to-thymine mismatches in the terminal nucleotide, using thresholds that varied according to library preparation protocols (partially UDG-treated libraries have a lower expected rate of damage due to the biochemistry of the library preparation process(61)). We estimated contamination rates from mitochondrial DNA based on the rate of mismatch to the consensus sequence using *contamMix* v1.0-10,(70) marking data from an individual as “questionable” if the upper bound of the 95% confidence interval for mismatch rate was in the range 90-95%, and marking data from an individual as “critical” or filtering it out from the dataset altogether if the upper bound was <90% (however, if we had an X chromosome contamination estimate for such individuals with an upper bound of <1% we marked them as uncontaminated as this methods provides a far more direct look at autosomal contamination levels than mitochondrial contamination estimates). We estimated contamination rates in males based on the rate of polymorphism on the X chromosome using *ANGSD* v0.923 for individuals with at least 200 SNPs covered at least twice,(71) marking data from an individual as “questionable” if the lower bound of the of the 95% confidence interval for mismatch rate was in the range 1-5%, and “critical” or filtering it out from the dataset altogether if the lower bound was >5%. For contaminated individuals with sufficient coverage we restricted to damaged molecules to reduce the effects of contamination.(72)

PCA

We carried out PCA in smartpca program of EIGENSOFT(73) using numoutlieriter: 0 and lsqproject: YES(25) parameters; the PCA was computed on present-day West Eurasians genotyped on the Human Origins array(10, 16, 25) with ancient samples projected.

ADMIXTURE analysis

ADMIXTURE analysis was carried out in ADMIXTURE(74) after pruning for linkage disequilibrium in PLINK with parameters --indep-pairwise 200 25 0.4 after which 989,562 autosomal SNPs were retained. K=8 was chosen (Fig. S 1) as the lowest value in which all 4 major components of West Eurasian variation appeared, with the AfontovaGora3(75)-maximized “Ancient North Eurasian” component not being present for lower K.

qpWave/qpAdm and development of 5-way model

qpWave(8, 76)/qpAdm(8) analyses were performed with v. 1201 of the software and details: YES and allsnps: YES parameters. The 5-way model was developed by examining models that fit the SA population as a whole, clusters of individuals without *a priori* assignment of labels, and the individuals themselves (Supplementary Text S2).

F4admix

F4admix is described in Supplementary Text S2 and originally in SI9 of (8) and consists of fitting f -statistics of the form $f_4(Test, O_1; O_2, O_3)$ as a sum of $\alpha_i f_4(Ref_i, O_1; O_2, O_3)$ where $Test$ is the admixed population, α_i are admixture proportions summing to unity from sources Ref_i . The f -statistics were computed in qpDstat(77) for both the entire dataset and by dropping each

chromosome in turn(78) to produce a block jackknife estimate.(79) F4admix produces smaller standard errors than qpAdm for low coverage individuals. Ancestry proportions and differences between individuals and populations are visualized with “ancestral variation diagrams” (Supplementary Text S3, Fig. S 3, Fig. S 4).

Y-chromosome haplogroups

The procedure for Y-chromosome haplogroup determination is described in Supplementary Text S5 which used the YFull YTree v. 8.09 phylogeny (https://github.com/YFullTeam/YTree/blob/master/ytrees/tree_8.09.0.json), obtaining information about SNPs from ISOGG YBrowse (https://ybrowse.org/gbrowse2/gff/snps_hg38.csv; accessed Oct 18, 2020), lifting coordinates from hg38 to hg19 using liftOver and intersecting with the SNPs present in the v. 8.09 tree. TMRCA estimates providing a chronological framework for different nodes were obtained from the YTree v. 8.09 metadata provided by yfull.com.(80)

Modeling of temporal change in ancestry

We used the mleHetGP function in the hetGP package in R(53, 81) to perform a maximum likelihood fit of a heteroskedastic Gaussian process on individual admixture estimates in which time (in years BP) is the predictor variable and an admixture proportion is the response variable. This allows us to visualize trends of ancestry without any assignment of individuals onto rigid by-period populations and is complemented by our analysis of admixture proportions by such archaeologically and genetically informed groupings.

Dating of admixture

We used DATES software v.3520 to estimate the number of generations since admixture for a Test population given two source populations(34) and a generation length of 28 years(54) to convert this into years.

Detection of relatives and estimation of homozygosity

Runs of homozygosity were detected in individuals with at least 400,000 autosomal SNPs covered using HapROH (82) as described in Supplementary Text S2 of (6)

Pigmentation inference

Pigmentation phenotypes of ancient individuals was performed with the aid of the HRISplex-S tool(83, 84) which takes as input diploid genotypes at diagnostic loci; we submitted 10 random replicates for each individual, generated from its genotyped likelihoods as described in (16) and Supplementary Text S3 of (6).

Radiocarbon Methods Penn State University

Bone samples for radiocarbon dating at Penn State University were received at the Human Paleoecology and Isotope Geochemistry Lab in the Department of Anthropology where they were pretreated, combusted to CO₂, and converted to graphite for AMS 14C measurement at the Penn State AMS Radiocarbon Laboratory (labcode: PSUAMS). Preparation methods follow those described in (34). Briefly, bone samples were initially manually cleaned with hand implements (e.g., Dremel tool, X-acto knives or similar) to physically remove adhering sediment, adhesives, and potentially altered outer bone surfaces. In general practice, subsampling of portions of bone with obvious contaminants was avoided when possible. All

samples were then sonicated in successive baths of ACS grade methanol, acetone, and dichloromethane for 30 min at room temperature to remove any remaining adhesives or consolidants; contamination is assumed a priori for all museum or archived samples. After a final rinse in 18.2 MΩ-cm H₂O, samples were demineralized in 0.5N HCl at 5°C from roughly 48 to 96hr. The remaining pseudomorph was subjected to a 0.1N NaOH bath, as needed, at room temperature for <1hr to remove humates, rinsed in 18.2 MΩ-cm H₂O, and gelatinized in 0.01N HCl for 12hr at 60°C. Crude gelatin yield was calculated by weight of the lyophilized gelatin, and % yield and gelatin quality determined the additional processing steps. Well-preserved samples were processed by ultrafiltration and less-well preserved samples went through amino acid hydrolysis and purification by modified XAD. Readers are referred to (34) for the specific procedures for each.

Purified >30 kDa gelatin or amino acid hydrolysate were subsampled and submitted to the YASIC labs at Yale University for EA-IRMS analyses (%C, %N, δ¹³C and δ¹⁵N) for quality assurance. C:N ratios range between 3.11 and 3.42 and indicate good sample collagen or amino acid preservation. Aliquots of ~2.1mg of UF gelatin or ~3.5mg of hydrolysate were combusted to CO₂ in sealed quartz tubes in the presence of CuO and Ag wire at 900°C and 800°C respectively. CO₂ was then converted to graphite via hydrogen reduction on an Fe powder catalyst at 550°C for 3hr with reaction water drawn off with Mg(ClO₄)₂. Graphite on Fe was pressed in targets for AMS measurement at the PSU AMS lab, and run on the NEC 1.5SDH-1 Compact AMS along with primary standards (SRM4990C; OXII oxalic acid), process backgrounds (Latton mammoth) and in-house secondary bone standards (e.g., Certain Site #2 Bison; ~1850 BP). Unknowns were normalized with respect to the OXII and corrected for fractionation using δ¹³C measured on the AMS (i.e., 13C+/12C+) following the conventions of (85). All radiocarbon dates were calibrated in OxCal version 4.4(86) using the IntCal20 curve(87) and are reported in calibrated years BCE/CE.

Fig. S 1 ADMIXTURE analysis (K=9). Populations with individuals at the top-25% of (A) Iran-Caucasus (sky blue), (B) Balkan hunter-gatherer (reddish purple), (C) Eastern hunter-gatherer (vermillion), (D) Anatolian Neolithic ancestry (yellow). (E) Other populations. Other components: blue (East Asian), bluish green (Native American), gray (Australasian), black (African).

Fig. S 2 F4admixture proportions. Populations with individuals at the top-20% of (A) CHG (blue), (B) EHG (red), (C) Levant_PPN (orange), (D) SRB_Iron_Gates_HG (pink), (E) TUR_Marmara_Barçın_N (yellow) ancestry. (F) Other Southern Arc populations.

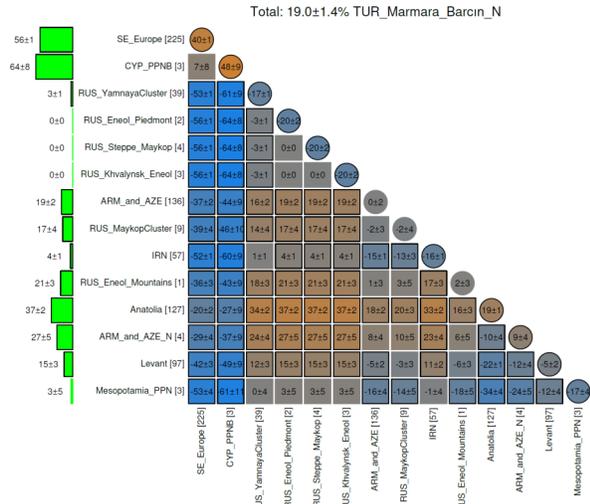
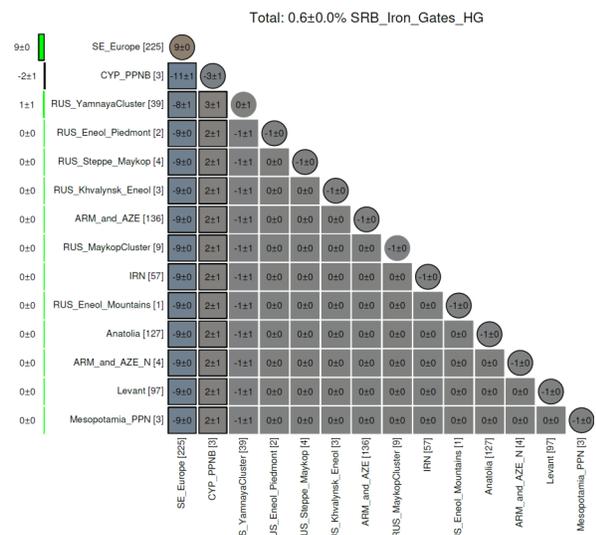
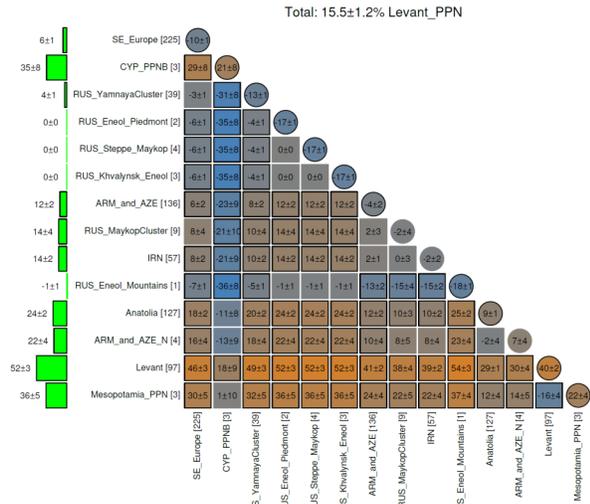
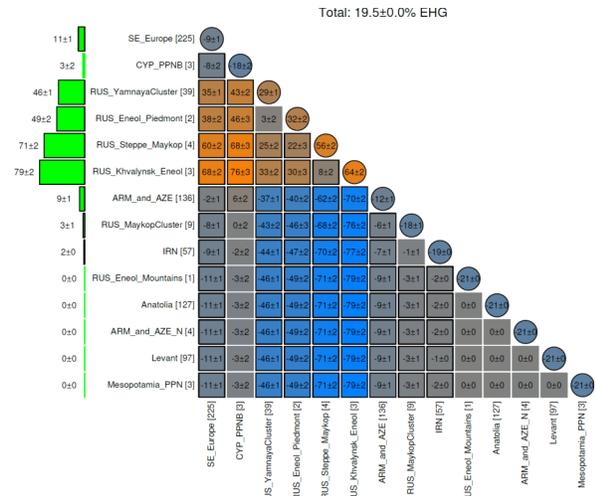
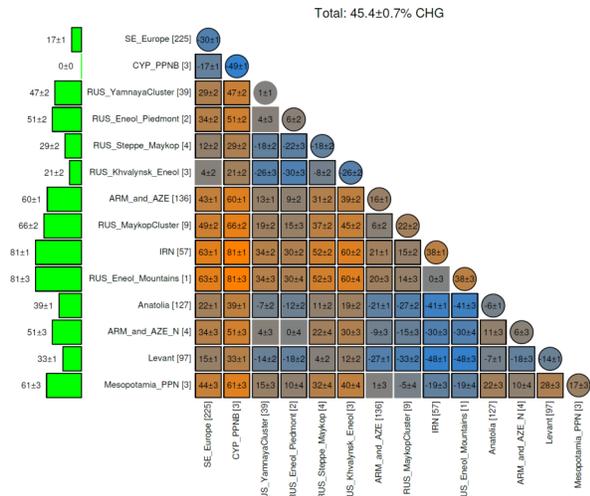
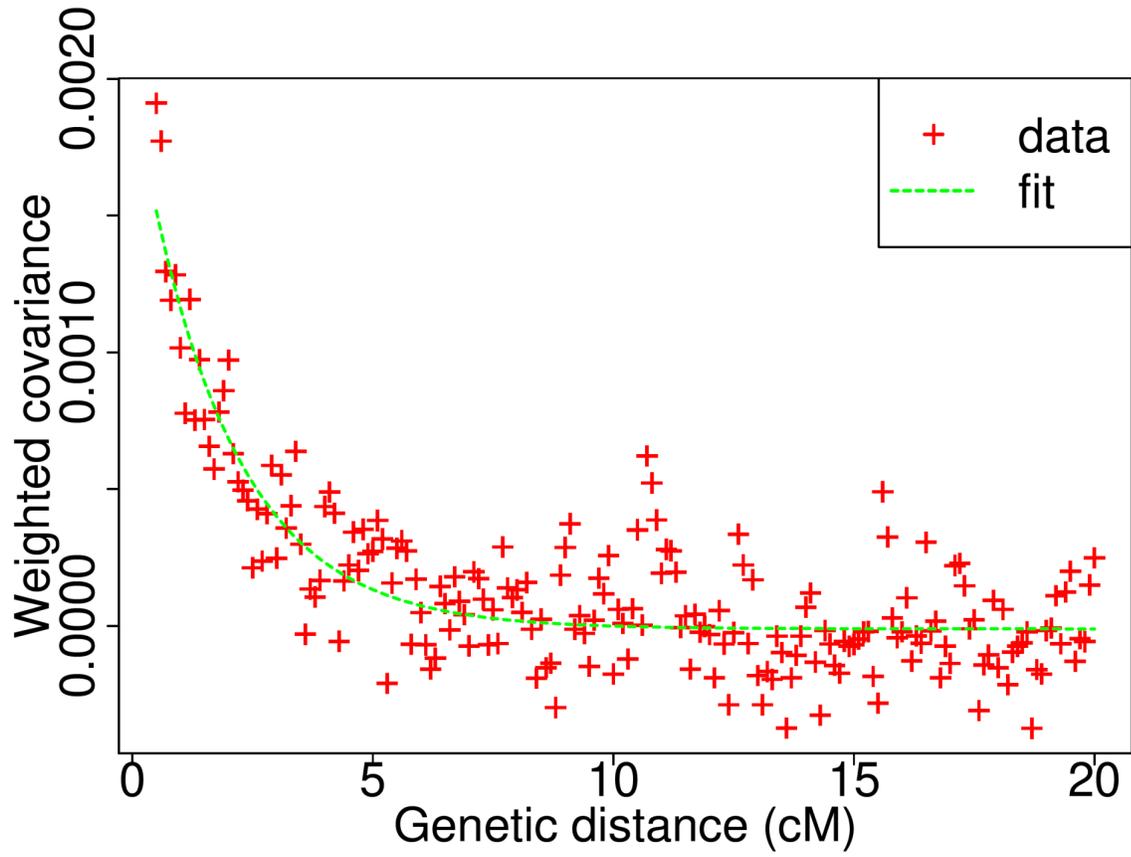


Fig. S 3 Ancestral Variation Diagram of Chalcolithic-Bronze-Early Iron Age across the Caucasus. More detailed analysis of Southern Arc populations can be found in Supplementary Text S3.

Fig. S 4 Ancestral Variation Diagram of Chalcolithic-Bronze-Early Iron Age from Anatolia to Europe. More detailed analysis of Southern Arc populations can be found in Supplementary Text S3.

A



B

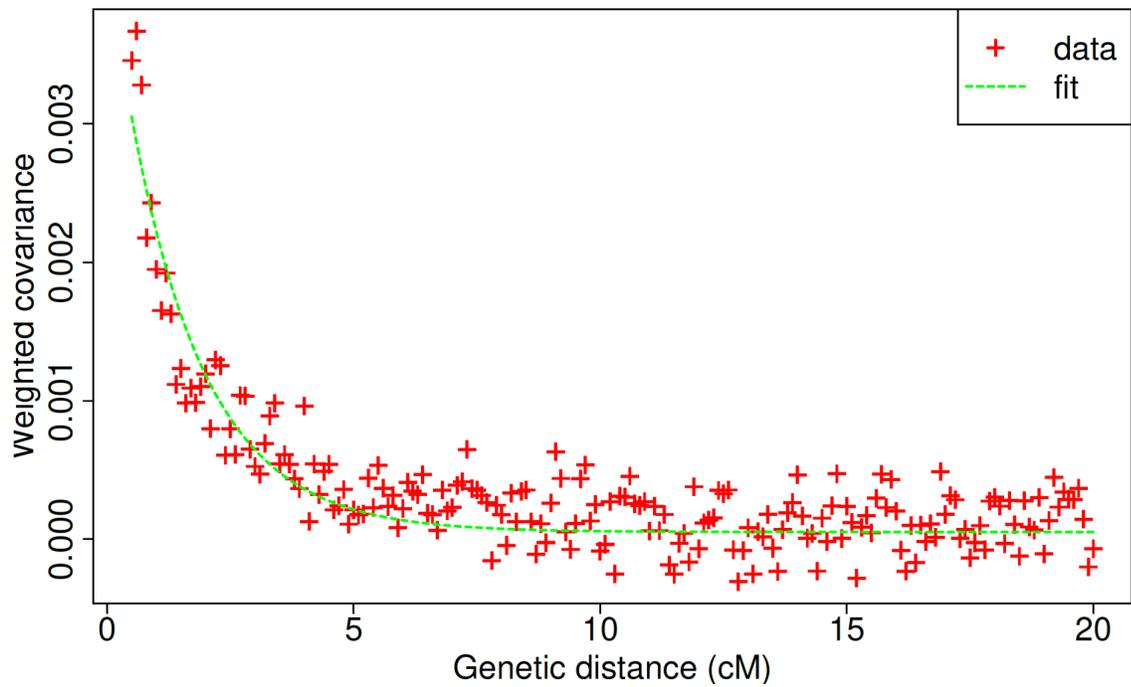


Fig. S 5 Admixture timing across the Caucasus. (A) C14-dated Bronze-to-Iron Age individuals from Armenia admixed 52.2 ± 8.0 generations ($1,460 \pm 224$ years) prior to their average date of 1119BCE, or ~ 2579 BCE (mid-3rd millennium BCE), assuming a generation length of 28 years,⁽⁵⁴⁾ and Early Bronze Age Armenia and Yamnaya cluster individuals from Russia as parental sources. (B) Yamnaya cluster individuals from Russia admixed 63.7 ± 10.6 generations ($1,785 \pm 297$ years) prior to the time they lived using EHG or Eneolithic individuals from Russia as one source and Chalcolithic individuals from Armenia, Azerbaijan, Iran, and Turkey in the Southern Arc as the other; their average radiocarbon date is 2770BCE, placing admixture to the mid-5th millennium BCE.

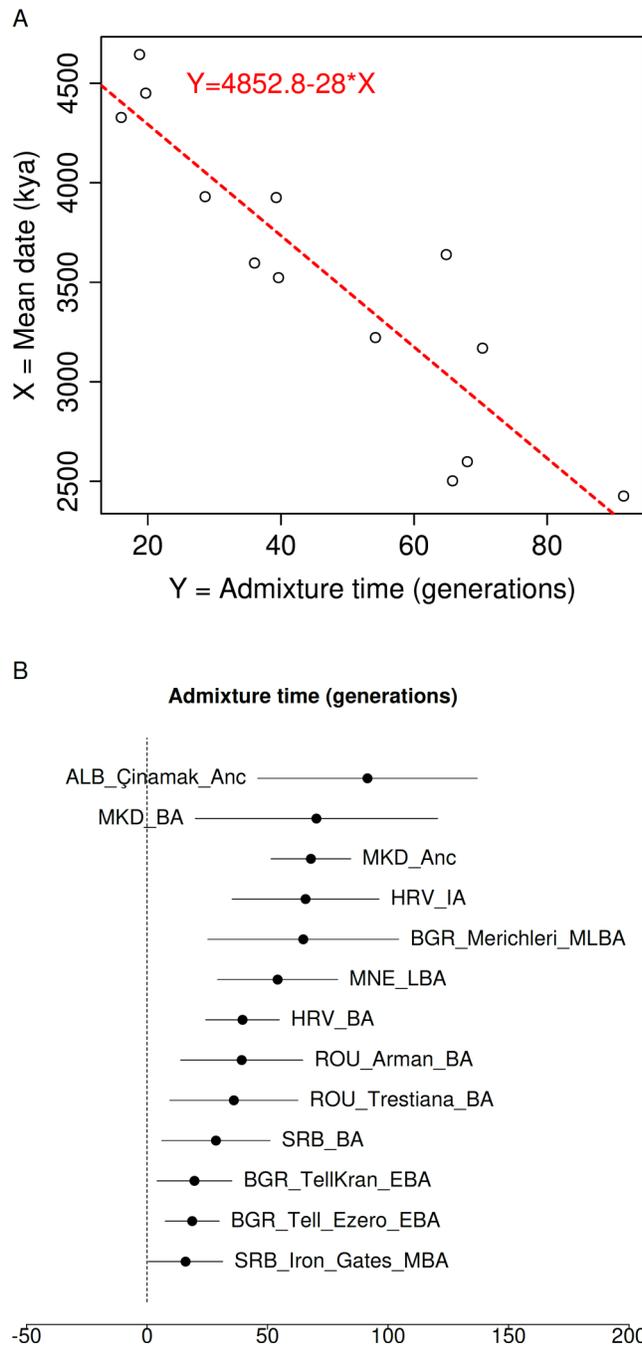


Fig. S 6 Admixture timing across Southeastern Europe. (A) Regression of population dates (using C14 dated individuals for each population) on admixture times in generations; more recent populations have older admixture times, and the regression places admixture between populations related to the SE European Neolithic and Yamnaya at $4,853 \pm 205$ years ago and the generation length at 28 ± 4 years, virtually identical to its independent empirical estimation of 28 years.⁽⁵⁴⁾ (B) Admixture times in generations of populations used in regression; this is the subset of Bronze Age, Iron Age, and Ancient populations for which admixture time was

significantly greater than zero ($Z \geq 3$) and could be estimated with a standard error < 20 generations.

Supplementary Text

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S1: Archaeological and Anthropological context of sampled individuals

In this section we describe the context of the sampled individuals. We list these alphabetically by country of origin.

Albania

Podgorie (Southeast Albania, Korça basin; Early Neolithic)

Contact: Rudenc Ruka

The Early Neolithic settlement of Podgorie (named very often in the literature Podgori) is situated in Southeastern Albania. It belongs to the northeastern periphery of the Korça basin, a rich and fertile high-altitude plain (ca. 850-860 masl), with numerous prehistoric settlement and burials sites. The settlement is located in the neighborhood of Kishnik, at the periphery of village Podgorie, at the foot of Mali i Thatë mountain. This archaeological site otherwise known as Pogori-Kishnik or Podgori 1, must not be confused with the nearby site of Podgorie-Luadisht that presents a different chronology and does not include the Early Neolithic component.

The site was first identified during agricultural activity by the local archaeologist Petrika Lera in 1970 and was initially thought to date to the Late Neolithic period (88) and (89): 52. It was however, quickly realized that the surface materials dated to the Early Neolithic period (90): 84-85. In 1974, P. Lera undertook test excavation that lead to the identification of Early, Middle and Late Neolithic, Eneolithic, as well as Early and Late Bronze Age components (89): 52-58.

Due to these interesting preliminary indications, systematic excavations were conducted at the site during 1982 by the Albanian prehistorians Muzafer Korkuti and Zhaneta Andrea, under the direction of Frano Prendi. The fieldwork focused in three different sectors, in a total area of 300m², and revealed ca. 3.2 m depth of archaeological stratigraphy, which ranged from Early Neolithic to the Bronze Age. The Early Neolithic was divided into three distinct phases according to pottery typology. Of particular note was the discovery of three Early Neolithic burials ((91): 112-13; (92): 277). Based on the presently published data, the Early Neolithic component of Podgori-Kishnik ranges between the end of the 7th millennium BCE to ca. 5600 calBC (93): 40; (94): 109; (95): 78, 81, 88–89; (96): 109.

One of the Early Neolithic individuals buried at Podgorie is included in this study:

- I15705/2708; Grave 2,1 (phalanx), genetically female.

This individual belonged to grave no. 2. The excavations have not been published systematically, consequently, no further evidence is provided on the exact location of the graves and other grave characteristics. It has been noted that they were found within the settlement and that they belonged to the Early Neolithic period, which is well supported by the radiocarbon date obtained in the course of this study 6223-6067 calBCE (7270±30 BP, PSUAMS-7927). This individual was included in the physical anthropological research conducted by the Albanian scholar Aleksandër Dhima, who associates it with the ‘gracile Mediterranean type’ (Dhima,

1985: 296). Based on anthropometric traits and morphological elements, Dhima's study focused on the formation and chronological development of anthropological types, seen in Albania ((97); for more on anthropological research history in Albania see (98)).

Tren cave 2 (Southeast Albania, Devoll area; Late Neolithic; Chalcolithic)

Contact: Rudenc Ruka

The archaeological site of Tren Cave 2, is located in Southeastern Albania, in the southwestern-most extremity of the Small Prespa Lake. The cave is on the western slope of a twin hill (western hill), at the bottom of Gryka e Ujikut gorge (ca. 860-870m asl).

The area was first explored during 1921 by the Swiss anthropologist and archaeologist Eugène Pittard, who noted the presence of a cave on the eastern slope of the twin hill (99): 40. This particular cave later became to be known as Tren Cave and was excavated under the direction of the Albanian prehistorian Muzafer Korkuti during 1966-1967, and more recently by the Albanian archaeologist Esmeralda Agolli (100). The archaeological record of the cave shows a long chronology that includes the Middle Neolithic, Eneolithic, Bronze Age, Iron Age, Roman, and the Early Middle Ages (101): 142-45; (102); (103); (104); (105): 166-67; (106): 182-83

The skeletal material included in this study comes from another cavity of the western slope of the twin hills, and on the opposite side of the entrance to the already known and explored Tren Cave. This cavity was most probably exposed during stone quarrying activity in the early 2000s and is presently accessed through an artificial entrance. It is not clear yet whether this large cavity is connected with the aforementioned Tren Cave. Therefore, for the purpose of this study, it has been named as Tren Cave 2. This particular cave was probably first identified thanks to a joint Italian-Albanian speleological explorations conducted during 2007 (107). It was only in 2009 that the cavity was visited by Albanian archaeologists. A number of archaeological remains, such as pottery and skeletal materials were collected, in relation to disturbed contexts due to illicit excavations.

The human remains included in this study belong to two different individuals:

- I13840/1241; Skull 1, 44 (petrous bone), genetically male.
- I13838/1239; Skull 2, 45 (petrous bone), genetically male.

Dukat (Southwest Albania; Bronze and Iron Age; Medieval period)

Contact: Rovená Kurti, Rudenc Ruka

The two burial mounds excavated near the village of Dukat in the 1970s (108), were located in the Plain of Dukat, in southwestern Albania. The plain extends northwest-southeast, from the southern end of the Vlora bay, where two seas, the Adriatic and the Ionian meet. The two tumuli were located at a distance of 1 km from each other, at the edges of the narrow, in the southeastern part of the plain. They were excavated during 1970s: Tumulus 1 excavated by Neritan Ceka (Ceka, 1974) and Tumulus 2 by N. Bodinaku (Bodinaku, 2002).

The necropolis of tumuli (the presence of other tumuli in this plane has been reported in the literature, Ceka, 1974: 131) was founded since the Early Bronze Age, a period to which has been attributed the central grave of Tumulus 2 (Bodinaku, 2002: 73-74). However, the main phase of the use of the tumulus includes the Late Bronze Age and particularly the Early Iron Age (11th-10th centuries BCE). The tumulus was reused in the Late Antique and particularly in the Early

Medieval period. Tumulus 1 was founded in the Late Bronze Age, while similar to Tumulus 2, its main phase of use belongs to the Early Iron Age. It was sporadically reused in the Late Iron Age (7th-6th centuries BCE) and during the Hellenistic and possibly the Roman period (109): 25-26

Two individuals from the tumuli of Dukat are included in the present study:

- I17622/2637; Tumulus 1, grave 10 (?) (molar tooth), genetically male, adult. Only the mandible has been preserved from the skeleton.
- I17623/2638; Tumulus 2, grave 38 (?), 12 (molar tooth), genetically male, adult. The age is estimated over 35 years old (35+). Only the skull and mandible are preserved from the skeleton.

Unfortunately, due to the poor labelling of the skeletal remains, both individuals cannot be safely associated with a specific grave context from any of the two tumuli excavated at Dukat. The individual I17622/2637 from Tumulus 1 most probably belongs to the graves included in the time span that covers the Late Bronze Age-Early Iron Age, which is the main period of the tumulus use.

According to the label found with individual I17623/2638, it could be associated with grave 38 of Tumulus 2. This grave has been dated to the Early Medieval Period (9th-10th centuries CE), which corresponds with an important phase of the reuse of the prehistoric burial mound. The two long sides of the grave pit were limited by medium size stones; similar stones were used for the covering. The skeleton was oriented east-west with the head to the west. It was found in an extended supine position, with both forearms folded over the lower torso (109): 40, fig. 24. The grave inventory included a bronze applique and an iron finger ring, as well as an iron ring found in the midsection of the skeleton.

Shkrel, Tumulus 099 (Middle Bronze Age)

Projekti Arkeologjik i Shkodrës (PASH) [The Shkodër Archaeological Project]

Contacts: Michael L. Galaty, Lorenc Bejko, and Sylvia Deskaj

Tumulus (mound) burials are common in Albania, including in northern Albania, beginning in the Early Bronze Age through the Iron Age. PASH located and mapped 82 mounds in Shkrel, in the province of Shkodër. One of these, numbered 099, was chosen for excavation, which took place in 2014. Ten tumuli in Shkrel (Dedaj) were excavated by Albanian archaeologists Bep Jubani in the 1980s and 90s. Jubani argued based on relative dating of archaeological finds in the mounds and graves that they were built and used in the Early Bronze Age. Tumulus 099, however, dates to the Middle Bronze Age, based on two AMS C14 dates on human teeth.

Tumulus 099 is located along the main, asphalt road into Shkrel, just south of a new prison. It was approximately 20 meters in diameter, and was 1.75 meters in height, composed of rock and soil. The mound had been excavated or looted in the past, exposing a central, stone-slab cist grave. The central grave contained fragmented remains of three different individuals, two adults and a juvenile. Diagnostic sherds from excavation as well as AMS radiocarbon dating of two adult teeth (1740-1610 BCE and 1885-1690 BCE) date the tumulus to the Middle Bronze Age.

Additionally, strontium isotope analysis performed on the latter tooth, dating to 1885-1690 BCE, indicate that that individual was likely of non-local, inland origin. One individual is included in this study.

- I8471/SD001, GT2811A; SD003, GT2811C (tooth), genetically male.

References: (110-112)

Çinamak (northeastern Albania-Kukës district; Bronze Age; Iron Age)

Contact: Rovena Kurti, Rudenc Ruka

The village of Çinamak is part of Kukës district, located in northeastern Albania, near the confluence of the White Drin (alb. Drini i Bardhë) and the Black Drin rivers (alb. Drini i Zi), and near the border with Kosovo. The region is very mountainous, in contrast to the Kukës basin and the river valleys which constitute the main suitable area for living. A significant number of prehistoric sites have been identified and excavated in the region, especially burial mounds.

The necropolis of tumuli of Çinamak was located on an elongated river terrace (1.2 km long and 120-140 m wide; around 150 m a.s.l.), along the left bank of the Black Drin River, which at present is covered by the waters of Fierza Lake. During 1969-1975, there were excavated 28 tumuli of this necropolis by Bep Jubani (113-117). This was a rescue excavation that preceded the construction of the Fierza hydroelectric power station. The necropolis included around 80 burial mounds, distributed along the river terrace, most of them organized in groups.

The ritual of burying the dead under a mound or tumulus was introduced to the region in the Early Bronze Age. According to the author of the excavation, only two tumuli from the necropolis of Çinamak were founded at such dates, tumulus 1 and 10 (this study includes individual I14689/1707; 2831-2480 calBCE, from grave 23 of tumulus 10; Fig. S 7). However, the main phases of the necropolis use include the Late Bronze Age (or the 15th-10th centuries BCE) and particularly the Late Iron Age (or the time span that includes the 7/6th-5th centuries BCE), when an important number of burial mounds were added to the cemetery. Several tumuli were continuously used or reused in the following periods, some of them up to the early Medieval period (113, 116).

Early Bronze Age

- I14689/1707; Tumulus 10, grave 23, 29 (petrous bone), genetically male.

This male individual belonged to grave 23 of Tumulus 10 of Çinamak. The radiocarbon date obtained from the bones 2663-2472 calBCE (4045±25 BP, PSUAMS-7926) supports the dating suggested by the author of the excavation for the earliest graves from this tumulus. Based mainly on the ceramic and stratigraphic evidence, he attributed to the Early Bronze Age the central grave of Tumulus 10 (or grave 27), as well as grave no. 26 (Jubani 1990). Both graves were positioned at the center of the mound. The central grave consisted of a slightly irregular rectangular pit of large dimensions (3.20 x 2.50 m; depth 0.80 m); the skeleton was found in a crouched position, on the left side (115): 42-43; no inventory was found in the grave. Grave no. 23 associated with the individual I14689/1707 was found 0.60 m from the center. It consisted of an oval shaped pit (dimensions 1.70 x 0.80 m), limited and covered by stones. The grave was

oriented northwest-southeast; inhumation was practiced, but no further details on the position of the skeleton are provided. No grave goods were included in the grave.

Late Iron Age

- I17640/2700; Tumulus 4, grave 19, 37 (tooth), genetically male, adult.
Estimated age is 20 – 29 years old.

Grave 19 of Tumulus 4 of Çinamak had an ellipsoidal shape (dimensions 1.70 x 0.80 m), and was lined and covered by stones. The skeleton was found in supine position, with the left arm folded on the chest; oriented east-west, with the head to the west. The grave inventory includes iron knives (2) and spearheads (2), an iron double axe, one or two iron pins, as well as a local one-handled vessel (I17). It dates to the Late Iron Age, or the 6th-5th centuries BCE.

- I16253/1943; Tumulus 14, central grave (grave 91), 28 (petrous bone), genetically male.
At the present state, only some fragments of the skull and the mandible are preserved.

This individual belongs to the central grave (grave 91) of Tumulus 14. The radiocarbon date obtained 658-403 calBCE (2405±20 BP, PSUAMS-7193) provides solid evidence for the foundation of the tumulus at the Late Iron Age, as suggested by the grave inventory. This absolute date is also consistent with I14688/1706 from the same tumulus.

The pit of the grave was lined and covered by stones; it measured 2.30 m x 0.90 m. The skeleton was oriented northwest-southeast with the head to the northwest; in supine and extended position. The grave inventory included two local cantharoi, two to three iron spears, the handle of an iron knife and an iron pin (I17).

- I14688/1706; Tumulus 14, grave 92, 27 (petrous bone), genetically male, adult.

Age is estimated to be over 45 years old (45+). The skeleton includes some fragments of the skull, right femur, left humerus and tibia.

This individual belongs to grave 92 of Tumulus 14. The skeleton was oriented northwest-southeast with the head to the southeast. Grave dimensions: 2 m x 1 m; in supine position. The grave inventory includes: a local one-handled vessel, an iron spearhead and an iron spear, as well as an iron pin (I17). It dates to the Late Iron Age or the 6th-5th centuries BCE.

- I16254/1944; Tumulus 16, grave 2, 26 (petrous bone), genetically male, adult.
Estimated age is 20 – 25 years old.

The skeleton preserves the skull and the inferior members.

Grave 2 of Tumulus 16 of Çinamak (dimensions 1.90 m x 1.00 m) was oriented northwest-southeast. The grave inventory includes fragmented local ceramic vessels, two iron fibulae and two bronze pins, and several bronze, amber and glass beads (I17). It dates to the Late Iron Age or the 6th-5th centuries BCE.

- I14692/1710; Tumulus 16, grave 17, 18 (petrous bone), genetically female.

Grave 17 of Tumulus 16 of Çinamak. The pit of the grave had a rectangular shape, and is lined by stones (dimensions 2.20 m x 0.90 m). The skeleton was oriented east-west, with the head to the east; in supine position. No grave goods were included in the grave. Tumulus 16 was founded in the Late Bronze Age, whereas most of the graves date to the Late Iron Age, or to the period that includes the 6th-4th centuries BCE (I17).

- I16256/1946; Tumulus 20, Grave 12, 21 (petrous bone), genetically female.

Grave 12 of Tumulus 20 of Çinamak was oriented east-west (dimensions 2.20 x 0.90 m). The grave inventory includes two local cantharoi (fragmented), an iron pin, one spindle whorl, one loom weight and several glass beads. It dates to the Late Iron Age or around the 7th-5th centuries BCE.

Individuals whose association with a specific grave inventory remains uncertain or is not known:

- I16251/1941; Tumulus 14, Grave 37, 30 (petrous bone), genetically male, adult.

Estimated age > 40 years old. The skeleton preserves the complete skull and some fragments of the inferior members. It remains uncertain if this individual from Çinamak belongs to Tumulus 14, grave 37 (as written on the associated label). The burial ritual practiced for grave 37 remains unclear. According to the notes of the author of the excavation (117), incineration was practiced and some of the bones were deposited in a simple pit grave, which included a number of fragmented vessels of different shapes and three glass beads. Consequently, the dating of this individual remains uncertain. Based on the different pottery fragments found in the pit it can be generally attributed to the interval between the 6th-1st centuries BCE.

- I14691/1709; no. of tumulus unknown, field inv. No 901, 25 (petrous bone), genetically female, adult. The age was estimated to be between 25 – 29 years old.
- I17633/2694; Tumulus no. unknown, field inv. 114, 34 (tooth), genetically male.
- I14690/1708; Tumulus 4, (grave unknown) field inv. 678, 35 (petrous bone), genetically male

Only fragments of the skull were preserved.



Fig. S 7 Tumulus 10 at Çinamak where the outlier I14689/1707 was unearthed (Albanian Institute of Archaeology).

These three individuals buried at the necropolis of Çinamak cannot be associated with a specific tumulus/grave context. Considering the long chronology of the necropolis, they could date from the Early Bronze Age to Early Medieval period; but more possibly to the interval that includes the Late Bronze Age and Late Iron Age. Individual I17633 likely belongs to Tumulus 20, because a family relationship was revealed with individual I16256 (1d relationship) from Tumulus 20.

Individual I14690/1708 most probably belongs to Tumulus 4, which was used during Middle/Late Bronze Age, then reused extensively in the Late Iron Age and sporadically in the Late Roman period (117).

Kënetë (northeastern Albania-Kukës district; Medieval)

Contact: Rovena Kurti, Rudenc Ruka

The necropolis of tumuli at Kënetë is located in northeastern Albania only few kilometers from that at Çinamak. It belonged to the lowest river terrace along the right bank of Black Drin River (alb. Drini i Zi), which at present is also covered by the waters of the Fierza Lake. From the nine tumuli identified along the terrace, six were excavated during the 1960s and 1970s (118, 119). The tumuli were arranged almost in a N-S line, at a distance of 10 to 15 m from each other. Few of them were founded since the Bronze Age, while the main phase of the use of the

necropolis dates to the late Iron Age or the 7th-6th centuries BCE. They were sporadically reused in the later periods.

One individual from Tumulus 4 of Kënetë is included in this study:

- I14622/1233; Tumulus 4, grave 6, 43 (petrous bone), genetically male.

Grave 6 of Tumulus 4 was a simple pit grave oriented north-south. Only two fragments of wheel made pottery were found in the grave. Tumulus 4 included 10 graves in total. According to the author of the excavation, the burial mound was founded in the Early Bronze Age (Jubani, 1992: 111) and continued to be used during Late Bronze Age and Late Iron Age. The radiocarbon date obtained from 773-885 calCE (1205±20 BP, PSUAMS-7198) suggests that the necropolis of Kënetë was also reused in the Early Medieval period.

Shtikë (Southeastern Albania, Kolonja Plateau; Medieval)

Contact: Rovena Kurti, Rudenc Ruka

The flat necropolis of Shtikë is situated on the northeastern edge of the Kolonja Plateau, in southeastern Albania. The necropolis was located on a high plateau to the eastern periphery of Shtikë village (1100 m asl.), at the foot of Gramoz Mountain range, on the actual border between Albania and Greece.

The excavation was carried out in 1969 under the direction of Damian Komata (120). There were excavated 40 graves in total, in an area of 130 m². The graves were relatively close to each other; there were cases when graves were touching, or at a distance that varies between 0.30 and 1.20 m. The architecture of the graves was quite homogenous: graves were limited by vertical stone slabs; irregular stone slabs were used for their covering. Most of them were oriented east-west. Only eight graves were associated with grave goods. The inhumation ritual practiced is also homogenous: the body was laid on the natural bedrock in an extended supine position; only the position of arms was relatively flexible.

The necropolis dates to the Early Medieval period.

One individual from this cemetery is included in this study:

- I13839/1240; Grave 36, 51 (petrous bone), genetically female, adult.

Estimated age is 40-45 years old (121): 316. The skeleton belonged to grave 36 of the necropolis. Dimensions: 1.62 m long; 0.55 m wide and depth 0.33 m. The length of the skeleton was 1.45 m, and it was found in an extended supine position, with both hands on the belly. The grave inventory included a pair of earrings and a bracelet. The radiocarbon date obtained from this individual is 889-989 calCE (1120±20 BP, PSUAMS-5943).

Barç (Southeast Albania, Korça basin; post-Medieval/Modern)

Contact: Rovena Kurti, Rudenc Ruka

The two tumuli of Barç were located on the eastern periphery of the Korça Plain, in southeastern Albania. The village of Barç is 2 km to the NE of Korça city. The tumuli were at a distance of 100 m from each other and very possibly were part of a necropolis of tumuli, as

traces of another damaged burial mound were identified at their proximity. They were discovered in the 1960s during agricultural activity in the plain. During the 1970s the two tumuli were excavated by Zh. Andrea (*122-125*)(Andrea 1971; 1974; 1976; 1985).

The biggest mound or Tumulus 1 included 181 graves. It was possibly founded in the Early Bronze Age. However, the main phase of tumulus use includes the Late Bronze Age and Iron Age. Tumulus 2 included 22 graves in total. The main phase of use includes the Late Bronze Age and Early Iron Age, and only few graves date to the Late Iron Age. According to the author of the excavation, only one grave (no. 13) was added in the Medieval period. Zh. Andrea notes in particular a group of graves, more specifically nos. 1, 3-5, 7-8 (*125*): 101-102, 250, figs. 12-13: all located near the eastern periphery of the mound and near the surface; all in an extended supine position, mostly oriented east-west; and with no grave inventory included. However, based on stratigraphic evidence, such as their association with the second (upper) main layer of the mound fill, where few graves of the Late Iron Age were also found, Andrea associated all these graves to the Late Iron Age. The radiocarbon dates obtained from several individuals included in this study that belong to this group of graves, provide clear evidence for the reuse of the mound in the post-Medieval/Modern period, or otherwise during the early phase of the Ottoman period. The radiocarbon dates obtained from several individuals included in this study that belong to this group of graves, provide clear evidence for the reuse of the mound in the post-Medieval/Modern period, or otherwise during the early phase of the Ottoman period which began in the 1380s in the region of Korça (where Barç is located) and was well-established at the beginning of the 15th century(*126*).

Five individuals from this group of later graves of Tumulus 2 at Barç are included in this study:

- I13835/1236; Tumulus 2, grave 7, 6 (petrous bone), genetically female, adult.

Her age is estimated between 30 – 40 years old. She has a mother or daughter relationship to I13837.

The skeleton preserves the complete skull and a fragment of the mandible. Traces of dental caries are present in the second mandibular molar, left side. This individual belongs to Tumulus 2, grave 7. The grave was oriented east-west. The skeleton was well preserved, in a supine extended position, with hands on the abdomen. No grave goods were found in the grave. Radiocarbon date obtained: 1644-1797 calCE (235±15 BP, PSUAMS-8291).

- I13837/1238; Tumulus 2, grave 4, 8 (petrous bone), genetically female, adult.

Her age is between 20 – 25 years old. She has a mother or daughter relationship with I13835.

The skeleton preserves the mandible and the skull. Tumulus 2, grave 4, to which this individual belongs, was cut by grave no. 5. Traces of carbonised wood in the grave suggest the use of a wooden coffin. The skeleton was oriented SW-NE. No grave goods were found in the grave. Radiocarbon date obtained from this individual is 1481-1635 calCE (340±15 BP, PSUAMS-8301).

- I13833/1234; ; Tumulus 2, grave 3, ind. 1, 2 (petrous bone), genetically male, young adult.

His age is estimated to be between 17 – 19 years old. The skeleton preserves only part of the occipital section of the skull and fragments of the mandible. It belongs to Tumulus 2, grave 3.

The grave was oriented east-west. The skeleton was well preserved (length 1.70 m), in a supine extended position, with hands on the abdomen. No grave goods were found in the grave.

- I13836/1237; Tumulus 2, grave 8, 7 (petrous bone), genetically female, adult.

Her age is estimated to be over 40 years old. The skeleton only preserves the skull. The skeleton derives from Tumulus 2, grave 8. The grave was oriented north-south. The skeleton was well-preserved, in a supine extended position, with the right hand on the abdomen and the left by the side. No grave goods were found in the grave. Radiocarbon date obtained from this individual is: 1452-1619 calCE (385±15 BP, PSUAMS-8300).

- I13834/1235; Tumulus 2, grave 1? (petrous bone), genetically male, adult.

His age is estimated to be over 40 years old. The skeleton is well presented.

The skeleton most likely derives from Tumulus 2, grave 1. The grave was oriented NE-SW, with the inhumation in a supine extended position. The radiocarbon date obtained from this individual was 1402-1439 calCE (515±20 BP, PSUAMS-5942).

Bardhoc (northeastern Albania-Kukës district; post-Medieval)

Contact: Rovena Kurti, Rudenc Ruka

The tumuli of Bardhoc were located few kilometers to the northeast of the necropolis of Çinamak and Kënetë, in northeastern Albania. They were found on the left bank of White Drin River (alb. Drini i Bardhë), on a lowland surrounded by low hills, at the foot of Mount Koritnik.

The tumuli were used since the Late Bronze Age, but their main phase of use belongs to the Late Iron Age or the 6th-5th centuries BCE. The author of the excavation notes the presence of eight graves from Tumulus 1, which are distinguished from the prehistoric ones because they were found near the surface of the mound; all in extended supine position and oriented east-west (with the head to the west); with no inventory included, apart from a few iron nails. He suggests that they might belong to a later period (127): 32-33. The four individuals from Tumulus 1 included in this study belong to this group of putatively later graves:

- I15707/2710; Tumulus 1, grave 19, 46 (petrous bone), genetically male, adult.

His age is estimated to be above 45 years old. The skeleton preserves the complete skull and part of the mandible, the left femur, the left tibia and the right humerus. The skeleton derived from Tumulus 1, grave 19. The shallow grave pit had an ellipsoidal shape and was cut into the bedrock. Skeleton was well preserved in the extended supine position, oriented east-west. The use of wood coffins seems possible as suggested by the presence of visible traces of carbonized wood and three iron nails. No other grave goods were found in the grave. We radiocarbon dated the skeleton to 1472-1632 calCE (355±15 BP, PSUAMS-7161) which supports the reuse of this prehistoric burial mound in the post-Medieval period and a dating at around the same date for all the eight later graves distinguished by the author of the excavation (nos. 18-21; 25-26; 29-30).

- I14687/1705; Tumulus 1, grave 25, 50 (petrous bone), genetically male, adult.

The estimated age is between 35 – 40 years old. The skull is fragmented, but other parts of the skeleton (both radius, ulnas and the left femur) are perfectly preserved. An accidental trauma was noted in the right radius. The skeleton derived from Tumulus 1, grave 25. The shallow grave

pit had an ellipsoidal shape and was cut into the bedrock. The skeleton was found in the extended supine position, oriented east-west. The use of wood coffins seems possible as suggested by the presence of visible traces of carbonized wood and four iron nails. No other finds were included in the grave.

- I14685/1703; Tumulus 1, grave 20, 47 (petrous bone), genetically female.

The skeleton derived from Tumulus 1, grave 20. Grave features very similar to I15707 and I14687 (grave nos. 19 and 25). No other finds were included in the grave.

- I14686/1704; Tumulus 1, grave 18, 49 (petrous bone), genetically male, adult.

The estimated age is over 45 years old. The skeleton only preserved the complete skull.

The skeleton derived from Tumulus 1, grave 18. The shallow grave pit had an ellipsoidal shape and was cut into the bedrock.

Pazhok (Central Albania; Modern)

Contact: Rovena Kurti, Rudenc Ruka

The necropolis of tumuli of Pazhok is situated 5 km southeast of the city of Elbasan, in central Albania. It is located in a plain, between the Devoll (to the right bank of the river) and Shkumbin rivers, at the point where the valleys of the two rivers converge. At the time of its discovery, 25 burial mounds were counted on the plain, most of them damaged due to agricultural activity. The mounds were spaced at a distance of 50 m to 200 m, and sometimes more. Seven of them were excavated systematically. The three first tumuli were excavated in 1960 by Selim Islami and Hasan Ceka, while four others were excavated in 1973 by Namik Bodinaku (*I28*): 95; (*I29*); (*I30*); (*I31*): 60. Although they were badly damaged, the excavations revealed that the necropolis was used since the Early Bronze Age, when the construction of Tumulus 1 started (with two graves and three individuals). However, the Late Bronze Age and Early Iron Age (until the 8th century BCE) is the period of its most important use during the late prehistory. The necropolis was reused in the Medieval period. However, according to the author of the excavation, an important period of its reuse belongs to the post-Medieval period (Tumulus 4 and 5, (*I30*): 85; (*I31*): 117-118), which is supported by the presence of jewelry, as well as a coin dated to the 17th century CE.

The only individual from the necropolis of Pazhok included in this study belongs to this late period of the reuse of the necropolis:

- I15706/2709; Tumulus 1, grave 18, 11 (petrous bone), genetically male.

His age is estimated to be above 45 years old (45+). At the present state, from the skeleton is preserved only the complete skull. The radiocarbon date is 1527-1660 calCE (270±13 BP). Based on the labels in the storage boxes, this individual seems to belong to Tumulus 1, grave 18. No detailed information is provided for this grave in the literature.

Anatolia/Turkey

Archaeological Overview of Genetic Variations of Turkey Samples

Atila Engin

Covering an area of 783,562 km² Turkey constitutes a bridge between Europe and Asia that has always functioned as an important gateway to both continents. The Anatolian peninsula has been a passage not only between these continents, but also had a role in the spread of Paleolithic Age hunter societies, especially those migrating from Africa to Europe. In the "Overview of Genetic Variation" study approximately 200 samples obtained from more than 30 archaeological sites in Turkey and dated to different periods ranging from the Neolithic to the Middle Ages were evaluated. The early periods through the Middle Bronze Age constitute about 35% of the samples, while the Late Bronze Age, Iron Age, Hellenistic and Roman periods and the Middle Ages make up the rest.

When evaluating the samples from Turkey archaeologically and anthropologically, it is necessary to ask from which context they originate: from intramural burials (graves in settlements) typical of pre-Iron Age sites, or from extramural necropolises (clustered graves outside settlements), landmarks of the Iron Age and later periods. Anthropological data further show that the samples evaluated belong to different age groups such as infants, children and adults. While burials in Neolithic and Chalcolithic sites belong to the simple earth grave category, pot graves, pithos burials, stone cist graves, chamber graves and rock-cut tombs are encountered in the Early Bronze Age and later periods. Pot graves were used for infants and children. Until the Iron Age people were buried generally in flexed position (*hocker*), but from the Iron Age it was customary to bury the dead flat on the back (dorsal position). Until the Byzantine period there was no unity of direction in which the body of the deceased was laid.

In the Neolithic period gifts accompanying the dead were generally scarce, while from the following Chalcolithic era pottery, ornaments, tools, weapons and food began to appear more frequently in the tombs. With exceptions in earlier periods, multiple burials are mainly found in Bronze Age cemeteries. Pithos graves in particular show that more individuals were buried in the same vessel. These pithoi apparently served as family graves.

Differences in burial customs, material cultures, technologies and lifestyle observed in different regions of the Anatolian peninsula indicate differences in population composition, while changes in this pattern may reflect new arrivals. Especially in the Iron Age, various burial customs could be found in the same necropolis indicating that the community included different ethnic groups.

The regions of Turkey have demonstrated cultural integrity with neighboring regions for thousands of years in human cultural history. It should be borne in mind, however, that geographical boundaries are a factor that largely determines the distribution of human cultures of the successive periods. While the Anti-Taurus Mountains and the mountain ranges in eastern Turkey allow migrations through east-west and north-south oriented valleys, the same mountain ranges have hampered connections between the Anatolian heartland and the southern and eastern regions, especially in harsh winter conditions. Therefore, Eastern Turkey shows ties to the Caucasus, while Southeast Turkey shows unity with the Mesopotamian and Syro-Eastern Mediterranean cultures. On the other hand, Northwest Turkey (North Marmara region), which is

part of Southeast Europe, has been linked to the Balkan cultures for thousands of years; the coastal region of West Anatolia has strong links with the cultures of the Aegean Sea basin.

Southeast Turkey is part of the Fertile Crescent including North Mesopotamia and the Northwest Zagros mountains as well, where the first farming villages emerged to replace hunter-gatherer communities. While incipient farming was concentrated in the Fertile Crescent, adjacent Mesopotamia in particular hosted innovations such as the first cities, writing, state bureaucracy (city-states), organized trade, and important technological developments. From the earliest times the Euphrates allowed cultures from the south to spread to the Upper Euphrates region. There are Aceramic Neolithic sites such as Caferhöyük and the Late Chalcolithic Ubaid and Uruk sites of Arslantepe and Değirmentepe which maintained strong links with the southern regions.

Findings of genetic variation confirm the spread of regional cultures in Turkey according to material cultures as described in archaeological studies. Neolithic developments of southeast Turkey and the Eastern Mediterranean are known to have spread across Anatolia. The samples from Boncuklu Tarla near Mardin are from occupation layers dated to the Pre-Pottery Neolithic A (PPNA). The earliest samples from Barcın, Menteşe and Ilıpınar Höyük near Bursa belong to a later phase of the Neolithic. It is important to note that periodic developments did not occur at the same time in every region. At the time when settlements arose in the Southeast and food production started, there were hunter-gatherer communities in Southeastern Europe. For this reason, the Neolithic, Chalcolithic and Bronze Ages in particular can be dated differently in each region.

There are many factors that trigger humans to move and relocate such as drought, wars, epidemics, population increases. Years of archaeological research show the (pre)history of Turkey as an important resource for cultural development and a crucial passageway of cultural diffusion from the Caucasus, Mesopotamia, the Levant and the Eastern Mediterranean to the west. That picture is confirmed by the samples in terms of genetic variation.

Migration movements were not only over land, but also by sea. Early seafaring took place in the Eastern Mediterranean and the Aegean Basin, where contacts between the mainland and offshore islands had existed since the early settlement phases of the Neolithic. However, it is known that organized maritime trade mainly emerged from the end of the 3rd millennium BCE and showed great development from the beginning of the 2nd millennium. Intensive relations of the Minoan and Mycenaean communities in the Aegean Basin with the North African coasts and the Eastern Mediterranean went by sea, and technological developments and traditions of the East reached the West also by sea.

When we follow the movements of the material cultures, it becomes clear that until the period of the Roman and Byzantine empires, which ruled over three continents, migrations mainly took place from East to West. Indeed, written sources state that there were also migrations from West to East during that period, and that large numbers of people were moved eastward to control the Eastern Mediterranean ports and the rich resources and trade routes to Mesopotamia, Syria and Egypt.

Mardin excavations

Boncuklu Tarla (Mardin, Dargeçit, Iısu; Pre-pottery Neolithic)

Contact: Nihat Erdoğan

Mardin Boncuklu Tarla represents an important stage in the succession of early food production cultures of the Near East. Sites attributed to these Aceramic Neolithic cultures were discovered in the Northern and Southern Levant and investigated from the 60's and 70's onward. As a result, the impression arose that food production had principally developed in those regions, whereas Anatolia and Iran were considered marginal to the core area. With the start of a long-lasting excavation campaign at Çayönü led under auspices of Robert Braidwood and Halet Çambel, this image has gradually been adjusted. Not only were various stages of crop domestication demonstrated at the site, but the Çayönü site also displayed a rarely observed full development of PPNA and PPNB architectural phases running from round huts to rectangular buildings (132-134).

The site of Boncuklu Tarla, dated to the Pre-pottery Neolithic (PPN) period, is situated on a slope. The excavations uncovered architectural remains close to the surface which were partially destroyed. The architecture of the upper levels, including the courtyard and the room layout, clearly corresponds to the cell period of the Pre-Pottery Neolithic, which is well-known from the excavations at Çayönü. Structures and rooms were paved with stones or pebbles. In addition, a terazzo floor paved structure was uncovered in the settlement. This structure was probably used as a public building. All graves in the settlement were found under house floors. They had no standard orientation. Most individuals were buried in flexed and semi-flexed positions. Apart from single graves multiple burials also occurred. The samples were taken from the early phases of the Pre-pottery Neolithic. Three samples are included in this study.

- I8432/26G-2017 (petrous bone), genetically female, infant

A few thin skull fragments and two teeth (first and second milk molar crowns) were recovered from the grave pointing to a neonatal (+/- 2 months; Moorrees et.al., 1963. Age determination by Alpaslan-Roodenberg).

- I8435/27G-2017 (petrous bone), genetically female, juvenile
- I14445/G56 (petrous bone), genetically female, adult

Tatika (Şırnak, Güçlükönak, Koçtepe; Chalcolithic and Early Bronze Age)

Contact: Nihat Erdoğan

Located on the banks of the Tigris River, just south of Koçtepe village, Tatika dates to the beginning of the Early Bronze Age. Extending to the west on a rocky hillside, this site would have been used as a cemetery rather than as a settlement. Where there were interconnected spaces, no upper structure remains of buildings were unearthed. Pits paved with stones at different depths we spotted in some of the structures. Some of these pits yielded numerous pottery sherds, while one pit revealed several jar burials. Almost all human remains uncovered in the site were interred in jars. Beside this, a small number of simple stone cists and earthen graves could be identified. The majority of buried individuals were likely to have been children and infants. Although traces of ovens and hearths appeared in the investigated area, there is no clear evidence of a substantial settlement. The painted and unpainted pottery of different sizes found

in the trenches are likely burial gifts. Twelve samples are included in this study. Three burials dated to the Late Chalcolithic period; nine are Early Bronze Age:

Late Chalcolithic period

- I4483/B7 (petrous bone), genetically male, infant.

This infant, buried in a small jar, is exhibited in the museum of Mardin. It belongs to the Chalcolithic period. The infant's age is assessed at ca. 1.5 months (studied by Alpaslan-Roodenberg; (135)).

- I4622/C8, 27G (petrous bone), genetically male, infant.
- I4480/E6, 15G (petrous bone), genetically female, infant.

Early Bronze Age

- I4481/E7, 6G (petrous bone), genetically female, infant. Sister of the infant I4478/E7, 7G.
- I4614/E6, 10G (petrous bone), genetically male, infant.
- I4615/B7, 27G (petrous bone), genetically male, infant.
- I4616/B8, 15G (petrous bone), genetically male, infant.
- I4617/C7, 10G (petrous bone), genetically female, infant.
- I4619/E7, 5G (petrous bone), genetically female, juvenile.
- I4620/E7, 4G (petrous bone), genetically female, infant.
- I4478/E7, 7G (petrous bone), genetically male, infant. Brother of the infant I4481/E7, 6G.
- I4621/C7, 9G (petrous bone), genetically male, infant.

Dara (Mardin; Roman / Byzantine)

Contact: Nihat Erdoğan

Dara was a garrison city built by the Roman Emperor Anastasius in the 6th century CE to protect the borders against the Sassanids; however, the first establishment of the settlement was Persian. The city was large, surrounded by a 4 km wall. There were enough water cisterns to meet the needs of a large population. Administrative buildings, religious buildings, houses, a bazaar and a large necropolis area were present. The necropolis was large enough to cover most of the city's western slopes. The area excavated here was located in the old stone quarries at the bottom of the western walls. The Great Gallery catacomb in this section was of a peculiar architecture. This three-story gallery has a rectangular plan and the two upper floors have tomb naves with arched pediments. In this section there were multiple burials. The lower floor, covered with blocks of bedrock and stone, looks like a cellar with a stone staircase to the upper floor. Here, a large number of human bones lay stacked on top of each other. The samples included in this study were collected in this gallery. In order to make room for new tombs on the upper floors, the bones from prior burials would have been collected in this area. In this way, the dead would wait for the day of apocalypse, while there would be room for new burials on the upper floors. In Dara different types of graves occur. Along with arched tombs carved into the

rock, chamber tombs, sarcophagus tombs carved directly into the bedrock and simple stone cists to a lesser extent were also found in the necropolis of the city. Late Christian simple cist graves were east-west oriented, but this unity of orientation did not apply to the other periods. Ten samples are collected in different places of the underground burial gallery in Dara. Five samples are included in this study:

- I4474/D5 (petrous bone), genetically male, adult.
- I4475/D6 (petrous bone), genetically male, non-adult.
- I4532/D7 (petrous bone), genetically male, non-adult.
- I4533/D9 (petrous bone), genetically male, adult.
- I4534/D10 (petrous bone), genetically female, adult.

Aktaş Mevki (Midyat, Mardin; Roman / Byzantine)

Contact: Ayşe Acar

The necropolis of Aktaş Mevki in the Midyat district of the province of Mardin is situated in the eastern part of the district, north of the Mor Abel and Mor Abrohom monasteries. It is classified as a first-degree protected archaeological zone. The cemetery consists of rooms carved on the west side of a low rocky area, all with skeletal remains. The 4 burial chambers are labeled A, B, C, and D. There were 3 boat shaped graves south of the front door of chamber A, and 3 north of the door. Furthermore, a sarcophagus in the eastern part of that chamber and scattered human bones on the floor. Chamber B, located north of chamber A revealed 2 carved tombs. Excavations on the floor of chamber B yielded human bones piled up at the foot of the northern wall. Northeast of chamber B there was an opening to adjoining chamber C. There was a niche right of the entrance. Chamber C included 6 carved tombs, one in the north and south, three in the east and one north of the entrance. Burial chamber D was the smallest in size. Here the bones of prior graves were stacked on one side to make room for later burials. There were 3 graves inside the room. The burial position of the skeleton in grave 1 of chamber D was identified as flexed, a position that was not observed in other graves. Coins, pottery vessels, beads and tear bottles were found inside the burial chambers. Dating of the coins confirmed these remains to belong to the Roman Period. Four individuals are included in this study:

- I5255/Chamber D; individual 1 (molar tooth), genetically female, adult.

This individual was buried in flexed position. The skull was intact except for the face. The metopic suture was detected in the frontal bone. The age was estimated to be between 30 and 35 years. Maxillar M3 and mandibular M1 were lost before death.

- I4613/Chamber A/G10 (petrous bone), genetically female, adult.

The skeletal parts were fragmentary. This woman's age was assessed between 25 and 35 years.

- I4539/Chamber C; individual 1 (petrous bone), genetically male, adult.

Post-medieval period. Forty-seven individuals were identified on the floor of Room C according to the lower jaw bones. The sex and age of the two sampled individuals (I4539 and I4540) could not be estimated due to the scatter of the remains.

- I4540/Chamber C; individual 2 (petrous bone), genetically male, adult.

This sample was also recovered from the mixed human remains spread on the floor Chamber C.

Barcın (Bursa, Yenişehir; Neolithic and Late Chalcolithic)

Contact: Jacob Roodenberg, Songül Alpaslan-Roodenberg

Barcın is the last of three prehistoric multi-period sites in the eastern Marmara region investigated from the eighties until recently by the Netherlands Institute for the Near East/Leiden and its annex, the Netherlands Institute in Istanbul. The burials included in this study were uncovered in the first years of investigations at Barcın Höyük (2005, 2006), when Chalcolithic and Neolithic deposits were excavated. Samples from two individuals are included in this study:

- I11949/557; UC-M10 - 2006 (phalanx), genetically male, adult

This sample was collected from the skeleton of a middle-aged individual buried in a courtyard in the upper layer of the Neolithic deposit (6200-6000 calBCE). The deceased lay on his left side in a contracted position. Wood fragments underneath the skeleton suggest that the dead had been laid on a board (136).

- I5395 (dup.I1584)/UN L11-2006 (petrous bone), genetically female, infant.

There are two skeletal samples for which we produced data: I1584 M10-111 (published in (10)) and I5395 UN_L11(2006). The genetic data from these two individuals potentially match. This means that the samples are either from the same individual or from two different individuals who were close relatives or identical twins. Infant UN L11's age is estimated to be between 9 and 12 months and the size of the petrous from which the sample was taken is compatible with this age. The other infant M10 111 is younger (unpublished research notes). Therefore, it seems highly probable that these two bones belong to infant UN L11. Bone sample I5395/UN L11 originates from infant skeleton UN-L11, buried on the bottom of a jar dating to the Late Chalcolithic period (3800-3600 calBCE) which was damaged at a later date. Beads made of bone recovered from this jar suggest that the child had worn a necklace.

İlıpınar Höyük (Bursa, Orhangazi; Neolithic, Late Chalcolithic, Byzantine)

Contact: Jacob Roodenberg, Songül Alpaslan-Roodenberg

Nearly fifty human burials were unearthed in the earliest levels of the Neolithic settlement (6000-5800 calBCE), uncovered over an area of nearly 400m² (136). These burials were found in courtyards adjacent to houses whose contours could be recognized by rows of wall posts, and sometimes also wooden floors. High mortality among infants is characteristic: this category, aged between 7-8 fetal months and 1.5 years, constitutes nearly half of the total burial population (137).

Forty graves dating to the Late Chalcolithic period (3800-3600 calBCE) were uncovered in the central sector. In part disturbed by the construction of the Byzantine cemetery and recent agricultural activities, these graves were simple, oval pits dug in the ground where the deceased were deposited on their sides with flexed limbs. Quite often the dead were accompanied by decorated pottery and copper tools, such as knives, axes, and once a dagger. Apart from this burial ground, İlıpınar did not provide evidence of contemporaneous habitation (138).

Investigations in the topsoil of the central sector of the mound, an area of 1100 m², yielded approximately 200 graves belonging to the end 6th-7th century of the Byzantine era (139). These were all single burial graves, built of large terracotta tiles, placed against each other to form a roof above the dead who were stretched on their backs, hands folded on the abdomen. When extrapolated, the number of graves spread over the entire mound may have reached a thousand, and even more if the surroundings are included. Given the rather short time span during which the cemetery was expanded -- the investigated graves suggest a time span of a few generations -- it may be assumed that the inhabitants of a settlement larger than a rural hamlet were buried at Ilıpınar. Personal belongings were scanty; only a few deceased were interred with personal effects such as finger and earrings.

Nine individuals are included in this study from Ilıpınar's following periods: 2 Neolithic, 4 Late Chalcolithic, 3 Byzantine.

Neolithic

- I3121/UAP W13 (petrous bone), genetically male, adult

The skeleton found in this grave belongs to an old male (>40 years old) who suffered from osteoarthritis and DISH. Lying on his left side, legs flexed and hands in front of his face, he was buried on a wooden plank that covered the bottom of the pit.

- I1510/1229; UAO-W13 (bone), genetically female, adult

This robust female skeleton belonged to the best-preserved skeletons of Neolithic Ilıpınar. Her age at death was estimated between 62 and 70 (Alpaslan-Roodenberg, 2008).

Age determination of the burials below is made by Ayla Sevim-Erol, Çilem Sönmez-Sözer

Late Chalcolithic

- I10542/UR U13 (petrous bone), genetically male, adult older than 40 years.
- I10543/UN V13 (petrous bone), genetically female, adult, middle-old aged.
- I10545/UD W12 (petrous bone), genetically male, adult, 35-45 years old.
- I10547/UD X12 (petrous bone), genetically female, adult, 25-35 years old.

Byzantine

- I10429/UC W13 (petrous bone), genetically female, adult, 25-40 years old.
- I10546/UD S13 (petrous bone), genetically male, juvenile, 3-5 years old.
- I10430/UK X12 (petrous bone), genetically male, juvenile, 12-14 years old.

Kuriki Höyük (Batman, Late Chalcolithic, Iron Age)

Contact: Elif Genç, Ayşen Açikkol-Yıldırım

Kuriki Höyük, one of the Upper Tigris Valley settlements, is located 14 km south of Batman city, 1 km southwest of Oymataş village, at the confluence of the Batman Çayı and the Tigris. The settlement is located on the east bank of the Batman River near the western edge of

the Raman Mountains. Kuriki Höyük consists of two small hills approximately 70 m apart (Kuriki Höyük 1 and 2). Together they cover an area of approximately 250x100 m. Excavations were carried out between 2009 and 2015 with the goal of documenting and rescuing cultural assets within the framework of the Ilisu Dam and Hydroelectric Power Plant Project (HEP). Occupation remains from the Late Chalcolithic-EBA I, Late Bronze Age, Iron Age, and Hellenistic-Parthian-Roman periods were uncovered at Kuriki Höyük. This study includes graves from the 4th and 1st millennium. Ten individuals are analyzed (2 from the Late Chalcolithic Period, 8 from the Iron Age).

Late Chalcolithic

- I14730/Locus 470; KH15AD (petrous bone), genetically female, infant.

An infant in a Late Chalcolithic jar grave was uncovered in layer IVb on the eastern slope of the K/23 plan square in Kuriki Höyük 1 (KH1). The mouth of the pot was closed with a large vessel sherd. The jar contained no grave goods.

- I14627/Locus 121A; KH12A (petrous bone), genetically female, adolescent.

A storeroom uncovered in layer IVb3 yielded this Late Chalcolithic burial. It belonged to an adolescent of ca. 12 years (\pm 36 months). The dead was lying in a flexed position on a thin layer of carbonized lentil and grain residues in the room. No grave goods were present. Radiocarbon date: 3645-3525 calBCE.

Iron Age

- I14635/Locus 40; KH12E (petrous bone), genetically female, adult.

A stone cist grave was found in the east part of the Necropolis area (N / 15 plan square) dated to the first millennium BCE. The deceased was laid in a flexed position in the east-west direction, head facing east. The cover stone of the grave was not preserved. The skeleton belonged to a young woman aged between 18 and 25 years. Grave goods were absent.

- I14734/Locus 226; KH13A (petrous bone), genetically male, juvenile.

This Iron Age grave was found in Kuriki Höyük 1 (KH1), L / 23 plan square, on the eastern slope of the mound. The child was buried in a flexed position in a simple earthen grave on the edge of the round pit. The dead was laid in west-east direction with the head facing south. The grave had destroyed Late Chalcolithic Age walls (of the IVb1 and IVb2 levels). No grave goods were found.

- I14733/Locus 79; KH12E (petrous bone), genetically male, adult.

This simple earth grave was found in the Necropolis Area (M / 16 plan square) dated to the first millennium BCE. The skeleton belongs to a middle-aged male between 35 and 45 years old. The dead was deposited in half-flexed position with his head to the east, his face to the north, and his hands folded in front of him. A bronze ring was recovered from the grave.

- I14731/Locus 181; KH15 ED (petrous bone), genetically female, adult.

This Iron Age stone cist grave was discovered in the east part of the Necropolis area (N / 18 plan square). The cover stone was preserved. Three adult individuals were buried in the grave.

Two lay on top of each other in a flexed position, while the bones from the third were found in one of the corners. The grave's orientation was northwest-southeast. No grave goods.

- I14644/Locus 104; KH14EB (petrous bone), genetically female, adult.

This Iron Age pit grave was unearthed in the west part of the Necropolis area (N / 14 plan square). The dead was laid in a north-south direction with her head to the south facing east. Although the grave was not well preserved, the flexed position of the dead was apparent. She was buried with two bronze bracelets, while a bronze fibula and a red split stone bead were on her left wrist.

- I14636/Locus 52; KH12E (petrous bone), genetically male, adult.

This stone cist grave, found in the same area, also dates to the first millennium BCE. The cover stone of the grave was not preserved. Deposited in flexed position, the deceased was oriented northeast-southwest. The badly preserved skeleton belonged to a middle-aged man. An agate bead was collected from the grave.

- I14735/Locus 18A; KH11E (petrous bone), genetically female, juvenile.

The above stone cist grave was found in the eastern part of the Necropolis area (N / 16 plan square) and dates to the first millennium BCE. Two skeletons were unearthed in the grave. The age of the child skeleton lying in flexed position in the grave was assessed at 3 years (\pm 12 months). The bones of the other individual were disturbed. Associated finds are an iron perforator and ring, two bronze earrings, and glass and faience beads.

- I16570/ Locus 160; KH13AG (molar tooth), genetically female, adult

This stone cist grave was found in the southern slope of Kuriki Höyük 1 which is dated to the first millenium BCE. The dead was placed in a flexed position in east-west direction. The cover stone of the cist was not preserved. Her head was oriented to the east facing to the north. No grave goods were found inside the grave.

Oylum Höyük (Kilis; Late Chalcolithic, Early and Middle Bronze Age)

Contact: Atilla Engin

Oylum Höyük, 7 km. east of the municipality of Kilis is situated near the town of the same name. Oylum lies in a zone where the Euphrates river valley reaches the North-Syrian lowlands. The mound measures 460 x 320 meters at the base, is 22 meters high in the north and 37 meters in the south and therefore one of the biggest mounds of Southeastern Anatolia.

The skeletons of Oylum Höyük dealt with in this article originate from two different areas, namely from the necropolis on the north slope of the mound including graves dating to the Early Bronze Age III-IV (2500-2000 BCE) and to the Middle Bronze Age I (2000-1800 BCE), and from intramural burials dating to the Middle Bronze Age II (1800-1600 BCE).

EBA graves generally have richer grave goods than MBA graves. The graves dated to EBA III-IV reveal five different types, simple soil graves, terracotta, cube, stone chest and chamber graves, while MBA I types are simple soil and chamber graves in which the dead were deposited in a flexed position. The chamber tombs contain multiple burials. Some terracotta graves, simple earthenware and cube graves are found deposited in the same pit. It is suggested that hut like constructions discovered among the EBA graves were used for food presentation in mortuary ceremonies.

In the Middle Bronze Age II of Oylum Höyük (1800-1600 BCE), the dead were buried under house floors, walls or in spaces between the houses. The first graves of that period were dug in the northwest area where the remains of the Middle Bronze I palace had been. Tombs from Middle Bronze II, consisting of simple earthenware, pottery, cube, chamber and pit graves, were generally poor in terms of grave goods. Some were multiple burial graves where the remains of the first deceased were shifted aside when a new corpse was added. Multiple burial graves usually include two skeletons; exceptionally four individuals were identified in a simple soil grave. Regardless of their age and sex the dead were generally laid in flexed position. Bones were rather poorly preserved.

One Late Chalcolithic (Uruk period) individual, 16 individuals dated to the Bronze Age, and 4 Byzantine period samples are included in this study. In 2000, a Byzantine cemetery was excavated in grids X42 and Y42 on the southern slope of the mound.

Late Chalcolithic (Uruk period; 3500-3000 BCE)

In 1991, the EBA1 - Late Chalcolithic Transition Phase and the Late Chalcolithic Uruk layer were excavated in trench AA11a (measuring 5 x 10 m). In this trench, Late Chalcolithic (Late Uruk Period) graves were uncovered under house floors.

- I14793/AA11a oby7 (petrous bone), genetically female, adult. Her age was estimated between 25 and 35 years.

Early Bronze Age

- I14792/N165 E75-OBY25 (petrous bone), genetically female. The age of this juvenile was assessed around 8 years old.
- I14794/Z10-OBY31-11 (petrous bone), genetically female, adult. This young female was lying in a simple earth grave. Her age was estimated between 17 and 25 years.
- I14797/Y10-OBY 102 SK:1 (petrous bone), genetically male, adult. The skeleton was found in a jar. Age estimation between 25 and 35 years.
- I14798/Y11bZ11a-OBY283sk:1 (petrous bone), genetically male, fetus. The bones of this 7.5 months old fetus were uncovered in a chamber grave.
- I16580/Y11b-Z11a-OBY 283 sk:2 (molar tooth), genetically female, adult.
- I16577/N170 E75/OBY1 (metacarpal), genetically male, adult. This simple pit burial was unearthed in 1991 during the excavations carried out in Grid N170 E75 on the northwest slopes of the mound.

Middle Bronze Age

- I14786/J22-OBY123 (petrous bone), genetically female, adult. Sister of I14785. The skeleton of a woman between 18 and 22 years old lay in a half-flexed position in this simple earthen grave.
- I14759/ K21-OBY128-Sk2 (petrous bone), genetically female, adult. In this simple earthen grave, remains of 3 individuals were found: two adults (a young female and a middle-aged male) and a ca. 6 months old infant. Bones of the young adult female

were disturbed probably to make room for a new burial. The other two were lying in a half-flexed position (Fig. S 8).

- I14784/K21-OBY128-Sk3 (petrous bone), genetically male, adult. Brother of I14789/K21-OBY155 and son of I14782/K21-10.

The remains of this man aged between 32 and 26 years was discovered in a half-flexed position lying together with the above-mentioned young woman (K21-OBY128-Sk2) and an infant.

- I14761/Y9-OBY20 (petrous bone), genetically female, adult.

This skeleton was found lying in a half-flexed position in an earth grave. Anthropological analysis has not been conducted yet.

- I14762/J22-OBY100 (petrous bone), genetically male, adult.

In this earth grave next to this adult male aged between 35 and 50 years, who was lying in a half-flexed position, remains of a 6 years old juvenile and a ca. 9 months old infant were uncovered.

- I14782/K21-10 (petrous bone), genetically male, adult. Father of I14789/K21-10 and I14784/ K21-OBY128-Sk3.
- I14785/J22-OBY121 (petrous bone), genetically male, adult. Brother of I14786.

This individual aged between 18 and 24 years was lying dorsally in this grave.

- I14788/K21-OBY167 (petrous bone), genetically male, adult.

Remains of two individuals were retrieved from this grave. Next to the adult male skeleton aged 17-25 years, there was a child of ca. 11 years old.

- I14789/K21-OBY155 (petrous bone), genetically female. Sister of I14784/K21-OBY128-Sk3. Daughter of I14782/K21-10.
- I16574/OY99-Y10/107 (metatarsal), genetically undetermined sex, adult.

This pit burial was unearthed in 1999 during the excavations carried out in Grid Y10 on the northwest slopes of the mound. The corpse had been buried in a position with the head to the northwest, body in the northwest-southeast direction. The upper body of the skeleton was on the back, legs on the right side. No grave finds were identified.



Fig. S 8 Middle Bronze Age II, simple inhumation in pit burial, Oylum Höyük, K21, 128.

Byzantine

- I14787/X42a-c-25 (petrous bone), genetically male, adult.
- I14790/X42a-c-3 (petrous bone), genetically female, adult. Mother or daughter of I14791/X42a-c-14.
- I14791/X42a-c-14 (petrous bone), genetically female, adult. Mother or daughter of I14790/X42a-c-3.
- I14760/X42ac-Y42ba (45-26) (petrous bone), genetically female, adult

References: (140-144)

Tilbaşar (Gaziantep; Bronze Age, Byzantine)
Contact: Elif Genç

Tilbaşar (Tilbeshar), 18 km north of the Turkish-Syrian border, Gaziantep, Oğuzeli district, is located near Gündoğan. The settlement is dominated by the Oğuzeli Plain which is irrigated by the Sacır Suyu, one of the western branches of the Euphrates. With its two lower cities, Tilbaşar Höyük covers an area of 55.7 hectares. It was inhabited during the Late Chalcolithic, Early Bronze Age, Middle Bronze Age, Late Iron Age and the Middle Ages. After the studies of 1994-2006, excavations were resumed in 2015 within the scope of the efforts to protect the cultural assets endangered by the construction of the Doğanpınar Dam in the Sacır Suyu. This study includes graves from the Middle Ages (7 individuals) and the Early Bronze Age (1 individual) unearthed during four years (2015-2018) of rescue excavations in the eastern part of the South Lower City. Eight individuals are analyzed from this site. Seven of those listed below were excavated in the medieval necropolis which is located in the southeast sector of the lower town. In all cases the dead were laid on the back in a simple pit grave.

Early Bronze Age

- I14649/Locus 22; TH15 BR1030 (petrous bone), genetically male, probably adult.

This Early Bronze Age horizon yielded skull fragments in the southeast sector of the Lower Town, inside a settlement building of-level 4. Skull fragments were found among the debris caused by a fire. The bones were exposed to high temperatures as a result of which the skull darkened and crushed. Above the skull parts, remains of two other skeletons were uncovered (Locus 16 and Locus 9). This spot has been radiocarbon dated 2308-2129 BCE.

Middle Ages

- I14652, Locus 15; TH15 BF1020 (petrous bone); genetically male, adult.

The grave was unearthed at a depth of 70 cm below the surface. The dead was deposited east-west with the head facing west. An iron nail was found on the right leg.

- I14645, Locus 50; TH15 BF1020 (petrous bone); genetically male, adult.

The grave was unearthed at a depth of 70 cm below the surface, the body oriented east-west, the head facing west. His hands lay on his abdomen. His right arm was under the neighboring skeleton L.52. No grave goods were associated with this grave. His height was calculated about 1.70 cm.

- I14651/Locus 65; TH15 BF1020 (petrous bone); genetically male, adult. Father or son of I14650/L28.

This grave was found at a depth of 80 cm below the surface, the body oriented southwest-northeast, the head facing southwest. Skeletal parts were not preserved below the waist. His hands lay on his abdomen. No grave goods were found.

- I14650/Locus 28; TH15 BF1020 (petrous bone), genetically male, adult. Father or son of I14651/L.65.

The grave was excavated at a depth of 75 cm below the surface, the body being in the same orientation as L. 65. The leg bones stuck under the neighboring grave L. 29. His height was 1.48 cm. No grave goods.

- I14647/Locus 2; TH15 BF1020 (petrous bone), genetically male, adult.

This grave was discovered at a depth of 25 cm below the surface; the individual was deposited east-west with the head facing west. Hands lay on the abdomen. It was located on the eastern edge of the square where irregular stones were accumulated. His height was calculated 1.66 cm. Grave goods were absent.

- I14648/Locus 11; TH15 BJ990 (petrous bone), genetically female, adult.

The grave was found at a depth of 30 cm below the surface. and the body was buried in an east-west direction with the head facing west. Her height was calculated at 1.55 cm. The upper part of the skull and her feet were not preserved. Her hands lay on her abdomen. There was an absence of grave goods.

- I16571/Locus 57; TH15 BF1020 (molar tooth), genetically female, adult.

This grave was uncovered in a simple pit at a depth of 80-95 cm below the surface. The dead was buried in dorsal position in east-west direction. The stature was estimated 1.75 cm. There were no grave goods. Above this grave another skeleton was found (Grave L58).

Devret Höyük (Amasya, Suluova; Late Chalcolithic and Early Bronze Age)

Contact: Atila Türker, Celal Özdemir, Ayşegül Şarbak, Alper Atmaca

Devret Höyük is located on the northern slope of Çakırdağı Mountain (Amasya Province) overlooking the town of Suluova. There are many illicitly dug pits opened by treasure hunters on the mound and therefore a rescue excavation was conducted in 2013. Excavations yielded five-layers (I-V) in the Chalcolithic and Early Bronze Age settlements. Seventeen graves were uncovered in the layers II-V (145) and it was established that, disturbed graves included, in total 21 individuals were buried under the building floors. These were all simple earth graves, some of them containing burial gifts(146). Seven individuals are included in this study:

- I5740/Grave MB.6 (petrous bone), genetically female, adult.

Age and sex could not be determined since the skeleton, found in Layers III-IV (inside the wall of Layer V) was badly preserved. Its burial position was half flexed. Grave goods were absent (Türker et al., 2018: 122).

- I7079/Grave MB.3 (carpal bone), genetically male, adult.

This individual was buried in a flexed position in layers III-IV (inside layer V). The lower half of the body was disturbed. A copper needle and a small necked pot accompanied the dead (Türker et al., 2018: 120).

- I7073/Grave MC.1 (long bone), genetically male, adolescent.

The skeleton was unearthed in layer II (inside layer IIb). His burial position was uncertain. The lower half of the skeleton was absent. There were no grave goods (146): 112.

- I5741/Grave MC.4 (petrous bone), genetically female, juvenile.

This skeleton was of an approximately 11 years old child from layer IV (inside layer V). He was laid on his back in a flexed position. There were no grave goods (146): 115.

- I5742/Grave MD.1 (petrous bone), genetically female, adult.

This was an adult female found in layer III (inside the layer IV). She was buried on her right side in a flexed position. There were no grave goods (146): 117.

- I5743/Grave MD.4 (petrous bone), genetically female, adult.

This grave contained two female skeletons buried in a back-to-back flexed position in a simple pit in layer I (inside layer III; (146): 117). The face of skeleton MD4 was turned south. There was a small necked pot as a burial gift.

- I5744/Grave MD.5 (petrous bone), genetically female, adult.

This skeleton was found in the same grave as skeleton MD.4 mentioned above. She was buried in a half-flexed position facing north. A small cup was buried with her.

Yassitepe Höyük (İzmir, Bornova; Early and Middle Bronze Age)

Contact: Zafer Derin

Osteological study is done by Alpaslan-Roodenberg

Yassitepe Höyük is situated in the coastal zone of the Aegean, in the middle of the the Bornova Plain which is closed to the east by the Belkahve Passage. It is an Early Bronze Age mound located in a residential area of İzmir and is excavated together with the site of Yeşilova (147): 177; (148):1. Since the surrounding plain was filled with alluvial deposits the burial mound is low and flat with a height of ca. 6.30 m. Located north of Manda river, the mound is 19 m above the sea level, approximately 200 meters measured along the north-south axis and 150 m along the east-west axis (149): 1-15;(150): 224.

Excavations at Yassitepe began in 2010 in area VI. Cultural layers started at just ten centimeters below the surface in the center of the mound. Hence, remains near the surface were partially destroyed due to agricultural activities and road construction. Fourteen layers containing four different cultural levels could be identified. The largest settlement, dated to the Early Bronze Age, was uncovered in an area where 14 dwellings could be identified. These dwellings belong to levels IIB 1 and IIB 2 (most of the dwellings are from the latter). Although roughly similar, in level IIB2, the dwellings were built as multi-room structures, while the ones in level IIB 1 were single-room dwellings(151). The EBA settlement of Yassitepe represents the traditional architectural style of Western Anatolia in terms of architectural order. It is known that the settlement form, which consists of a radial planned space arrangement and seems to open to a central courtyard, became widespread in Western Anatolia. Settlements with this type of architecture are also seen in residential areas such as Liman Tepe, Troya, Bakla Tepe, Beşik-Yassitepe and Demircihöyük during the EBA I period. This change in the interior architecture perhaps shows a difference in economic strength between the communities of the consecutive levels IIB 1 and IIB 2. The architectural plan of the IIB 2 level reveals that the settlement was made according to the “Anatolian Settlement Plan”. This consists of radially placed buildings, the outward facing walls of which were incorporated into the defensive wall surrounding the settlement (152): 223. Radiocarbon dates obtained from the Early Bronze Age levels of Yassitepe Höyük indicate a period between 3020-2900 BCE and 2880-2830 BCE. Level IIA of the Yassitepe mound is defined as Middle Bronze Age. This period was mainly recognized by remains of mudbrick architecture close to the surface. A small number of graves belonging to the Early Bronze levels represented by the III B culture level were brought to light. All these graves were unearthed in trench H19 to the north of the mound. Three individuals are included in the study, two Early Bronze age burials, and one Middle Bronze age burial:

- I5733/YE-YA’16-1 (petrous bone), genetically female, adult.

This Early Bronze Age grave contained a flexed burial oriented northwest-southeast.

The skeleton belonged to a middle-aged woman between 25 and 35 years old (153). The bones poorly preserved and fragmentary.

- I5735/YE-YA'16-2 (petrous bone), genetically female, adult.

This badly preserved Early Bronze Age burial was unearthed in the same area where grave YE-YA'16'1 was found. The skeleton in this grave was also in a flexed position, but buried south-north, hence in the opposite direction to the first grave (YE-YA'16-1). The dead of both burials (1 and 2) face west. No grave goods were found. The skeleton belonged to a middle- to old-aged woman. All bones were fragmentary. Osteoarthritic changes were noticed in her bones. Her dental condition was rather bad: 3 carious molar teeth among the inspected ones and a moderate level of tartar on the teeth from both jaws. Her upper front teeth presented linear enamel hypoplasia, which is a condition mostly associated with malnutrition and/or infections in the childhood. Considering her age her teeth, especially the incisors and canines were heavily worn.

- I5737/YE-YA'15-1 (petrous bone), genetically male, adult.

The Middle Bronze Age grave (YE-YA'15-1) was found in the southeast sector of the mound. This badly disturbed simple pit grave was unearthed among the MBA constructions. Although the position of the bones could not be determined exactly, the grave is thought to be oriented northwest-southeast. The badly preserved fragmentary bones belonged to a middle- to old-aged man. The skull and mandible fragments were covered with a thick layer of calcareous deposit which made examination difficult. His front teeth were heavily worn.

Halicarnassus, Eastern Necropolis (Bodrum, Early Bronze Age; Hellenistic)

Contact: Seda Deniz Kesici, Tayfun Selçuk, Emre Savaş, Sinem Köstak Boca Negra Valdes

Çukurbük, Gümüşlük necropolis

The Çukurbük Necropolis is located in the west of the Bodrum Peninsula, in the north of the Gümüşlük district, just across the Büyük Kiremit island. During the control excavations carried out by the Directorate of the Bodrum Underwater Archeology Museum in this region, pithos tombs dating to the Early Bronze Age were unearthed. Pithos tombs were generally placed on a slope overlooking the sea, in reservoirs formed into an easily shaped bedrock structure. There is no unity of direction in the necropolis area. The lids of the pithos tombs are supported with stones and covered. One individual (Early Bronze Age) is included in the study:

- I3294/GMŞ14.28P.PM1.SK1 (petrous bone), genetically male, juvenile.

The bones were found inside the pithos tomb PM1. The pithos was in a broken state with red paste and color differences due to poor firing. It has a height of about 60 cm; It is placed in the chamber carved into the bedrock in the northeast-southwest direction. The mouth of it was covered with a thin stone cover and the cover was supported with other stones. Inside the pithos, the skeletal remains of an individual were found in the earth fill, but the preservation of these remains was very poor and consists of fragments of the cranium and a few isolated teeth. The child was probably placed in a flexed position. No gift for the dead was found inside the pithos.

Yokuşbaşı necropolis

The necropolis unearthed during investigations in the center of the Bodrum peninsula (the area known as Yokuşbaşı, today outside the eastern walls of ancient Halicarnassus) is located under the current town. British archaeologist C.T. Newton excavated in Bodrum-Halicarnassus

in the 1850s and mentioned two main necropolis areas. In his book on these excavations, he defined the area as ‘Halicarnassus Eastern Necropolis’ but did not provide detailed information about the outline of the necropolis. Newton's studies suggest that the area was used extensively as a necropolis and called Kislelik. However, no comprehensive excavations have been conducted, except for a few salvage soundings excavations carried out by the Bodrum Museum. From the finds uncovered in 2015, it is understood that the necropolis was used extensively from the 4th to the first century BCE. In the tombs dating to the 4th century, Kerch-style late red-figure pelikes, kylixes, and a golden ring with a quartz seal were found. The other graves yielded mainly Hellenistic finds. Seven individuals (Hellenistic period) are included in the study:

- I3225/YKB15.51P.M1.SK1 (molar tooth), genetically male, adult.

This tomb was a 220cm long, 82cm wide, 78cm deep sarcophagus with a triangular lid, oriented southeast-northwest. In addition to pottery fragments, among which are a handle, rim and body of a pelike, the grave also contained a quartz stone golden seal ring with the effigy of a “washing Aphrodite”. Since the sarcophagus was destroyed before the investigations (probably by illicit digs), the skeleton’s position could not be determined. The age of the individual was determined as middle to old.

- I3308/YKB15.M8.SK1 (petrous bone), genetically female, adult.

This was a 205cm long, 90cm wide, 80cm deep stone cist built with stones, oriented northeast-southwest. Except for fragments of the cover stones, the upper part of the cist was not preserved. Skeletal fragments were found at two different levels in the grave. The individual found at the upper level was in a supine position and the head-foot direction was south / southwest-northeast. The position of the skeleton at the lower level was probably disturbed due to the burial above; skull fragments were collected from the grave’s southwest wall. The sample, collected from the individual found at the bottom, belongs to a young female according to the cranial features.

- I3309/YKB15.86P.M16.SK1 (petrous bone), genetically male, adult.

The interior of this northeast-southwest oriented stone cist grave measured 200 x 70 cm. The upper part was missing. The inner walls were built with stones and the bottom was covered with soil where the skeleton of a middle-aged male lay in a dorsal position.

- I3303/YKB15.86P.M14.SK1 (petrous bone), genetically male, adult.

The lid of this stone cist was destroyed. The grave was oriented northeast-southwest. Its inner part, 218 cm long and 88 cm wide, revealed the remains of two individuals. The position of one individual was unclear as the limb bones were recovered at the bottom of the tomb, suggesting that they were swept aside to make room for the other individual. The other individual lay in supine position, oriented southwest-northeast, with hands stretched on both sides.

- I3311/YKB15.86P.M7.SK1 (petrous bone), genetically male, adult.

This was a simple pit burial, 170cm long and 50cm wide. The boundaries of the tomb were delineated by a single series of stones. The skeleton of a middle-aged man was lying dorsally in the south-north direction with both arms stretched along body.

- I3310/YKB15.86P.M15.SK1 (petrous bone), genetically female, adult.

This stone cist grave, 280cm long and 135cm wide, was laid out in a northwest-southeast direction. The human remains were fragmentary. Four unguentaria (small ceramic bottles) were found as gifts to the dead.

- I3300/YKB15.51P.M15.SK1 (molar tooth), genetically male, adult.

This grave includes a cut stone sarcophagus in the northeast-southwest direction, 240cm long, 80cm wide and 90cm high. Pieces of a terracotta sarcophagus (grave M2) were found above this grave structure. The structure of M15 was formed from easily shaped stone blocks and its inner chamber is thought to be covered with lime and sandy plaster, because almost all of these plasters constitute the debris inside the grave. No grave goods were found except for cranial fragments belonging to an individual from the burial fill.

Stratonikeia graves (Muğla, Yatağan; Byzantine)

Contact: Bilal Söğüt, Ahmet İhsan AYTEK, Alper Yener YAVUZ, Esra Hilal KAYA

Stratonikeia, one of the ancient cities of inland Karia in Asia Minor (neighbour of Eskişehir, Yatağan district, Muğla Province). The Yatağan-Milas highway passes close to the northern edge of the ancient city. Since 2008, on behalf of the Ministry of Culture and Tourism and Pamukkale University, archaeological excavations, conservation and restoration work in Stratonikeia have been carried out by a team under the direction of Bilal Söğüt.

The oldest finds uncovered in Stratonikeia belong to the Early Bronze Age. The vast majority of standing remains, however, are dated to the Archaic and later periods. The city wall, gates, agoras, gymnasium, theater, temple, bouleuterion, baths, latrinas, colonnaded streets and a necropolis found in the settlement dated to the Archaic, Classical, Hellenistic and Roman periods. Beside these, the site includes churches, houses, colonnaded streets, arch and necropolis dating back to the Byzantine Period, as well as village squares, stone paved roads, Turkish baths, mosques, mansions, houses, a paint workshop, a bread oven, shops of various crafts, and cemeteries from the periods of the Anatolian Principalities (Beylikler Dönemi) the Ottomans and the Republic.

Here, the remains from ancient times to the present can be seen side by side. For this reason, Stratonikeia has been taken under protection as a living historical city.

Eleven individuals (twelve samples) are included in this study:

Byzantine period

- I20140/Burial 1 (petrous bone), genetically male, adolescent. Brother of I20141.
- I20141/Burial 2 (petrous bone), genetically male, adolescent. Brother of I20140.

The ages of the 2 individuals above were estimated at 16-18 and 15-17 years, respectively.

- I19539/15BCM05 (tooth), genetically female, adult.

From the long bones, the minimum number of individuals buried in the grave was inferred to be 7. Sex determination of three of the individuals are: 2 males and 1 female. The age of the female is determined to be between 32 and 43 years.

- I20187/14BCM12 (petrous bone), genetically male, adult.

A skeleton was found in an east-west oriented cist tomb (grave built with aligned stone slabs) east of the Gymanasion Propylon, buried in dorsal position with both arms joined on the abdomen. It belongs to a male aged between 34 and 47 years.

- I20574/15BCM16 (petrous bone), genetically female, adult.

The remains of two skeletons were found scattered in a cist tomb oriented east-west, positioned adjacent to the north wall of the south nave of the church. The age at death of the sampled individual was estimated between 20 and 30 years.

- I20144/15BCM21 (petrous bone), genetically male, adult.

In the north nave of the church, skeletal remains of two individuals were found in a cist type grave built in the east-west direction. The age of the skeletons was estimated between 45-50 and 13-15 years.

- I20142/15BCM23a, skull 1 (petrous bone), genetically female, adult.
- I20143/15BCM23b, skull 2 (petrous bone), genetically male, adult.

Number 15BCM23 is an east-west oriented cist grave, adjacent to the north wall of the south nave of the church. In the grave, scattered bones were found from which it was concluded that in total 6 individuals had been buried in the grave. Sample 15BCM23-a is from a female of 35-43 years old, while sample 15BCM23-b is from a male whose age could not be estimated.

- I20146 (dup. I20148/16BCM04-individual 3) /16BCM04-individual 1 (petrous bone). Genetically male, juvenile.
- I20147/16BCM04-individual 2 (petrous bone), genetically male, infant.

The cist grave (16BCM04) was built in east-west direction within the apse of the south nave of the church. The minimum number of individuals identified in this grave is 5. One of the skeletons was in dorsal position, the others were in flexed position. Age determinations are 0-6 months for a baby, 2-3 years for 3 juveniles, and 8-10 years old for another juvenile.

- I20145/16BCM09 (petrous bone), genetically female, young adult.

Two individuals were found in this grave (16BCM09): a child of 8-10 years old and a young adult between 18-21 years.

Reference: (154)

Pre-Urartian and Urartian

Contact: Rafet Çavuşoğlu, Hakan Yılmaz, Hanifi Biber, Sinan Kılıç, Timur Gültekin

Muradiye grave (Van, Muradiye, Babacan; Early Iron age)

The grave, disturbed by illicit digging, was rescued in 2014 by a team of the Van Museum (155). Pottery sherds, iron and bronze objects found in the grave were dated to the Early Iron Age.

- I14767/ Muradiye 1 (VMBk-1 2014; petrous bone), genetically female, adult.

This skull, which was left in the grave after illicit digging, belongs to an individual between 20-30 years old. The rest of the skeleton was missing.

Çavuştepe necropole (Van, Gürpınar; Iron Age)

According to an inscription in the Assyrian language, the Kingdom of Urartu was founded by Sarduri I (840-830 BCE) in the middle of the 9th century (156) and survived until the end of the 7th century. The capital of the Kingdom was Tushpa, located on the eastern shores of Lake Van; it was the power center of the state which was divided into regions, each ruled by a governor. After an expansion around 700 BCE to the north, the kingdom was destroyed about a century later (157, 158).



Fig. S 9 Çavuştepe Castle view from the northwest.

Çavuştepe Castle (the city of Sardurhinili), located near Gürpınar 20 km east of Lake Van, was an important royal center of the mid 8th century overlooking the highway extending from Tushpa to Lake Urmia (Fig. S 9). This castle was founded by Sarduri II, king of Urartu (765-734 calBCE) according to a cuneiform inscription of the Irmuşini Temple in the Lower Castle. It was initially excavated from 1961 until 1986 by a team led by Afif Erzen. A second series of

excavations in the castle started in 2014 under the responsibility of Rafet Çavuşoğlu and still continues.

Consisting of an “Upper Castle” and “Lower Castle”, it was erected on an east-west running mountain ridge and was protected by a system of trenches carved in the rock. The necropolis related to Çavuştepe Castle is located 1 km to the north where excavations have been carried out since 2017 (Fig. S 9). During these excavations important information about the society of Urartu and its burial customs was obtained. Several grave types could be identified such as stone chamber tombs, urn graves, cist graves and simple earth graves. Also a new grave type emerged in the necropolis, in which the dead were laid down in a flexed or semi-flexed position next to a single row of upright sandstone plates. We call this type “grave with aligned stone slabs” (Levha Taş Sıralı Mezar). Radiocarbon dating of the necropolis points to the second half of the 8th century for its use. As can be concluded from the rich finds of the Çavuştepe graves, where in addition to jewels of gold, silver, bronze, and semi-precious stones, a seal was retrieved, the dead belonged to the ruling class (159, 160); Fig. S 10.

- I19612/Grave 6; VÇN18-M6 (metacarpal), genetically male, adult.

The individual is placed in a simple grave pit dug into the ground. No archaeological finds were found in the pit. However, a broken Urartian pottery piece was retrieved from under the bones of the left foot of the skeleton. The individual was lying in full flexed position. His age was estimated older than 25 years.

- I14764/ Grave 7; VÇN18-M7 (petrous bone), genetically female, adult.

The individual was inhumated in flexed position in a simple earth grave. The woman was wearing a bronze ring on her left ring finger (fourth digit of her hand). Her age is estimated older than 25 years. Except for the foot bones the skeleton was intact.

- I14765/Grave 9; VÇN18-M9 (petrous bone), genetically male, juvenile.

This child was buried in flexed position in a simple earth grave, next to a sandstone plate placed along the east side of the burial pit. No archaeological objects were found. His age was estimated between 2 and 3 years.

- I19613/Grave 10; VÇN18-M10 (bone), genetically female, adult.

The burial pit is a simple earth grave aligned by sandstone slabs in the south-west direction. No archaeological objects were found in association with the dead. The bone remains belong to a woman older than 25 years. The cranium was missing, but mandible and postcranial bones were almost complete. Antemortem tooth losses were observed at the level of the right and left mandibular first molars.

- I20577/Grave 2-1; VÇN17 M2-1 (petrous bone), genetically female, adult.
- I19611/Grave 2-2; VÇN17 M2-2 (metatarsal), anthropologically male, adult

Two almost complete skeletons lying in flexed position were buried in this “grave with aligned stone slabs” (Levha Taş Sıralı Mezar). It is a simple earth grave, on the west side bordered by three sandstone slabs. One of the skeletons belong to a female (grave 2-1) who was older than 25 years, while the second skeleton (Grave 2-2) lying on top of the first deceased belongs to a male older than 35 years. The male’s teeth from both upper and lower chin were

severely worn. He had a healed fracture in his left eighth costa. Moreover, he suffered from severe osteoarthritis in his arm bone. There were rich grave goods. A total of 40 gold, silver and bronze earrings were found around the ear of the female skeleton (Fig. S 10). Two hair spirals, a silver neck collar with dragon head, a golden needle, a bronze amulet, and a decorated belt were retrieved from the female's grave. A belt covered the remains of the male. An agate seal was found between the two skeletons. These costly grave goods indicate that the deceased couple belonged to the Urartian elite.



Fig. S 10 Agate seal and golden jewelry from 'grave with aligned stone slabs' at Çavuştepe (VCN17 M2-2).

Samsun Museum rescue excavations (Tekkeköy-Büyükli; Cedit-Basarabya; Zafer-Azman; Hellenistic, Roman)

Contact: Uğur Akyüz, İlkay İvgin

Samples were taken from human bones recovered in burial chambers investigated during various rescue excavations in the province of Samsun carried out by Samsun Museum in 2012 and 2013. DNA was found in 7 individuals from 3 different locations and are included in this study.

Tekkeköy, Büyükli, Mahmatlı grave chamber (Hellenistic)

A grave chamber carved into coarse-grained sedimentary bedrock appeared in 2012 during road works in the locality of Mahmatlı, Büyükli quarter in the Tekkeköy district. This grave belongs to the chamber type that was most used in the ancient Amisos burial tradition. It has a

rectangular plan. The height of the chamber is 1.40 m and the ceiling is oval and shaped into a barrel vault. In addition, the floor of the tomb, which had no bench, was leveled with earth.

A total of 4 burials (1 cremation and 3 inhumations) were uncovered in front of the southwest and northeast walls of the chamber. The bones and the ashes remaining from cremation were collected in order to make room for the next burial buried at a later time and were stacked disorderly in front of the wall. Gifts belonging to the cremation burial were two terracotta unguentaria, the broken one from the Hellenistic Period, were found side by side in the northwest section.

Four complete and 2 fragmentary terracotta unguentaria, a golden diadem broken in three parts, and three corroded bronze coins and a fragmentary iron coin, possibly from a belt, were picked up from the grave. The coins could be dated to the Early Hellenistic Era between 320 – 63 BCE. One individual is included in this study.

- I5249/BU Grave 2 (bone), genetically male, adult. Burial number 2 adjacent to the cremation burial near to the southwest wall of the tomb was extended southeast-northwest with the skull at the southeast end. The dead was laid with his head facing southwest, his arms stretched along the body.

Cedit-Basarabya grave chamber (Hellenistic and Roman)

In 2013 this grave was uncovered in the Cedit district of İlkadım - Samsun. The rectangular single-room burial chamber carved in sedimentary rock measured 5.20 m. by 4.50 m. Inside, a door opening closed by stone blocks provided access to the burial chamber and 7 niches. The niches were of different shapes suggesting that they were made in different periods (Hellenistic - Roman and Late Roman). The grave chamber, which had an unusual architectural plan, yielded mainly terracotta artifacts (unguentarium, jug, oil lamp, rython fragment), a glass artifact (unguentarium) and metal artifacts (coins and sconces). Five individuals are included in this study:

- I4472/CE-Chamber 1: Individual 1 (petrous bone) Hellenistic; genetically female, adult.
- I4473/CE-Chamber 1: Individual 2 (petrous bone). Hellenistic; genetically female, adult.
- I4529/CE-Chamber 1: Individual 3 (petrous bone). Roman; genetically male, adult.
- I4530/CE-Chamber 1: Individual 4 (petrous bone) Roman; genetically male, adult.
- I4531/CE-Chamber 1: Individual 5 (petrous bone). Roman; genetically male, adult.

Zafer-Azman grave chamber (Hellenistic)

This burial chamber, carved in the sedimentary bedrock, was uncovered in 2013 during road works in the Azman district of Zafer village. Among the burial gifts there was a silver ring on the left hand of the dead and badly preserved bronze earrings. On the floor, torpedo-shaped sarcophagi and scattered bones from former burials were noticed. The burial chamber and the finds were dated to the Hellenistic Period. One individual is included in this study.

- I5228/ AZ Grave 2 (phalanx), genetically male, adult.

Gordion (Archaic and Late Hellenistic)

Contact: Janet Monge

The archaeological site of Gordion is located near the modern village of Yassihöyük approximately 100km southwest of the capital of Ankara in central Turkey. The site has been, more or less, continuously excavated by teams from the Penn Museum (University of Pennsylvania) in collaboration with the Museum of Anatolian Civilizations and with the Ministry of Culture and Tourism beginning in 1950. Gordion shows continuous occupation from the Bronze Age to modern times, over 4,000 years.

During the Hellenistic period, from which these samples derive, Gordion transformed into a large multicultural town including the spread of Celts or Galatians from western Europe. The human remains derive from the burial areas A and B of the Lower Town adjacent to the Citadel Mound at Gordion and were excavated between 1993 and 1995. The human skeletal remains recovered from the Later Hellenistic period show extensive evidence of Celtic sacrificial burial ritual including commingled human remains with animal bones, some with butchery marks, and pit burials along with evidence of extensive antemortem and perimortem trauma. All other human remains derive from traditional inhumations in a cemetery context. 6 individuals are included in this study (Archaic and Later Hellenistic).

- I4029/YH36111; GDN13, 1993 (tooth). Genetically male, age 20-35.
- I3917/YH47398; GDN333 (phalanx) and GDN322 (tooth). Genetically female, adult.
- I3916/YH45830; GDN56, 1995 (tooth). Genetically female, age 17-22.
- I4030/YH42653; GDN134, 1994 (tooth). Genetically male, juvenile, age 4-8.
- I6573/YH37301; GDN31, 1993 (tooth). Genetically female, age 30-45.
- I6574/YH43121; GDN145, 1994 (phalanx). genetically female.

Reference: (161)

South Bithynia graves

Apollonia ad Rhyndacum (Bursa, Gölyazı; Roman)

Contact: Mustafa Şahin

Excavations of the ancient city of Apollonia ad Rhyndacum are being conducted by the archaeology Department of Uludağ University (Bursa) under the auspices of the Bursa Directorate of Museums with the permission of the Ministry of Culture and Tourism. In 2016-17, 27 graves in 5 sectors of the necropolis of Apollonia were unearthed. In sounding IV, 4 graves were discovered. After stripping the surface of rubble used for camouflage, an enclosure (peribolos) formed by a dry wall was uncovered surrounding the 4 tombs: M5a, M5b, M5c and M5d (162): 72-79. Cremation was applied in all graves except in M5a. Therefore, the remaining bones of M5a were relatively better preserved comparing the cremation contents of the neighboring graves.

Grave M9 in the plan square/sounding 12E is located to the northeast of the wall of family grave M5. The burial area, extending in the northwest-southeast direction, was built by lining large shapeless stones placed on the bedrock as a dry wall without using mortar. In this area, two

graves placed one on top of the other were revealed: M9a and M9b. M9a is included in this study.

The floor of grave M9a, which is bordered by amorphous stones, constitutes the cover stones of the tomb located at the lower level. This simple earth grave is 230cm long, 137cm wide and 84cm high. Among the grave finds, apart from one coin there are three severely damaged pottery vessels and eleven nails. The coin indicates the middle of the 1st century BCE as the date of burial in the grave. However, the irregular borders of the grave and the fact that it was covered with rubble stones suggest that the coin ended up there by accident. Taking into account the date of the tomb located at the lower level, we are inclined to date the grave to a later phase, namely the 2nd century CE. Four individuals are included in the study:

- I14845/M5a (petrous bone), genetically female, adolescent.

Grave M5a was located in sounding IV (in squares 12D and 12E) and contained two individuals: an adult and an adolescent. It is believed to be a family grave.

- I16583/M4 (femur fragment), genetically male, adult
- I16584/M1 (metatarsal), genetically male, adult
- I16585/M9a (tooth), genetically male, juvenile.

The grave is covered by a fill with very large rubble stones. After the removal of this fill, skeletal fragments belonging to an upper body were found together with damaged but still preserved burial gifts. During the excavations most of the lower part of the skull, jaw bone fragments and an almost the entire row of teeth were uncovered. One of the most interesting finds of the grave is the coin that was found under the chin. From the neck of the skeleton, the ribs and spine are curved inward. The skeletal parts of the upper body and the thin rib bones were in very poor condition due to the humid environment.

References: (162-165)

Underwater Basilica (in Lake İznik, İznik/ Nikaia; Roman/Byzantine)

Contact: Mustafa Şahin, Ahmet Bilir

This section has been prepared for publication with the support of the General Research Project entitled “Early Christian Martyriums in the Light of the Basilica Church of the Lake of İznik” supported by the Scientific Research Projects Unit of Bursa Uludağ University.

The İznik Underwater Basilica, situated in the İznik (Nikaia) district of the province of Bursa was photographed in 2014 within the scope of a project entitled Documentation of Historical Cultural Heritage and Aerial Photography of the Municipality of Bursa. In the 2015 survey conducted under the scientific consultancy of Mustafa Şahin, the building was delineated with the help of a total station (tachymeter). The structure is approximately 50 meters from the shore, 41.32m in length, 18.61m in width, and is oriented along the east-west axis (Fig. S 11). The building has three naves, a narthex and an atrium. On both sides of the apse, which has an internal circular form and a flat wall on the outside, there are a prothesis and a diaconicon called pastophoria. There is a sarcophagus in the diaconic room measuring 1.97x0.70m (166): 75-86.

In general, the building's architecture is typical of an Early Christian basilica. During the 2015 surveys a total of 36 graves were found. While 18 of these tombs were located on the outer periphery of the building, 18 were traced inside: 6 of them in the middle nave, 6 in the narthex, 5 in the atrium and one in the north nave (167): 38. During the excavation seasons that continued in 2016 and 2017, many graves were encountered: sounding 4A yielded 7 more graves in the middle nave and 3 in the diaconicon section. Except for the sarcophagus in the diaconicon, all these graves, investigated in order to define the usage and age of the building, are of the roof tile type. The latter appears to be the general tomb in İznik's Underwater Basilica.

The skeletons were laid in the dorsal position, oriented east-west, on a tile floor inside the tomb. The roof tile tombs of İznik's Underwater Basilica are located inside as well as outside the building.

The fact that part of grave KM4 and the entire grave KM7 are located under the bema wall suggests that the graves existed before the construction of the Basilica (168). For this reason, it is thought that the area was used as a necropolis in the pre-construction phase and that the temple of Apollo, which Bakhtyanus mentioned as having been built outside the fortification, was located in that area before the necropolis existed. After the pagan temple was abandoned, a necropolis with a grave chapel may have been established in the area. With the decision to close the pagan temples during the Early Christian Era, the Christian structure may have been built on the foundations of this temple for the continuity of the sanctity of the spot (169): 15. However, during the excavations carried out so far, no such foundations from the previous phase could be identified.

The grave chapel in the area was probably a martyr's tomb. Saint Neophytos who was a defender of Christianity since his childhood, was subjected to martyrdom. He was tortured and executed outside the city walls and buried on the spot. Nikaia, which hosted the first ecumenical council meeting in 325 CE (The Council of Nicaea), became a stopover for pilgrims on their way to the holy land in later periods. The cult of Saint Neophytos, who was seen as protecting the city from various dangers, was embraced and respected by believers (170): 28. It is possible that the necropolis laid out in and around the basilica under the waters of İznik Lake was transformed into a sacred burial ground by the hosting of the tomb of martyr Neophytos. The human and animal remains were dark colored, almost blackened due to a long stay underwater. Nine individuals are included in this study (anthropological analysis by Alpaslan-Roodenberg).

- I8366/KM1a (petrous bone), genetically male and brother of I8367/KM3; juvenile.

This grave was adjacent and parallel to the north wall of the middle nave and north of sounding 4A in the middle nave. It was damaged due to a mortar layer. Since the two coins found in the grave were heavily corroded, no dating could be made. From the grave, an adult and a child were identified. The child's age was assessed ca. 2 years (135). The bones were covered with a thick chalky layer. The skull and the left orbit of the child presented porous lesions (cribra orbitalia and porotic hyperostosis).

- I8367/KM2 (petrous bone), genetically male and brother of I8366/KM1a; infant.

This grave was also found inside sounding 4A, with the short side to the east, adjacent to the bema (step) wall. The grave yielded a heavily corroded coin. His age is estimated 3 months from his long bone measurements (135). The bones were well preserved. The maxilla and feet bones were absent.

- I8368/KM3 (petrous bone), genetically female, infant.

This burial was uncovered next to grave KM2. A golden earring with a square bead insert, a circular bead and a coin were collected from the grave. Two infants aged ca. 1.5 and 6 months were identified (*135*).

- I8369/KM4 (petrous bone), genetically female, adolescent.

This grave appeared next to KM2 and KM3. The eastern end of the grave, whose cover tiles were scattered, was stuck under the bema wall. Among a few collected coins, one could be dated 378-383 calCE. This individual's age was assessed at 14 years (epiphyseal union timing was applied for age determination). The bones were relatively well preserved; foot bones were lacking. Right orbital roof presented porotic lesions (cribra orbitalia).

- I8370/KM5 (petrous bone), genetically male, infant.

The grave was completely collapsed and yielded no additional finds. The infant was one year old (*135*). The remaining bones were a fragmentary skull, pelvic parts, and a right humerus.

- I8372/KM6 (petrous bone), genetically female, adult.

This was destroyed by a later wall; no finds. The bone sample is radiocarbon dated to 335-418 calCE (1670±20 BP, PSUAMS-5520). The young woman's age was determined to be between 17 and 25 years (*153*). Her height was calculated at 162.4 cm (*171, 172*). Linear enamel hypoplasia (LEH), which is a useful health indicator during childhood, was noted in the mandibular front teeth. Although she was young, her dental health was rather bad considering periosteal changes such as caries, abscess and antemortem tooth loss in her lower jaw due to carious teeth.

- I8373/KM7 (phalanx), genetically female, adult.

The grave was the most interesting among the roof tile graves. No finds. This woman's age was estimated between 35-45 years (*153*). She had two abscesses in her right lower jaw and thick dental calculus deposits on the labial surface of her mandibular and maxillar teeth. Her height was 154.3 cm. (*171, 172*).

- I8371/KM8 - Grave 9 (petrous bone), genetically female, juvenile.

This burial was found in the diaconicon section. The badly preserved bones belonged to a woman between 35 and 45 years. Her skull presented rather masculine sex features. Her height was calculated 164.4 cm. Osteophytic changes were observed due to osteoarthritis.

- I14799/KM9 (petrous bone), genetically male, juvenile.

Bones were scattered throughout the diaconicon section and poorly preserved. The bones belonged to a 2.5 years old juvenile (*135, 173*).

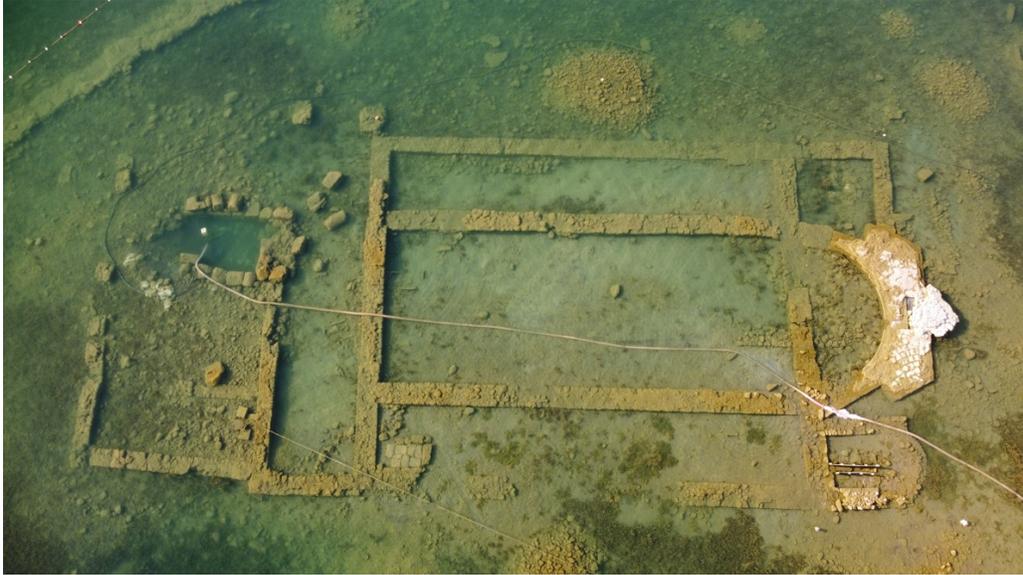


Fig. S 11 Underwater Basilica (in Lake İznik, İznik/ Nikaia, Turkey)

Yenişehirkapı (İznik; Nicaea; Late Roman/Early Byzantine)

Contact: Mustafa Şahin, Serkan Gündüz

Yenişehir Kapı is the present name of the gate to the south of the *Cardo maximus* (central north-south street of an antique city), and one of the four main gates of Nicaea. In 2017, under the auspices of İznik Archeology Museum, rescue excavations were carried out under the scientific consultancy of Mustafa Şahin in five different trenches. Five soundings revealed graves of various forms. The first sounding is located in the eastern part of the Yenişehir Gate. A total of 10 graves of different various were identified from different levels in the trench, measuring 5x5 meters. The graves were discovered in the northern part of the trench at a depth of 126 and 237 cm. The majority of the graves, which were of the “Torpedo Grave” type and the “Roof Tile Grave” type, contained infants. Six individuals are included in this study:

- I14833/M2 (petrous bone), genetically male, infant.

The grave was found at a level of 133 cm below the surface. The grave form is a “torpedo” (43 cm long). Grave cover was made of mortar. The corpse was oriented west-east.

- I14843/M3a (petrous bone), genetically male, infant.
- I14844/M3b (petrous bone), genetically male, infant.

Remains of two babies were found in a 60 cm long torpedo grave M3.

- I14840/M6 (petrous bone), genetically female, infant.

This was a disturbed grave where a few fragmentary bones of a young baby were recovered.

- I14839/M7 (petrous bone), genetically female, infant.

A badly preserved Torpedo grave contained a skeleton in dorsal position. According to the place of the skull, the dead was buried in west-east orientation.

- I14842/ NK17 YKS1 (disturbed grave)), genetically female, infant.

Zeytinliada, Meryemana Manastırı /Virgin Maria Monastery (Erdek, Balıkesir; Early Byzantine)
Contact: Fadime Suata-Alpaslan, Nurettin Öztürk, Berna Kavaz-Kındıgılı

Zeytinliada, one of the Marmara Sea islands in the vicinity of the Kapıdağ Peninsula within the borders of the Balıkesir province, is the closest island to Erdek (174). Because of the olive trees on the island, it is called Zeytinliada. There is no precise inscription on the date of foundation of the monastery that was built there. In light of the excavations carried out since 2007 at Zeytinliada, it is possible to date the foundation of the monastery to the 4th century CE. From this date to the 14th century, it was in use with additions and changes. The Kyzikos Hadrian Temple, which was considered as the eighth wonder of the world in ancient times, was located at a distance of 7 km from the island. According to historical sources (175): 217. this temple was turned into a church with the name of the Virgin Mary during the reign of Leon I (457-474 CE). There is a high probability that a temple of Apollo could be found here in line with the architectural finds recovered from the nearby hot water spring and from the excavations. A baitylos, a meteorite or black stone held sacred, was unearthed in the 2016 excavations. The wide base of this stone was flattened and the upper part had been given a narrowed aniconic appearance. It is thought that the stone was cut into two and used as a cult image. Zeytinliada Monastery includes a baptistery, a chapel, retreat rooms, an open-air area for worshipping, an altar area, a holy spring, cisterns, baths, pools, ovens, latrines, a warehouse, a workshop, a harbor, a western church, an underground church and a boathouse. Among the human skeletons found in sarcophagi, seven samples are included in this study:

- I14821/ZK-41 (petrous bone), genetically female, between 25 and 35 years old.
- I14823/ZK-59 (petrous bone), genetically male, ca. 9 years old juvenile.
- I14831/ZK-65 (petrous bone), genetically female, ca. 46 years old.
- I14832/ZK-68 (petrous bone), genetically male, between 25 and 35 years old.
- I14820/ZK-77 (petrous bone), genetically female, between 30-35 years old.
- I14822/ZK-82 (petrous bone), genetically female, between 17-25 years old.
- I14824/ZK-106 (petrous bone), genetically male, adult.

Samantaş, Değirmendere, Çapalıbağ locations (Muğla, Yatağan; Archaic Sub-Geometric period, Byzantine, Ottoman)

Contact: Ahmet İhsan AYTEK, Sabiha Eriş Pazarcı, Esra Hilal Kaya, Alper Yener Yavuz

New graves were found at Samantaşı in 2016 during mineral exploration in the region. Following a protocol signed by the museum and the mining company, salvage excavations started in places within the mining license area that are registered as third degree protected archaeological find spots. These locations are Samantaşı in the Yeşilbağcılar district and Değirmenderesi and Çapalıbağ in the Turgut district. The Çapalıbağ graves were studied as part of a systematic archaeological excavation. The tombs were found in a very different place and level than Byzantine-era tombs. There were wooden boards on the dead in the graves, as in Muslim graves. The burial direction of the skeletons is within the framework of Islamic rules (it

is also evident in the images). As a result of the excavations carried out under this protocol, the following graves were unearthed;

-A Byzantine necropolis was found at Samantaşı. Here 455 graves of different architectural types were unearthed together with a small chapel.

-A necropolis belonging to the Archaic period was discovered at Değirmenderesi, where 297 tombs built using different architectural arrangements have been unearthed. The data obtained here are also important in terms of belonging to the only known necropolis in Western Anatolia from the Archaic period. In the same necropolis 3 rectangular-planned structures were unearthed built with slate stones.

-Although the Çapalıbağ site does not constitute a genuine necropolis, pithos graves dating to the Bronze Age could be uncovered in many spots.

Çapalıbağ graves (Muğla; Byzantine, Ottoman)

12 samples are included in the study.

- I20571/18CS206 (petrous bone), genetically male. An almost complete skeleton of a man between 25 and 30 years old.
- I20329/18CS220 (petrous bone), genetically female, subadult.

Bones collected in this sounding (18CS220) pointed to the presence of 2 young individuals: an adolescent between 15 and 20, and a juvenile between 10 and 12 years old.

- I20327/18CS228 individual 1 (petrous bone), genetically male, adult
- I20328/18CS228 individual 2 (petrous bone), genetically female, adult

Skeletal parts from 3 individuals were identified in the grave 18CS228: an infant ca. 2-3 years old, and a woman and a man, both between 32 and 43 years old.

- I20570/18CS237 (petrous bone), genetically female, adult

Remains from 5 individuals were identified among the bones found in this grave: 2 males 40-45 and 34-47 years old; 3 women, respectively between 32 and 43, between 25 and 35, and a young female older than 20.

- I20572/18CS249 (petrous bone), genetically male; adult between 40 and 45 years old.
- I20573/18CS267 (petrous bone), genetically male; adult between 34 and 47 years old.
- I20326/18CS286 (petrous bone), genetically male; juvenile between 12 and 14 years old.
- I20324/18CS291 (petrous bone), genetically female; juvenile between 3 and 4 years old.
- I20325/18CS292 (petrous bone), genetically female, adult.

Among the bones excavated in this grave (18CS292), 3 individuals were identified: next to remains of a ca. 20-27 years old female, there were bones from 2 other individuals. Their sex and age determinations could not be made, because only a few skull fragments were available from them.

- I20322/18CS294-individual 1 (petrous bone), genetically male, adult.
- I20323/18CS294-individual 2 (petrous bone), genetically female, adult.

Skeletal remains from 3 individuals were identified in the grave, 18CS294: 2 males aged between 34 and 47 and 25 and 35 respectively, and a female between 20 and 25 years old.

Değirmendere graves (Muğla; Archaic, Sub-Geometric, Early Byzantine)

Twelve individuals are included in the study:

- I20232/18DDM74 (petrous bone), genetically female, adolescent.

Two individuals (between 12-15 and 15-21 years old) were identified in this grave. They were numbered as individual 1 and 2.

- I20226/19DDM02-individual 1 (petrous bone), genetically female, infant. Sister of I20229.
- I20227/19DDM02-individual 2 (petrous bone), genetically female, infant.

Two infants were identified among the bones found in the grave 19DDM02: the age of the infant skeleton with the most bones was estimated between 0-6 months. The few bones present from a second infant made an age determination impossible.

- I20229/19DDM05 (petrous bone), genetically female, juvenile. Sister of I20226. Almost complete skeleton of a ca 10 year old child. It was buried with an east-west orientation.
- I20228/19DDM18 (petrous bone), genetically female, infant. Bones from two infants were found in this grave: one of 0-6 months and a slightly younger infant.
- I20224/19DDM44-individual 1 (petrous bone), genetically male, juvenile (son of I20225).
- I20225/19DDM44-individual 2 (petrous bone), genetically male, adult (father of I20224).

In grave 19DDM44, oriented northwest-southeast, skeletal remains from 4 individuals were uncovered: Individual 1 is a male buried in a supine position and older than 45. Individual 2, who was represented only by scattered bones, was between 30 and 35 years old, while individual 3 and 4 were juveniles respectively 9-10 and ca. 12 years old.

- I20233/19DDM86-individual 1 (petrous bone), genetically female, adult.
- I20257/19DDM86-individual 2 (petrous bone), genetically female, adolescent.

Two burials were found in grave DD19M86 which was oriented east-west. Examination of the bones indicated 4 individuals. Individual 1 was a woman between 28 and 35 years and individual 2 an adolescent between 13 and 16 years old. Remains of two other individuals identified in the grave were a 6 to 8 years old child and a man between 40 and 50.

- I20231/19DDM88 (petrous bone), genetically male, adult.

Here skeletal remains of 3 males and 1 female were excavated. Two male individuals were estimated between 35 and 47, while a third male was between 40 and 50 and a female between 32 and 45 years old.

- I20258/19DDM96 (petrous bone), genetically male, adult.

The skeletons of two individuals in the dorsal position were found in this east-west oriented grave. Both skeletons were determined as male, aged between 43-46 and 34-47 years.

- I20230/19DDM97 (petrous bone), genetically male, adult.

In this grave remains of two individuals were unearthed a juvenile and an adult between 40 and 50 years old.

Samantaş graves (Muğla; Byzantine)

Seven individuals are included in this study:

- I20259/16SM169 (petrous bone), genetically male, juvenile.

The skeleton was uncovered in dorsal position. The skull, found on the west side of the tomb facing south, belonged to a 8-9 year old child.

- I20261/16SM174 (petrous bone), genetically male, adult.

This skeleton was also found in dorsal position with the skull in the west part of the tomb. It is that of a male 34-47 years old.

- I20260/16SM180 (petrous bone), genetically female, juvenile.

A skeleton of a 5-6-year-old child was found in this grave. The skull in the west part faced north.

- I20266/17SM60-B1 (petrous bone), genetically male, adult.

There were skeletal remains of 3 individuals in the grave. The sample was taken from individual 2, a 30-35 year old woman.

- I20320/17SM118 (petrous bone), genetically male, juvenile. The skeleton of a 6-7 year old child was uncovered in the grave.

- I20264/18SM83-individual 1 (petrous bone), genetically male, infant. Brother of I20265.
- I20265/18SM83-individual 2 (petrous bone), genetically male, infant. Brother of I20264.

Six skeletons were retrieved from grave 18SM83, one in dorsal position and five others only as scattered bones. Individual 1 and 2 could be identified from the scattered bones. The badly preserved remains did not allow age estimation.

Camandıras and Dalagöz graves (Muğla; Roman)

Contact: Ahmet İhsan Aytek, Alper Yener Yavuz

During highway construction works graves were unearthed between Stratonikeia and Lagina (Yatağan district). Excavations were carried out in locations called Camandıras and Dalagöz situated 400 and 450 m south of Lagina. During the excavations 34 graves were detected in Camandıras and Dalagöz. Architectural artifacts brought from the Hecate sanctuary in Lagina were also found in the graves. These graves are thought to constitute a necropolis belonging to one of the villages near Lagina. The skeletons are not numbered as they were found during road construction works. The minimum number of individuals was 15 (by considering the left femur). Among them there were 14 adults and 1 juvenile (between 2 and 4 years old). Sex determination of 11 individuals was made: 7 males and 4 females were identified. The age of the females was estimated between 20-30 years (2 individuals) and 30-40 years (2 individuals). Males' age was estimated for 3 individuals between 20 and 30 and for 4 individuals between 30-40 years. Four samples (3 individuals) are included in the study:

- I20000 (dup. I20002/Individual 3) /Individual 1 (petrous bone), genetically male, adult.
- I20001/Individual 2 (petrous bone), genetically female, juvenile.
- I20139/Individual 4 (petrous bone), genetically male, adult.

References: (176-178)

Armenia

Early Farming Societies

The Aratashen-Shulaveri-Shomutepe Archaeological Complex (Late Neolithic)

Contact: Pavel Avetisyan

The first agricultural settlements in the modern-day territory of Armenia date back to the Late Neolithic. The archaeological cultural tradition typical of this period is commonly referred to as the Aratashen-Shulaveri-Shomutepe complex and settlements belonging to this are located between the Kura and Araxes Rivers (The Territory of the Kura-Araxes Interfluvium). The Late Neolithic settlements are represented by multi-layered mounds clustered on the banks of tributaries of the Kura and Araxes Rivers. Among these are the settlements of Aratashen, Aknashen, and Masis Blur located in the Ararat Valley, which are artificial mounds with an area of up to 1 hectare. The cultural layers are between 3.5-4.5 m high and have been radiocarbon dated to ca. 6000-5250 calBCE. The materials of a number of sites of the Urmia Basin and Lake Van, particularly the materials of Tilki Tepe located on the south-eastern shore of Lake Van, indicate that the southern boundary of this culture reached the basins of Lake Van and Urmia.

Study of Early Holocene sites dating back to the 10th to 7th millennium BCE (Apnaghgyugh-8 cave, Gegharot-1 open-air, and Lernagog-1 settlement) do not allow answering questions of whether the Neolithization processes in the region were largely a result of migration or diffusion mechanisms. The Late Neolithic inhabitants of the Ararat Valley were undoubtedly sedentary farmers, but they were also engaged in long-distance animal herding and covered large territories during the seasonal movement toward pastures. The acquisition of obsidian from a wide number of sources within modern-day Armenia, the presence of obsidian from the Lake Van area, and the imported Halaf pottery in all three settlements indicate that the inhabitants of the Ararat Valley had close cultural relations with the bearers of the Halaf culture. Evidence of drastic changes in the subsistence system of early agricultural societies dates to the final phases of the Eneolithic/Chalcolithic period (4300-3400 calBCE). The geography of the settlements generally expands; in addition to the alluvial plains, the foothills and mountain river gorges also become inhabited. In addition to the long-term habitation mounds, we begin to see the appearance of temporary settlements and the use of caves for habitation or protection. The excavations of the Areni-1 Cave and the semi-permanent/seasonal settlement of Godedzor show the dominance of a subsistence economy, expansion and intensification of various vital activities, and clear directionality of cultural links. In particular, there is ample evidence for the connection of the inhabitants of Areni-1 and Godedzor with the populations of Lake Van basin, north-western Iran and eastern foothills of Zagros. Moreover, the materials from Godedzor (3600-3400 calBCE) show that at least a part of the population of this settlement for half the year lived on the shores of Lake Urmia and spent the other half of the year on the bank of the Vorotan River in southern Armenia. These data are the best evidence of long-term direct contact of populations living in different regions.

References: (179-182)

Aknashen (Late Neolithic)

Contact: Levon Aghikyan, Ruben Badalyan, Aram Yardumian

The site of Aknashen-Khatunarkh is located in the Ararat valley, in the basin of the Sevjur (Metsamor), at an altitude of 838 m, in the province (*marz*) of Armavir. The site is an artificial hill (*blur*), with an area of about 1 hectare, and the thickness of the cultural layer is about 5m. The excavations of the site have been conducted since 2004 by the Armenian-French joint expedition directed by R. Badalyan, A. Harutyunyan, and C. Chataigner. The site belongs to the Neolithic “Aratashen-Shulaveri-Shomutepe” archaeological complex and dates back to the first half of the sixth millennium BCE. Human remains are attested from both a cultural layer of the synchronous deliberately committed burial (Tr.6, UF 11, F.15) and as household waste (unburied remains of a newborn). The burial (Tr.6, UF 11, F.15) was unmarked and otherwise there were no outward signs of its presence. The skeleton was placed on the left side, oriented northeast-southwest, the head was oriented northeast, facing south. The lower limbs of the skeleton were open, the upper ones are in semi-contracted condition, directed to the knees. The skull was fragmented. The skeleton was in anatomically integral condition, while the skull was fractured and prostrated.

- I3931/Aknashen 2014, Trench 6, UF 11, F15 (humerus), genetically male, newborn.

References: (180, 183, 184)

Masis Blur (Late Neolithic)

Contact: Kristine Martirosyan-Olshansky

The Late Neolithic settlement of Masis Blur is located on the ancient left bank of the Hrazdan River, approximately 3km northwest of Masis city. The settlement’s artificial mound was destroyed in the early 1970s; however, subsequent excavations of the site revealed nearly 3 meters of Late Neolithic layers below the modern surface. Exploratory excavations conducted by G. E. Areshian in 1985-1986 identified architectural remains and a rich material assemblage, which Areshian ascribed to the Late Neolithic. Systematic excavations by the Armenian-American team at Masis Blur resumed in 2012 are ongoing. The agro-pastoral community at Masis Blur was established sometime at the end of the 7th millennium BCE and thus far, the last preserved occupation phase at the site dates to ca. 5375 calBCE. The architecture at Masis Blur is comprised of individual dwelling units with no internal architecture or features. These are made of pisé, though unfired mud brick elements have been detected in later occupation phases with the heaviest 20th century destruction. The dwelling units are connected by courtyards which contain numerous small, circular storage bins, cobble-lined hearths, fire pits, and semi-circular walls which likely served multiple purposes (e.g., dividers, benches, find shields, etc.) The material assemblage is rich in obsidian and bone tools, faunal and botanical remains, ground and polished stone artifacts, and objects of personal adornment. The pottery from the site comes mostly from the ploughzone and intrusive pits, suggesting that the inhabitants of the site did not begin to use and produce pottery until the final occupational phases, at the end of the 6th millennium BCE. The preserved layers of the settlement attributed to the Aratashen-Shulaveri-Shomutepe archaeological complex date between ca. 6200-5375 calBCE. One sample from Masis Blur is included in this study.

- I3930/Masis Blur 2014, Trench 07/13SE, Burial (tooth), genetically male, adult.

Burial 1 was excavated in 2014, making it the third Neolithic burial found at Masis Blur to date. The two other burials, an adult male and an adult female, found in 1985 in individual graves were accessioned to the National History Museum in the 1980s, however the current project was not able to locate these materials in the Museum's collections. Burial-1 belongs to an adult male between 35-40 years of age. The individual was buried under a compacted earthen floor, in the supine position, slightly leaning towards his right side; his left arm, bent at the elbow, was placed across his abdomen, and his head was oriented northeast. Burial goods (obsidian blade fragments, bone tools, beads, and a pendant) were found both with the remains and in a small pit below his feet. The burial was dated to 6665 ± 25 cal. BP using a tooth from the individual (PSUAMS-3057).

References: (185-189)

Early Complex Societies

Contact: Pavel Avetisyan

In Armenia, Bronze-Iron Age archaeological monuments (cultural layers, residential and burial architecture, the typology of material culture, etc.) form 8 "archeological complexes" in the academic literature: "Kur-Araks culture" (KA) – Early Bronze Age; "Early Kurgan Culture" (EK) – first phase of the Middle Bronze Age; "Trialeti-Vandazor Culture" (TV), "Sevan-Artsakh Culture" (SA), "Karmirberd Culture" (KB), "Karmirvank Culture" (KV) or "Van-Urmian Ceramic Culture" – second and third phases of the Middle Bronze Age; and "Lchashen-Metsamor Culture" (LM) – Late Bronze-Iron Age. Here we discuss the KA and EK.

The first phase of changes in the cultural environment of the region becomes visible from 3400 / 3300-2900 BCE and is connected to the emergence and dominance of new archaeological cultures in the Kura and Araxes river basin, and the spread of this KA culture to the upper reaches of the Euphrates in Turkey (e.g., Arslan Tepe, Norshun Tepe), and to the western region of the Iranian highlands (Godin Tepe). The earliest evidence of complex societies in the territory of Armenia also appears in the context of the formation of the Kura-Araxes cultural landscape. Many hypotheses have been put forward regarding the origin of this culture. However, in the absence of appropriate ancient DNA data, no objective facts have been offered about the extent of genetic continuity between the Eneolithic and Kura-Araxes cultures in the area of the spread of the KA culture. At the same time, the earliest known complexes of the KA cultural complex are concentrated in the territories of the Kura and Araxes river basin (the Territory of Kura-Araxes Interfluvium). The abundance of KA sites in the Kura-Araxes basin dated to the second half of the IV millennium BCE and their appearance in the upper reaches of the Euphrates-Tigris, the Iranian plateau, the North Caucasus, as well as in northern Syria and the Levant (the so-called "Kura-Araxes expansion") only at the end of the IV and the beginning of the III millennium also indicate that the origin of Kura-Araxes cultural complex lies with territory of the Kura-Araxes basin. The appearance of exclusively KA cultural assemblages, at the end of the IV millennium BCE and the beginning of the III millennium BCE at Eneolithic settlements located thousands of kilometers apart and represented by significantly different Eneolithic cultural assemblages should be seen as a direct result of the first wave of the "Kura-Araxes expansion." The production of the distinctive KA pottery tradition, the settlements typical of valleys and highland regions, the burial complexes, artifacts of ritual practice, miniature figurines, and unique decorative motifs leave little doubt that we are dealing with the formation of a society or

societies that created a homogeneous cultural environment and with a large part of this society engaged in the active processes of acquisition of new territories ("expansion"), combined with "integration" processes.

Between 2900-2500 / 2400 BCE, segmentation (localization) of the cultural environment resulted in a number of archeological cultures or local variants of the KA culture being formed. From 2900-2600 BCE (KA IIA sub-phase), nearly the entire territory of Armenia is dominated by "Shresh-Mokhrablur" and "Karnut-Shengavit" cultural complexes. In this period, processes typical of the Ararat valley and neighboring territories become most widespread, especially towards the south-west, reaching the regions of the Tigris and Euphrates and Levant (second wave of the Kura-Araxes expansion). From 2600-2400 BCE (KA IIB sub-phase) the "Aygevan-Shengavit" and "Ayrum-Teghut" complexes dominated, with monuments belonging to archaeological culture to the north of the Caucasus becoming commonplace in the Kura basin. We also begin to see appearance of kurgan burials and artifacts not part of the KA complex: the "Early Kurgan" (EK) culture.

During the second half of the third millennium BCE, kurgan pottery previously seen in Armenia only in the Kura basin almost entirely replace the "Aygevan-Shengavit" and "Ayrum-Teghut" groups. These post-KA complexes are represented by burial fields within abandoned settlements of the Araxes basin. The material assemblages of these burials allow us to synchronize them with the EK culture from 2450-2200 BCE (Middle Bronze Age I Phase) From the southern foothills of the Caucasus Mountains to the Kura Basin, complexes with burial structures of unprecedented size (kurgans) become dominant; it is in such complexes that artifacts very typical of the regions located north of the Caucasus are often recorded. In contrast, further south, more traditional KA archaeological features remained common although in the Araxes River basin only burials in abandoned settlements (Sos Hoyuk, Shengavit, Dvin, Aknashen); there are also Mayisyan burials not associated with any settlement. South of the Araxes, particularly in the upper reaches of the Euphrates River, the KA culture continued to flourish, with large settlements with palatial complexes appearing (Norşuntepe).

The archaeological strong influences from the north in the Kura Araxes basin starting from 2600/2500 BCE coincides with our genetic findings in this publication of major new inflow of population from north from the Caucasus to the Kura River.

References: (190-202)

Talin Cemetery

Contact: Pavel Avetisyan

The Talin cemetery is spread within the limits of Talin town, which is located on the southwestern slopes of Mt. Aragats, at 1600m elevation above sea level. The Early Bronze Age burials were mainly opened in the eastern part of the cemetery. In 1990-1992, four Early Bronze Age burials (N^o 7, 10-12) and one ritual platform were excavated. Early Bronze Age burials were also excavated in 2013 (N^o 110, 111, 113, 115, 116).

- I1657/ TA3/L5, Tomb 15; Talin 3, 2013, Tomb 115, Skull 5 (petrous bone), genetically female.

The burial cell is lined with slabs, and contained the remains of 6 individuals. One complete skeleton was placed on the right side in flexed position; the rest of the highly fragmented skeletal remains were in a heap under the northern wall of the chamber. A single cup was found within the pile of human bones.

References: (203, 204)

Shengavit Cemetery

Contact: Hakob Simonyan

The site is located in the Shengavit community of Yerevan, on the left bank of the Hrazdan River (nowadays the eastern shore of the artificial Yerevan Lake), on a flat-topped plateau 930m above sea-level; it once occupied more than 6 hectares. Its art is represented by statuettes of men and women as well as animals including rams, goats, bulls, horses, and lions; it also includes phallic amulets made of pebbles, tuff and baked clay. A variety of jewelry was widely distributed: necklaces, amulets, earrings and pendants; the most ancient gold products of Armenia were found in the burials of the upper class of Shengavit. A large number of weapons were present including obsidian and bone arrowheads of various types, and stones for slings. Ten tuff statues of deities up to 70cm high were found, as well as cult hearths/altars, in which the eternal flame burned made of baked clay with a diameter of about 1m and a depth of 20-25cm. Burials were carried out outside the defensive walls, in a necropolis dug into the cultural layers of an abandoned quarter of the ancient city. In 1965, Sandro Sardaryan excavated four big tombs and five small burials; further excavations by Hakob Simonyan in 2004-2005 uncovered five burials, one of which we analyze here. Burials with stone walls were recorded, but no cromlechs or burial mounds.

- I14346/Shen05t4; Locus 051; Tomb no. 4; 2005 (long bone) Genetically female

The floor of the grave was 50 cm below the ground level. The bones of sacrificial animals and burial accessories were placed in a circle of stones and fragments of clay bricks (1.1m x 1.0 m). At the top was half of a bowl, and a little to the north was another, richly decorated. Below them was the lower jaw of a young woman, which was divided into two parts, and next to it was placed the half of a small cup. To the west were a human shoulder-bone, jagged obsidian and flint tools, and a single rib of cattle. The following human bones were identified: a) the lower jaw of a 25-30-year-old woman, B) a pair of shoulder bones stacked on top of each other, C) one palm-bone, and d) one rib. Under the pile of bones of the woman, the right half of a child's pelvis opened, and under it, on the floor, the woman's clavicle. This placements of remains corresponded to a ritual of dismembering the corpse, and dividing and placing half of vessels in the grave.

References: (205, 206)

Karnut Archaeological Complex

Contact: Levon Aghikyan, Ruben Badalyan

The Karnut Archaeological complex is located in the western edge of its eponymous village in the Shirak Region. At 1625m above sea level, the site sits on the eastern border of the Shirak plain, where it meets the western edge of the Pambak Ridge. Its settlement occupies the lower

section of the western slope of Surb Minas Mountain (1745m above sea level), an andesite-dacite formation with a relative elevation of ~175m.

Initial work at Karnut was conducted by R.S. Badalyan in 1981-1985, 1987, and 1990. During this time, 400 m² of settlement was excavated. The settlement had a single layer and was attributed to the end of the Early Bronze Age (EBA). The resumption of excavations (by R.S. Badalyan and L.A. Aghikyan) was due to the discovery of EBA burials on the territory of the village. All the burials have cist chambers. Burial 2 (single burial) belongs to the first phase of the Kura-Araxes culture (3500/3350 – 2900 BCE), most likely its final stage (KA Ic). Burials 1 (single burial), and 6, 8, and 9 (collective burials) are dated to the second phase (KA II: 2900 – 2600/2500 BCE). Burial 11, which contains no materials, is undated. The practice of moving previously interred individuals to make room for a new interment is evidenced in burial 8. The presence of materials and anthropological remains in front of chambers entrances was recorded in burials 6 (Fig. S16) and 9.

- I14812/ Karnut-2017, Tomb 9, Δ16 (petrous bone), genetically female.
- I13599/ Karnut 2017, Tomb 9, Δ9 (petrous bone), genetically female.
- I16706/ Karnut 2017, Tomb 9, Δ10 (tooth), genetically female.
- I16707/ Karnut 2016 Tomb 5, Δ6 (tooth), genetically male.
- I17499/ Karnut 2016 Tomb 6 Δ9; Karnut 2016 Tomb 6 Δ2 (cranial bone), genetically male. (Fig. S 12)



Fig. S 12 Karnut. Tomb 6.

References: (203, 207)

Berkaber, Dzhoghaz Cemetery, Tavush district

Contact: Hakob Simonyan and Gregory Areshian

Archaeological monuments of different epochs - from the Early Bronze Age to the Middle Ages - were found on the right Bank of the Voskepar river, now the Joghaz reservoir near the

village of Berkaber. They stretch out in an almost continuous strip, up to two km long, and occupy the slopes of the hills bordering this part of the valley from the East, as well as a vast sandy terrace between the foot and the steep bank of the river, now the bank of the reservoir. This includes an extensive settlement of Kura-Araxes culture and its associated burial grounds, archeological complexes of Bedeny culture, burials of the early stages of the Late Bronze Age, a cemetery of Hellenistic era and a contemporary settlement, and a settlement the late Middle Ages.

In 1986 in the area “Meydanner” three architecturally very similar tombs were excavated that are associated with the Kura-Araxes culture (excavations led by G. Areshian and H. Simonyan). They are crypts of a sub-rectangular plan, which were ground structures oriented E-W with the back of the crypts sunk into the hillside. The walls of the crypts are built with dry masonry of rolled boulders and large pebbles. In the ground part, the thickness of the walls formed two or three rows of masonry. The crypts probably had a wooden roof. The upper part of the crypts was cut off during the construction of the road. In the preserved part of crypt 1, the remains of more than 50 people were found. The vast majority of the bones were found in a mixed state, the result of periodic reburials during the functioning of the family or ancestral crypt. DNA analysis of skeletons from the mausoleum of Dzhogaz 1, first published in this article, proves that people with close family ties were buried in the same mausoleum, which makes the theory of successive burial of the deceased from the same large family in the ancestral tombs of their ancestors more than convincing (I14340/ DZH86M.t1.02, Tomb no. 1, 1986; (2) DZH86M.t1.04, Tomb no. 1, 1986; (3) DZH86M.t1.09, Tomb no. 1, 1986; (4) DZH86M.t1.07, Tomb no. 1 (petrous bone), genetically male. Father.or.sonI14343). However, individual undisturbed crypts indicate the placement of the dead on their side in a crouched state. More than 60 vessels were found, most of which are ornamented. Also found were flint inserts for sickles, flakes of obsidian and flint, beads, 13 bronze pins and spiral temporal rings in one and a half turns, and the remains of sacrificial animals and coals. Of particular interest is a double-leaf mold made of baked clay for casting metal.

- I15132/DZH86M.t1.10; Tomb no. 1, 1986 (petrous bone), genetically female.
- I16920/DZH86M.t1.05; Tomb no. 1, 1986 (tooth), genetically female.
- I14340/ DZH86M.t1.02, Tomb no. 1, 1986; (2) DZH86M.t1.04, Tomb no. 1, 1986; (3) DZH86M.t1.09, Tomb no. 1, 1986; (4) DZH86M.t1.07, Tomb no. 1 (petrous bone), genetically male. Father.or.sonI14343.
- I14339/DZH86M.t1.01; Tomb no. 1, 1986 (tooth), genetically male.
- I14341/DZH86M.t1.03, Tomb no. 1, 1986; (2) DZH86M.t1.06, Tomb no. 1, 1986 (tooth), genetically male.
- I14343/DZH86M.t1.05; Tomb no. 1, 1986 (tooth), genetically male.

From Early States To Territorial Kingdoms

Contact: Pavel Avetisyan

Starting from the XXIII century BCE, Kura-Araxes and Early Kurgan culture are no longer evident. There are drastic changes in the ways of organizing and appropriating space, and in many features of the economy, burial rites, cult and beliefs. These transformations show that we are dealing with the end of the establishment of complex societies in the highlands, and the

embryo of early state formation. This period is bookended at the X century BCE, when part of the territory of modern Armenia was included in a single state, the Van Kingdom.

The last quarter of the III millennium BCE (and not earlier than the XIX century BCE in southern Armenia) is marked by the Trialeti-Vanadzor cultural complex (TV) (2200-1800/1700 BCE, Middle Bronze Age, II phase). In most regions, only burial structures are documented, suggest that we are dealing with mobile, nomadic herders. From this stage, pottery typical of TV gradually becomes more widespread: black vessels with line and dot incised decorations in the upper and middle Kura basin, painted vessels in Nakhijevan and in the Marand, Lake Van and lake Urmia basins and Mush; and a mixture of the two in the main part of Armenia. The distribution and timing of the complexes suggests a south-to-north cultural expansion, leading to the merging of the realms typical of the northern and southern cultural zones of the region.

Beginning in the XVIII century BCE a new wave of regional cultural environment transformation started, spanning the basins of Urmia and Van lakes, the Araxes River, and the areas adjacent to the middle reaches of the Kura River. In the above-mentioned areas new archaeological cultures displaced the TV complex: the Sevan-Artsakh (SA) Karmir Berd (KB) and Karmir Vank (KV) archaeological cultures, which differ by painted pottery complexes of distinctive styles, and have features typical of settled societies (in contrast to the nomadic lifestyle of the TV). The TV cultural complex in the upper reaches of the Kura River persisted into the XVII century BCE, despite significant changes. In the Araxes River and Lake Urmia basin, archaeological cultures with mosaics of traits of the KB and KV, and the TV, appeared.

After the turn of the XVI-XV centuries BCE, a more homogeneous cultural environment appeared known as Lchashen-Metsamor (LM) culture. Hundreds of fortress-settlements and large necropoleis testify to dense and widespread habitation. Chariots including military chariots were found in the tombs of the Lchashen-Metsamorian elite, with numerous examples of Mitannian seals. From the XV-XIII centuries BCE the region is marked by symbols of power belonging to the Kassite dynasty of Babylonia (seals, balance-weights, etc.) in tombs of women. This *is* presented with manifestations of a demographic explosion. As evidence of a demographic explosion in this Late Bronze Age Phases I and II period, the number of cemeteries known from throughout the area between the Kura and Araxes rivers from the XVIII-XVI centuries BCE does not exceed a few dozen (in exceptional cases up to 200-250 burials); in contrast, there are many sites dated to the XVI/XV-XIII centuries BCE with burials reaching in some cases up to 1.5-2 thousand. At the turn of the XIII-XII centuries BCE, there is archaeological evidence of a decline in human activity. At Lchashen, Artik, Gegharot, Tsaghkahovit, and to some extent also at Karashamb, hundreds of burials dated to the XV-XIII centuries BCE are excavated, while graves from the XII to XI centuries BCE are sporadic or absent.

In the Early Iron Age (XII/XI–IX centuries BCE), a number of sites in the Ararat Valley (Metsamor, Dvin, Shamiram etc.) began to be used more intensively than ever before, a process that extended to the upper reaches of the Euphrates River and also involved appearance of new types of pottery connecting the region to the present-day territory of Georgia (Pre-Urartian layer of Karmir Blur, Sheytandagh, etc.).

Radical changes of the social-cultural landscape during the first millennium BCE are connected with the process of formation and expansion of the Kingdom of Urartu whose center of power was in the Lake Van region of Turkey. According to the inscriptions of the Assyrian king Shalmaneser III, between 860-850 BCE Urartu was a quite powerful state and the latter's invasions against "Aramu the Urartian" and afterwards the Sarduri, the son of the ruler of Tushpa Lyutibri, started the long-lasting Assyrian-Urartian conflict. Menua was the first of the kings of

Van to start the conquest of the sub-Araxian countries and their inclusion in the frame of Urartu. During the VIII century BCE the main part of modern Armenia was included in the Urartian state; in this context, it is notable that XI-IX century BCE graveyards located in the Ararat valley, the foothills of Aragats, Shirak plain and Lake Sevan basin radically decreased in their usage starting in the IX century BCE.

In the IX/VIII-VII centuries BCE, numerous graveyards dated are recorded in the northern regions of Armenia. Both cuneiform inscriptions and excavations suggest that the Urartian centers were heavily influenced by the western and southern regions of the kingdom. Starting from the VII century BCE, the region is impacted by mutual penetrations of Van-Tospyan and Lchashen-Metsamorian cultures, and separate intrusive elements from the Scythian culture.

In the Achaemenid, Hellenistic, and Late Roman periods, city centers are affected by the mutual penetration of cultural elements typical of different areas. The testimonies of historians of the displacement of populations by the rulers of the Artashesid dynasty from Cappadocia, Levant and other regions, and their settlement in Armenian cities are important to keep in mind in light of the ancient DNA evidence presented in this study..

References: (192, 208-214)

Tavshut Cemetery

Contact: Levon Aghikyan

The village of Tavshut is located in the Shirak region in north-western Armenia, about 5 km south of the Armenian-Georgian border. Initial excavations at the Tavshut archaeological site were carried out in 2018-19 by Sepasar expedition under the control of Dr. Larisa Yeganyan from Shirak Regional Museum. Two Early Bronze Age burials dated by ¹⁴C analysis to the Middle Bronze Age (second half of 3rd millennium BCE). (Tomb 1 and Tomb 2) were excavated in the 2018-19 season. These tombs were pit inhumations surrounded by stone cromlechs, and covered with capstones each containing a single individual with fragmented vessels. The description of Tomb 1 in the present publication is based on L. Yeganyan's field report.

- I14813/ Tavshut-Tomb2 (Bagheri Chala) (petrous bone), genetically male.

Noratus Necropolis

Contact: Ashot Philiposyan

An archaeological expedition led by A. Philiposyan excavated 26 burials near Noratus, located on the western bank of Lake Sevan. The burials mainly date from the Middle Bronze Age (Sevan-Artsakh culture) to the Kingdom of Van (Urartu). The Middle Bronze Age examples are mostly pit burials, while burials of the Late Bronze and Iron Age are of the “stone cist” type. They are surrounded by cromlechs. The burials are oriented mainly from east to west. In the burial chambers, which contain both individual and group burials, the skeletons lay in the fetal position, with women placed on their left side and men on the right.

- I18479/P5808 Noratus; Tomb 24; LM culture; LBA-3 (petrous bone), genetically female.
- I18467/ P5778 Noratus; Tomb 19; LM culture; LBA-2 (petrous bone), genetically female.
- I18468/ P5779 Noratus; Tomb 1; LM culture, EIA-1 (petrous bone), genetically male.
- I18469/ P5780 Noratus; Tomb 10; EIA-2 (petrous bone), genetically male.

- I18470/ P5781 Noratus; Tomb 1; LM culture, EIA-1 (petrous bone), genetically male.
- I18472/ P5783; Noratus; Tomb 21; LM culture; LBA-2 (petrous bone), genetically female.
- I18481/ P5810; Noratus; Tomb 1; LM culture, EIA-1 (petrous bone), genetically male.
- I18486/ P5815; Noratus; Tomb 19; LM culture; LBA-2 (petrous bone), genetically male.
- I18487/ P5816; Noratus; Tomb 20; LM culture; LBA-1 (petrous bone), genetically female.
- I19321/ P5852; Noratus; Tomb 1; LM culture, EIA-1 (petrous bone), genetically male.
- I19323/ P5854; Noratus; Tomb 18; LM culture; LBA-1 (petrous bone), genetically male.
- I19324/ P5855; Noratus; Tomb 3; LM culture, EIA-2 (petrous bone), genetically female.
- I19325/ P5856; Noratus; Tomb 21; LM culture; LBA-2 (petrous bone), genetically male.
- I19326/ P5857; Noratus; Tomb 4; LM culture; LBA-3 (petrous bone), genetically male.
- I19328/ P5859; Noratus; Tomb 21; LM culture; LBA-2 (petrous bone), genetically female.
- I19329/ P5860; Noratus; Tomb 19; LM culture; LBA-2 (petrous bone), genetically male.
- I18483/ P5812; Noratus; Tomb 4; LM culture; LBA-3 (petrous bone), genetically female. mother.I18276
- I19322/ P5853; Noratus; Tomb 3; LM culture, EIA-2 (petrous bone), genetically female.
- I19327/ P5858; Noratus; Tomb 2; LM culture; LBA-3 (petrous bone), genetically male.
- I18478/ P5807; bur 21-7; (2) P5861; bur 15 (petrous bone), genetically male.

References: (215-219)

Nerkin Getashen Cemetery

Contact: Ashot Philiposyan

The Nerkin Getashen cemetery (sometimes called the “Demer” necropolis) is located on the south-western shore of Lake Sevan, and was first investigated by archaeologist Gedeon Mikaelyan in the 1960s. From 1989-1991 the archeological expedition of the Institute of Archeology and Ethnography of the National Academy of Sciences of the Republic of Armenia excavated 40 tombs in the preserved part of the necropolis. The excavated burials are dated to the XXI-IX centuries BCE. The burials are partially surrounded by stone cromlechs. The orientation of the tombs varies, with some tombs having an east-west orientation and others a north-south orientation. Tombs containing individual and collective burials have been excavated. In the burial chambers, the skeletons lay in the fetal position with women placed on their left side and men on their right. Within the group burials, skeletons were sometimes found in the sitting position.

- I15732/2665; Nerkin Getashen; Tomb 23; LM culture, LBA-2 (petrous bone), genetically male.
- I15733/2664; Nerkin Getashen; Tomb 1; LM culture, LBA-2 (petrous bone), genetically male.
- I15734/2663; Nerkin Getashen; Tomb 23; LM culture, LBA-2 (petrous bone), genetically female.
- I15749/2627; Nerkin Getashen; Tomb 4; LM culture, LBA-3 (petrous bone), genetically female.
- I15729/2668; Nerkin Getashen; Tomb 4; LM culture, LBA-3 (petrous bone), genetically female.

- I15730/2667; Nerkin Getashen; Tomb 11; LM culture, LBA-2 (petrous bone), genetically female.
- I15748/2628; Nerkin Getashen; Tomb 7; LM culture, LBA-2 (petrous bone), genetically female.
- I15750/2626; Nerkin Getashen; Tomb 8; LM culture, LBA-2 (petrous bone), genetically female.
- I15731/2666; Nerkin Getashen; Tomb 11; LM culture, LBA-2 (petrous bone), genetically male. Son.I18166.

References: (220-227)

Sarukhan Cemetery

Contact: Ashot Philiposyan

The Sarukhan cemetery is located in between the Sarukhan and Karmirgyugh settlements of Gavar District of the Gegharkunik Province of the RA. In 1984-86 an excavation led by archaeologist A. Philiposyan, excavated 17 tombs here, which generally date to the XV-VI/V centuries BCE. Burials are stone cists with an east-west orientation. Tombs containing individual and group burials were excavated. In the burial chambers, the skeletons lay in the fetal position, with women placed on their left side and men on the right.

- I20440/P6643; Sarukhan; Tomb 6; LM culture, LBA-3 (petrous bone), genetically female.
- I20443/P6661; Sarukhan; Tomb 3; LM culture, EIA-2 (petrous bone), genetically male.
- I20436/P6639; Sarukhan; Tomb 4; LM culture, LBA-2 (petrous bone), genetically male.
- I20439/P6642; Sarukhan; Tomb 9; LM culture; EIA-2 (petrous bone), genetically female.
- I20441/P6644; Sarukhan; Tomb 12; LM culture; IA-2 (petrous bone), genetically male.
- I20444/P6662; Sarukhan; Tomb 5 Achaemenid period (petrous bone), genetically male.
- I20437/P6640; Sarukhan; Tomb 14; LM culture, LBA-3 (petrous bone), genetically female.
- I20438/P6641; Sarukhan; Tomb 8; LM culture, EIA-2 (petrous bone), genetically female.
- I20442/P6645; Sarukhan; Tomb 17; LM culture, EIA-2 (petrous bone), genetically female.

References: (215, 220, 228, 229)

Lchashen cemetery (LBA)

Contact: Pavel Avetisyan

Lchashen cemetery is spread on the eastern side of the village with the same name, in close proximity to the Lchashen fortress. It was covered by the waters of Lake Sevan until 1950 and was discovered after the drainage of the lake. Systematic excavations started in 1955 in an expedition led by H. Mnatsakanyan and were completed in 1975. A total of 231 tombs were excavated, some representing “royal graves” containing chariots including military chariots, and many unique examples of bronze miniature sculptures. The excavations restarted in 1980s led by L. Petrosyan and were continued until 2006, uncovering about 235 graves. The earliest burials are attributed to the Phases I and II of the Middle Bronze Age; there are also graves with materials characteristic of the Phase III of the Middle Bronze Age. However, the majority belong to Phases I and II of the Late Bronze Age. The chambers of the graves of the Phase I of the Late

Bronze Age are mainly dug into the sediment. The chambers of the burials of the Phase II of the Late Bronze Age are represented by cist graves, and are mainly individual burials, although several are group burials. This study analyzes materials of the graves of Lchashen I cemetery (excavated between 1980-1990), and burial № 229 from Lchashen II (2006).

- I18166/3315; ? 19; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18167/3316;15; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18168/3317; 1, burial 5; Lchashen; LM culture; LB-2 (petrous bone), genetically male.
- I18267/3318; 15/013; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18269/3320; 9; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18270/3321; 7, burial 9; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18271/3322; 4; Lchashen; LM culture; LB-2; (petrous bone), genetically female.
- I18272/3323; burial 8/2; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18273/3324; 14; burial 10; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18274/3325; 229; Lchashen; LM culture; LB-3 (petrous bone), genetically female.
- I18275/3326; 5, burial 19 (or 18?); Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18276/3327; 44105; Lchashen; LM culture; LB-2 (petrous bone), genetically male.
- I18277/3328; burial 3/2; Lchashen; LM culture; LB-2 (petrous bone), genetically male.
- I18278/3329; burial 17/6; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18279/3330; bur 916/8; Lchashen; LM culture; LB-2 (petrous bone), genetically female.
- I18280/3331; 13, burial 18; Lchashen; LM culture; LB-2 (petrous bone), genetically female.

References: (230-232)

Karashamb Cemetery

Contact: Pavel Avetisyan, Varduhi Melikyan

The Karashamb cemetery is situated 1.6 km south of the village Karashamb, in the Kotayk Province, on one of the terraces of the right bank of the Hrazdan River gorge. Today, the preserved segment of the necropolis occupies an area of about 3.5 hectares and is only a fraction of the original burial field. Systematic archaeological excavations occurred in 1981-1984 and again in 2009-2015. Over 1500 tombs have been recorded, dating from the Middle Bronze Age through the Iron Age II (the last quarter of the III millennium BCE to the second quarter of the I millennium BCE). The tombs are represented by round cromlechs and the majority contain single interments, although there are also some group burials. The deceased were placed either on their right or left side and the remains are in their anatomically correct position, but there are also tombs in which the remains were placed into piles in various locations of the burial chamber. In the later burials, most skeletal remains are incomplete, missing various skeletal parts.

There are also tombs which contain burials from multiple periods. These types of burials can be divided into two main categories: The first consists of tombs where the second (later) burial was placed within the fill of the tomb and the original burial chamber remained undisturbed. In the second category are tombs from which the original burial, both the deceased and accompanying burial goods, were removed, and the second (later) burial was placed into the chamber along with the burial goods. In this case, the original (earlier) burial consisting of the haphazardly gathered skeletal remains and the damaged burial goods were reburied on top of the roof slabs of the chamber and covered with soil.

For this study, samples were analyzed from tombs dating to the various phases of the Late Bronze and Iron Ages. The majority of the submitted samples, particularly those excavated during the 2009-2015 seasons belong to the second and third phases of the Lchashen-Metsamor archaeological culture: LM II: Tombs No. 435, 436, 513, 549, 591, 592, 593, 595 (XIV - XIII centuries BCE) and LM III: Tombs No. 361, 362, 478, 482 (XIII-XII centuries BCE). The first phase of the Iron Age is represented by Tombs No. 542, 570, 571, 604, 606 (LM IVA: XII-XI/X centuries BCE).

In Tomb No. 444 burials derive from three different periods. The lower burial contained three skeletal remains with materials typical of the early stages of the second phase of the Lchashen-Metsamor complex (LM II: XV – XIV centuries BCE). The succeeding burial was represented by a single skeleton and pottery dated to the XI – IX centuries BCE (LM IVB). The upper (last) burial is represented by remains of 5 distinct individuals and materials dated to the first quarter of the VII century BCE and first half of the VI century BCE (LM VB).

- I16220/1910; 606-1; LM culture; LBA-2 (petrous bone), genetically male.
- I16217/1907; 10; LM culture; LBA-3 (petrous bone), genetically female.
- I19331/ P5939;1; LM culture; LBA-3 (petrous bone), genetically male.
- I19332/P5940;6; LM culture; LBA-3 (petrous bone), genetically male.
- I19333/P5941;38; LM culture; LBA-3 (petrous bone), genetically male.
- I19334/ P5942;1985; LM culture; LBA-3 (petrous bone), genetically male.
- I19335/P5943; 549; LM culture; LBA-2 (petrous bone), genetically male.
- I19336/P5944; 595; LM culture; LBA-2 (petrous bone), genetically male.

- I19337/P5945; 604; LM culture; EIA-1 (petrous bone), genetically female.
- I19338/P5946; 482; LM culture; LBA-3 (petrous bone), genetically female.
- I19339/P5947; 362; LM culture; LBA-3 (petrous bone), genetically female.
- I19340/P5948; P7868; Burial 513; LM culture (premolar tooth), genetically male.
- I19341/P5949; 592; LM culture; LBA-2 (petrous bone), genetically male.
- I19342/P5975; 478; LM culture; LBA-3 (petrous bone), genetically female.
- I19343/P5976; 606-1; LM culture; EIA-1 (petrous bone), genetically male.
- I19344/P5982; 591; LM culture; LBA-2 (petrous bone), genetically female.
- I19345/P5983; 5; LM culture; LBA-3 (petrous bone), genetically male.
- I19346/P5984; 2; LM culture; LBA-3 (petrous bone), genetically male.
- I19347/P5985; ?; LM culture; LBA-3 (petrous bone), genetically female.
- I19348/P5986; 435; LM culture; LBA-2 (petrous bone), genetically male.
- I19349/P5987; 570; LM culture; EIA-1 (petrous bone), genetically male.
- I19350/P5988; 361; LM culture; LBA-3 (petrous bone), genetically female.
- I19351/P5989; 436; LM culture; LBA-2 (petrous bone), genetically female.
- I19352/P5990; 593 M2; LM culture; LBA-2 (petrous bone), genetically female.
- I19353/P5991; 542; LM culture; EIA-1 (petrous bone), genetically male.
- I19354/P5992; 3; LM culture; LBA-3 (petrous bone), genetically male.

References: (233-236)

Keti Archaeological Complex (BA_IA)

Contact: Pavel Avetisyan

During 1969-1979 in the area of the Keti village three Early Bronze Age settlements and three graveyards in their neighborhood were recorded. In the area adjacent to the “Karakari sar” settlement one Early Bronze Age burial was excavated (Keti II, tomb № 6); in the necropolis of the “Gorner” settlement three (Keti III, tombs № 1-3); and near the Sghnakhner settlement in the cemetery “Karot hogher” five (Keti I, tombs № 4, 5, 7-9). All graves contain group burials with 2 to 7 individuals. In Burial № 6, double usage of the chamber is recorded. Besides the Early Bronze Age burial, two more individuals were placed in later periods. The materials from the Keti graves are characteristic of Phase I of the Kura-Araxes culture (3300-2900 BCE), with skeletal remains rarely found in their correct anatomical position.

- I17182/2821; Burial 6/1 (petrous bone), genetically female.
- I17183/2822; 4; (petrous bone), genetically male.
- I17184/2823; burial 8/2 (petrous bone), genetically male.
- I17308/2824; burial 4/6 (petrous bone), genetically male.

References: (237, 238)

The Black Fortress cemetery

Contact: Anahit Khudaverdyan

The cemetery was located near the Aleksandrapol tower in the city of Gyumri. All of the burials there appear to have been interments typical of the Late Bronze - Early Iron Ages (XIV–IX BCE) and oriented in an east-west direction (expeditions leader Sergei Ter-Margaryan). Intentionally interred remains of small animals were common. A female warrior was discovered in grave N 37 in Black Fortress necropolis (Khudaverdyan, 2012, 2014). The fracture of the left ulna was a parry (“night-stick”) fracture at about 7.6 cm from the distal end of the ulna. The left-sided predominant fracture means that during the combat, the woman had been most likely exposed to direct blows to the defensive shield (the power transmitted from the end of the shield to the ulna), or direct blows when the forearm was used to ward off the blow (Khudaverdyan, 2012, 2014; Kricun, 1994; Pretty and Kricun, 1989). Here skeletal remains are consistent with the assumption of her being a horsewoman.

- I18162/3162; 7; LM culture; LBA-3 (petrous bone), genetically male.
- I18163/3163; 39; LM culture; LBA-3 (petrous bone), genetically male.
- I18164/3164; 37; LM culture; LBA-3 (petrous bone), genetically female, adult.
- I18165/3165; 27; LM culture; LBA-3; (petrous bone), genetically male.
- I18248/3167; 6; LM culture; LBA-3; (petrous bone), genetically female.
- I18247/3166; 9; LM culture; LBA-3; (petrous bone), genetically female.

References: (232, 239-242)

Archaeological sites of the Teghut mining zone

Contact: Pavel Avetisyan, Suren Hobosyan

Dzori Gegh Archaeological Complex

The Dzori Gegh medieval village is located on the left bank of the Shnogh River, south of Shnogh village. It contains pottery fragments, metal artifacts, and engraved stone fragments. The complex was excavated from 2010-2012 during which the expedition uncovered fragments of Early Bronze Age structures, a cist grave dated to the XV-XIV centuries BCE, and early Medieval graves with tiled walls. The cist grave we analyzed contained a wide-mouth clay jar, two pots, and one bowl.

- I16120/2360 Dzorigegh; Tomb, LM culture, LBA-1 (petrous bone), genetically male.

Teghut Cemetery

In 2009, exploratory excavations were carried out in the southeastern part of Teghut village, in the Tkhkut area. Two slab stone tombs were excavated, which, according to the burial goods, date to the IX-VIII centuries BCE (№ 2009/1 and 2009/2). The burials contained clay vessels of various sizes, bronze rings, needle, and fragments of iron artifacts. In 2010, excavations were carried out on the territory of the kindergarten located near the Teghut School. Six slab stone tombs (№. 1-6) dated to the XIII-XII/XI centuries BCE were excavated; large clay vessels were found on the burial chamber floor of three of the excavated tombs. Human remains, placed either on the right or left side, were recorded in tombs No 4 and 5.

- I16554/2218 Teghut; tomb 1; LM culture; LB-3 (petrous bone), genetically male.

Bagheri Tchala Archaeological Complex

The Bagheri Tchala Archaeological Complex is located south-west of the village of Shnogh, on the left high bank of the Kharatanotsi Jur stream of the Shnogh River. Pottery fragments and building outlines were first noticed during the construction of a mine tailings dam. Subsequent excavations uncovered two winepresses and 4 jars of different sizes placed near one of the presses. Excavations undertaken in 2011 uncovered 38 tombs dated to the XII/XI-IX centuries BCE, which had an east-west orientation, and each was covered with 2-4 slabs. A notable feature of all the tombs was the presence of small wine jars in the burial chambers. These were placed within pits dug into the floor of the burial chamber. Along with the wine jars, there were clay vessels of various sizes, bronze and iron weaponry, bronze jewelry, as well as carnelian and paste beads.

- I14066/1065; 3 or 12; LM culture, EIA-2 (petrous bone), genetically female.
- I14588/1188; 14; LM culture, EIA-2 (petrous bone), genetically male.
- I14601/1203; 5; LM culture, EIA-2 (petrous bone), genetically male.
- I14602/1204; 7; LM culture, EIA-2 (petrous bone), genetically female.
- I14603/1206 LM culture, EIA-2 (petrous bone), genetically female.
- I14605/1207; 16; LM culture, EIA-2 (petrous bone), genetically male. Brother.I14619
- I14606/1208; 28; LM culture, EIA-2 (petrous bone), genetically male.
- I14618/1229; 22; LM culture, EIA-2 (petrous bone), genetically male.
- I14619/1230; 9; LM culture, EIA-2 (petrous bone), genetically male.
- I14620/1231; 21; LM culture, EIA-2 (petrous bone), genetically male.
- I14065/1064; 3 or 12; LM culture, EIA-2 (petrous bone), genetically male.
- I14621/ 1232; 25; LM culture, EIA-1 (petrous bone), genetically female. Mother.I14618
- I16216/1906; 7; LM culture, EIA-1 (petrous bone), genetically male. Son.I14065.son.I14066
- I14617/1228; 10; LM culture, EIA-1 (petrous bone), genetically male. Son.I14603.son.I14619

Bragdzor Cemetery

The Bragdzor cemetery is located south-west of the village of Shnogh, on the eastern foot of Mount Gugut. Eight Early Iron Age tombs (IX-VIII centuries BCE), all partially damaged, were excavated. The cist graves contained individual interments placed on the right or left side. The cist graves also contained clay vessels of different sizes, bronze jewelry, iron decayed daggers, and cornelian and paste beads.

- I16536/2216; 5; LM culture; EIA-2 (petrous bone), genetically male.
- I16553/2215; 6; LM culture; EIA-2 (petrous bone), genetically male.
- I16546/2213;1; LM culture; EIA-2 (petrous bone), genetically male.
- I16547/ 2214; 3; LM culture; EIA-2 (petrous bone), genetically male.

Bover Cemetery (EIA-Pre-Urartian period)

The Bover cemetery is located south of the village of Shnogh. A total of 61 tombs were excavated between 2009-2015, 58 dating to the IX-VIII/VII centuries BCE, two dating to the XII-XI centuries BCE, and one to the XV-XIV centuries BCE. Two to four stone slabs were used to cover the burial chamber, which have an east-west orientation. All the burials are comprised of individual interments placed either on the right or left side. The tombs contained various clay

vessels, including pots, jars, and single handled pitchers, as well as bronze bracelets, iron spears, single handled or handless wine cups, cornelian and paste beads. In several tombs, large pots, which possibly had originally been filled with wine, were in a pit dug into the eastern corner of the burial chamber. These pots were covered with flat stones fragments and the skull of the deceased was placed on top of the slab stones.

- I16116/2356; 51; Bover; Tomb 51; LM culture; EIA-1 (petrous bone), genetically female.
- I16117/ 2357; 7; Bover; Tomb 7; LM culture; Urartian period (petrous bone), genetically male.
- I16376/2355; 32; Bover; Tomb 32; LM culture; Urartian period (petrous bone), genetically male.

Bardzryal (Bardzrel) Archaeological Complex

The Bardzryal (or Bardzrel) shrine sits on top of a hill to the west of the village of Teghut. On the rocky slope of the hill, leading towards the south, there are five successive terraces, which have been reinforced with large granite retaining walls. In 2012-2013 and 2017, 107 tombs dated to the IX/VIII-VII centuries BCE were excavated. The tombs were heavily damaged during agricultural activities and some were completely devoid of archeological material. The cist graves contained individual instruments placed either on the right or left side, though some tombs contained only highly fragmented and poorly preserved human remains. The materials recovered from the tombs include clay vessels of various sizes, bronze jewelry, bracelets, iron weapons and tools, as well as cornelian and paste beads.

- I14054/1042; 104-1; LM culture, Urartian period (petrous bone), genetically male.
- I14057/1045; 93; LM culture, Urartian period (petrous bone), genetically male.
- I14051/1039; 32; LM culture, Urartian period (petrous bone), genetically female.
- I14052/1040; 12; LM culture, Urartian period (petrous bone), genetically female.
- I14053/1041; 76; LM culture, Urartian period (petrous bone), genetically male.
- I14055/1043; 79; LM culture, Urartian period (petrous bone), genetically male.
- I14056/1044; 67; LM culture, Urartian period (petrous bone), genetically male.

Pijut Archaeological Complex

The Pijut archaeological complex is located south-west of the village of Teghut, on the left bank of Dukanadzori Jur stream of the Shnogh River. The site was significantly damaged by land amelioration processes during which the medieval cemetery and various medieval buildings were destroyed. In 2010 material remains dated to the Early Bronze Age, the Late Bronze Age, the Early Iron Age, and the Hellenistic and Medieval periods were discovered. During 2014-2015 in the western, elevated part of the ancient settlement, 27 slab stone burials dated to VIII/VII-VI centuries BCE were excavated. The slab stone chambers, which were oriented east-west, were covered with 2-3 slabs. All tombs contained individual interments placed either on the right or the left side. In the southernmost part of the burial field, Early Bronze Age artifacts and fragments of stone buildings were discovered. Among the 1st millennium BCE tombs, a single, well-preserved tomb (№ 17) dated to the XXVII/XXVI-XXV centuries BCE . This tomb contained four clay vessels, a bronze earring, and paste beads.

- I17180/2819; burial 13; LM culture; (petrous bone), genetically male.

- I17181/2820; burial 11; LM culture; (petrous bone), genetically female, adult.
- I16219/1909; 4; LM culture (petrous bone), genetically male. Son.I17181
- I16191/1826; 8; LM culture (petrous bone), genetically male.
- I16193/1828; 25; LM culture (petrous bone), genetically male.
- I16194/1829; 26; LM culture (petrous bone), genetically male.
- I16195/1830; 13/2; LM culture (petrous bone), genetically female.
- I16537/2817; 4; LM culture (petrous bone), genetically female.

The Urartian period from the Teishebaini (Karmir Blur) necropolis

Contact: Hakob Simonyan

We present genome-wide data from 12 individuals from the Karmir Blur (Teishebaini) necropolis, dating to approximately 1100-600 BCE, adding to the four individuals previously reported. The group of monuments of Karmir Blur is located in the southwestern district of Yerevan, on the left bank plateau of the Hrazdan river (according to cuneiform sources of the VII century BCE, the Ildaruni River) in the Ararat valley. On the northern edge of the flat plateau, at the edge of the canyon of the Hrazdan river rises a hill on which in ancient times stood the citadel of the city of Teishebaini of the Urartian kingdom.



Fig. S 13. General view of the burial ground Karmir Blur from the east.

The excavations in Karmir Blur (Fig. S 13) started in 1939 and continued until 1971. The excavations uncovered separate parts of the citadel-palatial complex of the city of Teishebaini built by king Rusa II (685-645 BCE). Pre-Urartian settlement was also recorded. Three layers or horizons as well as separate burials were discovered, testifying to three construction phases of the Pre-Urartian Karmir Blur, dated from 1200-900 until the invasions of King Argishti I. After the fall of Teishebaini, the site continued to be occupied from the V-III centuries BCE.

In 2013-2016, an expedition led by Hakob Simonyan found and examined a section of the necropolis of the along the southern edge of which the Shirak — Argavand bypass road. On a plot of 400×20 m, 281 burials were examined, mostly of the same age as the Urartian city (Fig. S 13). The entire burial ground is completely covered with a layer of pebbles. The tombs are mostly earthen, with niches at the bottom of some. Also found were tombs with walls lined in the lower part with river pebbles or crushed tuff and basalt, and spacious burial halls of the nobility. Most of the burial chambers were surrounded by previously unknown peculiar structures - cromlech rings. Trenches were dug around the graves in the clay soil, which were filled with river pebbles in a clay solution. Women were buried lying on their left side with bent limbs, and men were buried on their right side. There was a widespread ritual of dismemberment (decarnation) and decapitation (beheading) of corpses, possibly of sacrificed slaves. In some burials, their number reaches three dozen; corpses were laid on top of each other in several rows, and the master lay in the center. Some skeletons were buried face down, with obvious signs of violence, as if they were killed and thrown into the grave.

- I11853/ KB15T3S3; Tomb no. 3, Skeleton no. 3, 2015 excavation (tooth), genetically female.

The tomb was surrounded with a belt-like cromlech (magic circle fence) of diameter 3.5m, which was formed by digging a trench into the virgin soil, and filling it with river pebbles fixed with clay solution. Located in the center of the cromlech, the grave pit was filled with earth. The river stones formed a kind of “stone armor” with a thickness of 60cm. Bones of sacrificial animals and people were found on the stone fill. At the bottom (at a depth of 50-90cm), at least nine dismembered skeletons (skulls) were found stacked on top of each other: young women and men from 20 to 25 years old. Grave goods included vessels of black and red, a copper/bronze bowl, bracelets, earrings, chains with sea cowries, fibula, needle, buttons, beads, rings, an iron sickle-shaped knife, dagger, spearhead, bracelet, processed agate and carnelian beads, and bone spinning wheel.

- I11855/ KB15T8S5; Tomb no. 8, Skeleton no. 5, 2015; KB15T8S6, Tomb no. 8, Skeleton no. 6, 2015 excavation (tooth), genetically female. On the south-east corner of the grave on a depth of 82 cm skull number 5 in upside down position was unearthed with a bronze chain near the back of the head.
- I13032/ KB15T8 L802/2; Tomb no. 8, Locus 802, 2015 (tooth), genetically female.
- I13031/ KB15T8 L802/1; Tomb no. 8, Locus 802, 2015 (tooth), genetically male, adult.

This tomb was surrounded with a belt-like cromlech 30cm high, made in a similar way as that of Tomb 3. Fifteen cm deep from the surface of the virgin soil, were black clay vessels and fragments of bones, “sacrificed” during the funeral rite. At a depth of 25-55cm was the skeleton of a “bodyguard” immured in a stone-clay solution. He was wearing typical Urartian white and blue beads, a bronze earring, a ring, and shell coins. At a depth of 55-105cm, in the southern part of the grave, at least 6 dismembered skeletons were found stacked on top of each other. In the case of SSSa11 / 160, I13031, Dr. Armen Martirosyan noticed a 2.5 cm diameter injury on the left side of the skull with smooth edges, indicating that the wounded man survived and lived for at least 3-4 years. In different layers of the burial were clay vessels of black and brown colors, bronze necklaces, bracelets, earrings, rings, beautifully processed agate, carnelian, glass, faience beads, and disconnectors. All these artifacts and rites are characteristic of the Urartian culture.

On clay vessels, along with Urartu pottery, traces of the local culture of the early Iron Age can in some cases also be traced.

- I13035/ KB15T20S2; Tomb no. 20, Skeleton no. 2, 2015 (tooth), genetically male.

The grave is the only one of the 281 excavated graves that was surrounded by a cromlech built from large river stones. Fragments of sacrificial pots, obsidian, and human bones were found in a grave pit at a depth of 10-40 cm. At a depth of 60 cm, there were the bones of a sacrificial lamb. At 60-90cm, two skeletons were found near each other: 20-25 years of age. The skeleton in the West (#1) lay on its back, slightly turned to the left, its right arm was bent to the pelvis (hip), the left arm was under the right arm of the skeleton in the East. The pelvis was almost completely separated from the body. In the right hand was placed an iron spear, and above it a copper/bronze military badge with a relief image of lions. Two iron daggers and an arrowhead rested on his ribs. The Eastern skeleton (#2) from which we obtained DNA lay on its back with its mouth open, its slightly bent arms folded on its hip in the shape of the letter L. Under the head there were the bones of a young sheep. Next to the skull was a bronze arrow. A broken iron knife was found between the skull and the vessel. A large bovine bone was found under the eastern wall of the grave pit, and a fourth iron knife was found below, with second iron arrowhead attached. To the south was a thick iron ring, which contained 2-3 cervical vertebrae of a small child (identified by anthropologist Armen Martirosyan). In the southern part of the chamber, the remains of a dismembered skeleton were uncovered under the feet of the skeletons. It is likely that both young men received injuries that dismembered their skeletons, plausibly as soldiers who died in battle as they were buried fully armed. During the funeral, there were sacrifices of animals and slaves. From under the skulls, there were small beads made of paste and cornelian, and under the skeleton, about 110 cm deep on the bottom, a bronze bowl with two long bones. In a niche in the wall, there was a small vessel, beside another small pot with a pipe-like neck, an iron ring and an exquisite iron hook.

- I3892/ 3, Tomb 7, Cranium 3; (2) 6, Tomb 7, Cranium 5? Left lower molar #3 (tooth), genetically male.
- I3890/ 1, Tomb 7, Cranium 1 (tooth), genetically female.

At a depth of 90-100cm, a female skeleton was found in flexed position, lying on her left side, with head to the North and legs bent. Her arms were bent at the elbows: the right arm at a right angle, and the left was raised up and placed under the head. Under her feet, on the southern edge of the grave pit, lay 3 disconnected skulls (skulls) one being the source of ancient DNA, and dismembered other bones (Fig. S 14). In all probability, they were slaves sacrificed during the funeral. On the floor of the burial pit were found black clay vessels, a copper/bronze bracelet, a ring, a pendant, beads made of faience, agate, and carnelian.



Fig. S 14 Karmir Blur grave 7.

- I3938/ 8, Tomb 32, Cranium 3, left lower molar #2 (tooth), genetically male.
- I3945/ 12, Tomb 32, left lower jaw-teeth (tooth), genetically female.

Bones of sacrificial animals and people, teeth, phalanges, fragments of broken black and red ceramics were found on the stone embankment up to a depth of 25cm. In the second layer, 40 cm deep, was the femur of a man. At a depth of 50cm, skull N1, half preserved, broken into many pieces, had the lower jaw missing. At a 65cm was skull N2, which was fragmentary and from a child. In the central section of the grave at a depth of 80-90cm, a skeleton of a male in fetal position lying on the right side was found (skull N3). The skeleton was in the northern section oriented to the west, incomplete, broken to many pieces. The chest was in a preserved anatomical state. The left wrist was bent in the elbow and stretched to the norths. Under the body is the right hand-parallel to the left, folded at the elbow. A sample was taken from the jaw. On the floor of the burial were 5 black-burnished vessels, a bone spindle wheel, an iron dagger, beads of Egyptian faience, of blue glass, cornelian, bronze pipe-shaped beads.

- I3944/ 15, Tomb 25, Cranium (tooth), genetically male.

Fragments of broken pottery, a bone spinning wheel, and bones of sacrificial animals and people were found on the stone embankment and in the upper layer of the burial pit. Two arm bones, the ulna and radius, belonged to an adolescent; the spinning wheel belonged to the adolescent who was sacrificed and buried with the master. At 90cm depth, a skeleton of a young man was found, buried in flexed position on his right side, with his head to the North. The hands are bent at the elbows and wrists so that the palms are in front of the deceased's face; we obtained DNA from this individual. On the floor of the burial pit were found black clay vessels, an iron arrowhead, spears with a narrow feather and an unclosed sleeve, a dagger, a large carnelian bead, and small white beads (from faience). On the floor were two clusters of ribs and fragments of animal bones.

- I16118/2358; 4; (petrous bone), genetically female.

- I16119/2359; 2/1 43102 (petrous bone) Armenia_Achaemenid_Hellenistic. Genetically male.

References: (215, 243-249)

Lori Berd necropolis (LBA, Late Urartu)

The Lori Berd necropolis occupies an area of several hundred hectares on a high plateau located between the Dzoraget and Urut rivers (the tributaries of Debed). The large cemetery in the neighborhood of the city of Stepanavan has been excavated since 1969 and continues to be studied, and span the period between the III millennium BCE to the VI-V centuries BCE. The settlement of Lori Berd includes layers belonging to the end of the Middle Bronze Age and the early phases of the Late Bronze Age.

Despite plundering, the great tombs of Lori Berd still contain archaeological materials of great importance including a large number of rich ornamented ritual vessels, beads of stone and precious metals, and other items. Some burials were secondary: the bodies were left in the open for a time, and then the bones were bundled and placed in the grave. It is also possible that the bodies of the deceased were exposed to birds of prey before being buried, potentially providing archaeological evidence for ancient Zoroastrian burial practice. After a certain period the bodies were decomposed or defleshed and secondarily buried.

Ritual dismembering of human skeletons is also registered in the Lori Berd site. Cut marks are V-shaped notches across the external surface of a bone. Ritual dismembering was a common occurrence in the Caucasus. In burials 105 and 107 only the right part of the individuals were included.

In this study burials № 105 and 106 are included, containing materials characteristic to the late Uratian phase, as well as samples from tombs № 5, 102, and 103, with remains of materials attributed to the Late Bronze Age Phase III (1250-1150 BCE).

- I13948/1823; 5; Lori Berd; LM culture; LBA-3 (petrous bone), genetically male.
- I16196/1831; burial 102; Lori Berd; LM culture; LBA (distorted tomb; petrous bone), genetically male.
- I13947/1822; 105; Lori Berd; Late Urartu; (petrous bone), genetically male.
- I13949/1824; 106; Lori Berd; Late Urartu; (petrous bone), genetically male.
- I15663/1825; 103; Lori Berd; LM culture; LBA (distorted tomb), genetically male.

References: (250, 251)

Harjis Cemetery

Contact: Pavel Avetisyan

The cemetery is located at the southern suburbs of the village with the same name, adjacent to the settlement containing layers of mid I millennium BCE. The area occupied by the site was intensively used since ancient time and the external features of the graves are not preserved. Some of the graves were excavated by O. Khnkikyan. Inside the chambers, with elongated quadriform shape, the skeletal remains were recorded in irregular anatomical position, together

with animal bones. Numerous archaeological materials uncovered from the graves are characteristic for the VII-VI centuries BCE.

- I18159/3147; 4; LM culture; Post-Uratian period; (petrous bone), genetically female.
- I18160/3148; 5; LM culture; Post-Uratian period; (petrous bone), genetically female.
- I18161/3149; 6; LM culture; Post-Uratian period; (petrous bone), genetically male.
- I18236/3144; 1; LM culture; Post-Uratian period; (petrous bone), genetically female.
- I18237/3145; 2; LM culture; Post-Uratian period; (petrous bone), genetically male.
- I18238/3146; 3; LM culture; Post-Uratian period; (petrous bone), genetically male.

Aghitu-3 Cave (Vorotan valley; Late Hellenistic)

Contact: Andrew W. Kandel, Boris Gasparyan, Nelli Hovhannisyanyan, Beatrix Welte

Excavations at Aghitu-3 Cave in the Vorotan valley focused on Paleolithic deposits inside the cave. The excavations also unearthed evidence of Bronze Age, Iron Age, Classical and Medieval occupations based on different styles of pottery present at the site. In front of the cave, the team discovered an undisturbed tomb from the Middle Classical period. This basalt construction contained the well-preserved remains of seven individuals, four of which were radiocarbon dated to the 1st century BCE. Associated grave goods included three silver coins (also from the 1st century BCE), bronze and iron objects, intact ceramic vessels, beads of glass and stone, preserved wooden hafts, and traces of a wooden base underlying the skeletons. Since the skeletons were numbered in the order removed, Individual 1 represents the uppermost, and Individual 7, the lowermost of the burials. 3 samples are included in this study.

- I1639/ Aghitu 3,2012, Tomb1, Individual 1 (petrous bone), genetically female.

Anthropological sex determination matches the genetic data. Tooth wear, the degree of ossification of the cranial sutures, the general postcranial ossification and characteristics of physical decline suggest an age at death of 20-30 years. Based on femur length, height is estimated at 1.56m. Many of the grave goods mentioned were associated with Individual 1, the last individual buried in the tomb. A coin found in this individual's mouth was minted during the reign of King Phraates III (70-57 BCE) or King Phraates IV (38-2 BCE). Given the range of radiocarbon dates, an attribution to King Phraates IV seems most likely.

- I1637/ AG3/1/20, Aghitu 3,2012, Tomb 1, Individual 2 (petrous bone), genetically male.

Osteological and genetic sex determination matched. The status of ossification of the cranial sutures, the maxillary sutures, the pubis' symphyseal surface, and the mandibular angle all support an age estimate of 50-65 years, the oldest individual of the tomb. Based on femur (M1) length, a height of 1.70 m is calculated. The burial of Individual 2 preceded Individual 1 based on the burial sequence and juxtaposition of the skeletons.

- I1636/ AG3/30; Aghitu 3 2012, tomb 1, individual 7 (petrous bone), genetically male.

Compared to the other skeletons, Individual 7 was poorly preserved. While analysis of the incomplete hip bone and cranium suggests a feminine individual, the genetic analysis indicates a male. Based on the state of ossification, an age in the early twenties (20-25 years) is likely, but body height could not be determined. Radiocarbon dates range from 173-93 calBCE (KIA-48942), while a coin found in this individual's mouth stems from the reign of King Gotarzes (95-90 BCE). The aDNA studies also show a parental relationship between Individuals 7 and 2. Based on the sequence of burial, dates, and coins, Individual 7 is interpreted as the father, and Individual 2, as his son.

References: (252, 253)

Yerevan-2 cave

Contact: Benik Yeritsyan

Yerevan 2 Cave was discovered and studied by archaeologist B.G. Yeritsyan in 1968. The site is located in the Hrazdan River canyon, at a distance of 300 m from Yerevan 1 Cave. It is a small cave with a height of 1.75m, 4m long and 3m deep and is located at 900-910m above sea level and 10-15m above the river. In 1968-1969, two flint flakes with traces of Mousterian style modification, were discovered inside the cave, as well as Middle Paleolithic obsidian core and tools and fossilized bones. Holocene humans remains were recorded by Yeritsyan during the 1973 excavation season, which belong to *Homo sapiens* and are represented by a lower jaw and vertebrae (*vertebra cervicalis* I, axis I). The individual's age is 20-30 years. The lower jaw preserves three teeth from both sides: M1, M2 and M3. In 1974 another isolated tooth was discovered, an upper first molar.

- I10252/ ARME_YERE2, 1968, sondage 5; (2) P7833, Burial 3, ind. 1 (probably Middle to Late Classical Period; tooth), genetically female.

References: (254-256)

Agarak Archaeological Complex

Contact: Pavel Avetisyan

The monument is located in the western part of Agarak village, on the western bank of the Amberd River. It occupies an area of more than 200 hectares, stretching from Agarak village to Voskehat village. The area of the volcanic tuff platform of the northern complex was excavated in 2001-2008 and 2012-2014. A multi-layered habitation was opened here by excavations. The ancient layers of the settlement date to the second (end of XXIX-XXVII/ XXVI centuries BCE) and final (first half of XXVII/XXVI-XXV centuries BCE) stages of the Early Bronze Age Kura-Araxes culture: Agarak Ia and Ib. The next period of settlement is represented by the materials of the last stage of the Middle Bronze Age (XVIII/XVII-XVI centuries BCE) - Agarak II. In the Late Bronze Age, a fence was built to protect this platform, most of which has been preserved (XVI/XV-XV/XII centuries BCE) - Agarak III. The complex was used for burials during the period of the Urartian Kingdom and a pot burial was found together with a rock-cut tomb. The pot burial contained an Urartian seal (VIII-VII/VI centuries BCE) - Agarak IV. In the VI/IV centuries BCE - IV/VI centuries CE, Agarak became a city where large structures and burials of this phase - Agarak V - were excavated. The next stage, Agarak VI - of the settlement is represented with materials of the V-XIII centuries CE with the remains of buildings. In the XII-XIII centuries CE, burials also took place within some parts of the medieval settlement, particularly in the area of the ruined early medieval structure. For this study samples were submitted from three of medieval period burials, which are dated to the XII- XIII centuries CE based on radiocarbon dating.

- I1659/AGL40; Agarak, burial n 21 (petrous bone), genetically female.

- I1660/ AGL36; Agarak, burial n 6 (petrous bone), genetically female.
- I1630/ AGR34C; Agarak, 2013, Tomb 5 (petrous bone), genetically female.

References(203, 257-259)

Bosnia-Herzegovina

Klakar (Neolithic (Sopot culture) and Eneolithic periods)

Contact: Dusan Boric

The site of Lanište in Donji Klakar is located near the town of Basanski Brod represents a low rising tell settlement with layers dating to the Neolithic (Sopot culture) and Eneolithic periods. It is found in a floodplain near the Sava River (Benac 1964: 40–42). The site was discovered at the end of the 19th century and at that time was investigated by Ćiro Truhelka from the National Museum of Bosnia and Herzegovina in Sarajevo (Truhelka 1906, 1914). In 1960, small archaeological excavations were conducted by Branko Belić. Human remains from this site consist of one whole skull with a mandible and a separate mandible. A tooth from the latter was included in the study.

- I19561/SK3 (premolar), genetically male.

Bulgaria

Dzhulyunitsa – Smardesh (Veliko Tarnovo; Early Neolithic)

Contact: Nedko Elenski

Age estimation of the infants was made by S. Alpaslan-Roodenberg.

Dzhulyunitsa-Smardesh is a multi-period site of approximately 10 hectares established on a terrace of the Middle Yantra river in north central Bulgaria. During excavations stretching from 2001 until today, graves of different periods have been discovered dating from the Early Neolithic to the Late Iron Age.

- I11134/ Grave 9 (petrous), genetically female, infant.

Uncovered in quarter 3610 at a depth of 76.79cm, this grave belongs to the Dzhulyunitsa II phase. The skeleton of a newborn was found on the surface of a brown layer. There are no traces of a grave pit.

- I11135/ Grave 10 (petrous), genetically male, infant.

Grave 10 was uncovered in quarter 3609 at a depth of 76.63cm. It belongs to Dzhulyunitsa II. Again no traces of a grave pit. The age of this infant is estimated at 40 weeks, estimation according to the ulnar bones (dry bone fetal measurements: (260)).

- I11270/ Grave 11 (femur fragment), genetically male, infant.

A burial, also attributed to Dzhulyunitsa II, was uncovered in quarter 3609 at a depth of 76.44cm. This infant's age is estimated at 38 weeks from his femur (dry bone fetal measurements: Fazekas and Kosa, 1978). The grave was partially disturbed by bioturbation having displaced the human bones. The skull has remained intact.

- I17981/ Grave 13 (petrous), genetically female, adult.

The grave of a young individual was excavated in district 3402. It belongs to the end of the Early Neolithic phase called Dzhulyunitsa IV. No grave pit was noticed. The skeleton was found in flexed position on its left side and was oriented southwest.

Yabalkovo (Southeast Bulgaria; Early Neolithic)

Contact: Krassimir Leshtakov, Vanya Petrova, Nadezhda Todorova

Yabalkovo, is a more than two hectare Neolithic flat site that was occupied at the turn of the 7th and 6th millennia BCE. Showing similarities in its material culture with the early Karanovo, it yielded the remains of 9 individuals including 7 adults and 2 children. Among them is a female aged 25-35 buried in a simple grave pit with an almost intact vessel as a possible grave good (burial 3) She was found on her right side in contracted position, oriented ESE-WNW, head facing north. Age at death was assessed based on dental evidence (261).

- I2528/Yaba 3; Yabalkovo No.3 (petrous bone), genetically female, adult.

References: (3, 261)

Malak Preslavets (Early Neolithic)

Contact: Krum Bacvarov

The site of Malak Preslavets is situated on the northeastern shore of Lake Malak Preslavets, less than 200 meters from the bank of the Danube River (Silistra District). It was partially excavated in 1985–86 by a team directed by Ivan Panayotov. Nineteen early Neolithic burials were found on the site's periphery; its unexcavated part is now flooded by the lake. The cultural deposit was disturbed by recent construction activities. The pottery assemblage mostly belongs to the Criş culture but certain vessel types of the Dudeşti period have been identified as well. Thirteen crouched inhumations were revealed, six on the right side and five on the left side; two more primary burials were disturbed and thus rendered unidentifiable. Two contexts seem to represent remains of secondary burials, and the rest could be either disturbed inhumations or secondary burials. No grave goods were recovered; however, some of the burials yielded animal bones and/or river clam shells. Most skeletal remains were assessed by physical anthropologists.

- I6354/ MP7; S27, burial 12, sample 7 (long bone), genetically male.

A juvenile (14–16 years old) buried crouched on the right side, with the head to northwest. This seems to be the most tightly flexed burial at Malak Preslavets, with the legs pulled up and hands in front of the face.

References: (262, 263)

Smyadovo (Northeast Bulgaria; Late Copper Age, Early Bronze Age)

Contact: Stefan Chohadziev, Bisserka Gaydarka

Smyadovo is a prehistoric site in Northeast Bulgaria consisting of a tell and nearby cemetery. The latter contained 32 graves with 36 individuals buried over a long period from the mid-5th millennium to the beginning of the 4th millennium calBCE. This corresponds in the local

chronology to the Late Copper Age and the Early Bronze Age. Three samples are included in this study

- I2428/ 37; 12-13, infans II (molar), genetically male. *Infans II* (12-13 years old)

The grave was found in sq.23 at a depth of 0.73 m. The skeleton was in a flexed position on the left side. The skull was highly fragmented, with missing upper jaw and half lower jaw. The long bones are well preserved. A stone shat-hole hammer axe and four sherds were deposited as grave goods. Dates to the Late Copper Age.

- I2180/Smyadovo 20, Grave 26 (molar), genetically female, adult.

The grave was found in sq.32 at a depth of 0.98 m from the surface. The skeleton was in a flexed position on the right side. Three flint artefacts, a bone tool, two ceramic vessels, 22 nacre beads, a lump of ochre and snail shells were deposited as grave goods. Dates to the Early Bronze Age.

- I2177/15 Grave 20C (molar), genetically male, adult.

The grave was found in sq.33 at a depth of 0.75 m. Five skeletons were found in the grave pit. The skeleton marked as 20C was stretched on his back. Four of the individuals, including 20C, were embraced in pairs facing each other. A silver spiral and a small lump of slag were deposited as grave goods. Dates to the Early Bronze Age.

References: (3, 264)

Merichleri – Kairyaka Necropolis (South Bulgaria; Bronze Age)

Contact: Stanislav Iliev, Victoria Russeva

During excavations in 2011-2012, Tumulus 1, which is located on a hill ridge on the left bank of the Maritsa River near the town of Merichleri, Haskovo region, was excavated. The tumulus is 32m in diameter and 2.5m in height. The stratigraphy of Tumulus 1 shows at least three periods of accumulation of mound deposit. Seven graves were investigated, dated from the last quarter of 4th - 3rd and 2nd millennium BCE. The primary grave N 7 presents cremated bones, later burials have been carried out with inhumation ritual. Graves of the individuals N 4 and 6 were placed in a wooden structure, which resembles a dwelling with double sided roof, covered with soil. Two samples (Merich 2/individual 5, and Merich 4/individual 6) were published previously . In this new study another individual was analyzed from this site:

- I8429/Grave 4 (petrous bone), genetically female, juvenile.

Individual N 4 was placed immediately above individual N 6 in the same pit (there is a 0.25 m thick layer between the two skeletons). The skeletal remains present a child of an early age, laid in a “hocker or flexed” position on its left side, oriented west-east. The skull and the feet are colored with red ocher. No grave goods were discovered associating the dead. The radiocarbon analysis dates the grave back to the beginning of 3rd millennium BCE.

References: (3, 265)

Sabrano (Nova Zagora; Early Bronze Age)

Contact: Volker Heyd and Ilia Iliev

A small part of the site of Sabrano (Nova Zagora region, South-East Bulgaria) was investigated in 2009 during rescue excavations related to the “Trakia” motorway construction (Site 12). This revealed Late Neolithic (late 6th – early 5th millennium BCE) pits, an Early Bronze Age (EBA) inhumation grave and an EBA ditch as well as 1st millennium BCE pits. The EBA grave contained 4 individuals buried in extended position (two adult – 1A and 1B, and two infants – 1C and 1D). The grave inventory consisted of 7 vessels and dates, due to two 14C dates to the time around 3000 BCE. We thank the directors of the excavations - Dr. Anelia Bozkova and Dr. Zhivko Uzunov – for kindly giving us access to this sample. One sample is included in this study.

References: (266, 267)

Mogila, Grave 25 (Yambol region; Early Bronze Age)

Contact: Volker Heyd and Ilia Iliev

The kurgan of Mogila (Yambol region, South-East Bulgaria), 3.20 m high and with a diameter of 37.60 m, was excavated in 2004. It yielded 30 graves, of which 10 can be classified as Yamnaya, dating to the Early Bronze Age. Grave 25 belong to the first phase of secondary graves, brought into the mound next to the central Yamnaya grave, no. 29, but without disturbing it, however stratigraphically above grave no. 28. The grave pit was rectangular, 1.9m long and 1.2m wide. It was covered by wooden planks, each 0.25m wide, found at a depth of 1.55m under the top of the mound. Except of the skull, of which however the jaw was preserved, the grave was undisturbed. The burial, orientated WNW (head)-ESE and placed on an organic mat, was laid out supine with flexed legs, which were later falling to both sides, creating a frog-fork position. No equipment but slight ochre traces. Anthropologically an adult (mature age) man. One sample is included in this study.

- I18801/Mogila grave 25 (molar), genetically male. Mature adult.

Reference: (268, 269)

Tell Kran (south central Bulgaria; Early Bronze Age)

Contact: Krum Bacvarov, Kathleen MacSweeney, Clive Bonsal, Vassil Nikolov, Desislava Andreeva

A small tell site of late Neolithic and Early Bronze Age date in Upper Thrace, with a base of 80 X 70 meters and 5 meters high. Eight jar burials of babies/fetuses were found under house floors or next to houses in the EBA III layers. Jugs and jars were re-used as burial containers. Eight jar burials were osteologically examined. Three of the babies were full term foetuses, one was about 32 foetal weeks, another was 36 foetal weeks, while two were slightly older and had perhaps lived for a few weeks. Two of the babies had been dismembered before being placed in the jars.

- I19455/Tell Kran 2009; grave 8, sample 36 (outside jar; long bone), genetically female.
- I19452/Tell Kran 2009; urn 6, sample 33 (long bone), genetically male.
- I19454/Tell Kran 2009; burial 8. spit 5, sample 35 (long bone), genetically male.
- I19451/ Tell Kran 2009; Urn 5, sample 32 (long bone), genetically female.

- I19453/Tell Kran 2009; burial 7, sample 34 (long bone), genetically female.
- I19456_d/Tell Kran 9; 4th removal, sample 37 (long bone), genetically male (Fig. S 15).



Fig. S 15 Micro-excavation of burial 9 from Tell Kran (Kathleen McSweeney & Krum Bacvarov).

References: (270, 271)

Nova Zagora (south central Bulgaria; Early Bronze Age)

Contact: Krum Bacvarov

Stratified site excavated in the late 1980s and early 1990s. The partially destroyed deposits measured ca. 1 m depth and revealed four “building horizons” dating back to the EBA III. Six jar burials of babies were found in association with house floors or between houses. Large pots ca. 30 cm high were re-used as burial containers. Only one jar burial was osteologically examined (Context G4). This contained the fairly complete remains of a full-term foetus, with some evidence of dismemberment.

- I19462/Nova Zagora, sample 43 (long bone), genetically female.

References: (270, 272)

Tell Ezero (south central Bulgaria; Early Bronze Age)

Contact: Krum Bacvarov

Prehistoric tell site measuring 200 X 145 m (base) and 10 m high. It was first excavated in 1952, and more recently by a joint Bulgarian-Russian project in the 1960s and early 1970s. It was occupied in the late Neolithic, the Copper Age and the Early Bronze Age. The contents of four jar burials were osteologically examined (Contexts 1, 2, 4 and 5). Context 4 contained two individuals. Three of the individuals were full term fetuses and two were about 38 weeks in vivo. Four of the babies displayed clear evidence of dismemberment in the form of cut marks at major joints.

- I19461/Tell Ezero; burial 5, sample 42 (long bone), genetically female.
- I19460/Tell Ezero, burial 4 (ind. 2). sample 41 (long bone), genetically female.
- I19457/Tell Ezero; burial 1, sample 38 (long bone), genetically male.
- I19459/Tell Ezero, burial 4 (ind. 1), sample 40 (long bone), genetically female.
- I19458/Tell Ezero, burial 2, sample 39 (long bone), genetically male.

Reference: (270)

Boyanovo (Mound 3; EBA)

Contact: Stefan Bakardzhiev, Ilia Iliev, Victoria Russeva

Mound 3 is one out of three tumuli situated near the village of Boyanovo, South-East Bulgaria, Thracian Plain, Tundzha river valley. The tumuli are studied in the 2010 archaeological season. They are situated on a rocky height North-East from the village, tumulus N 3 (N 6009 after the numbering in the Tundzha Project, held 2009-2015 years) being the most eastern one. It is 1.60 m height and has a diameter of 27.40 m in its basis. Its periphery is marked with a stone ring with an inner diameter of 8.20 m. Under the mound a rectangular pit was found, 3.8 m long, 3.10 m wide and 1.12 m deep, dug into the ancient soil surface and filled with stones. Under the stone filling, on the bottom of the pit three rectangular pits were excavated containing three burials, graves N 2-4. In grave N 2 bone remains from two skeletons and a single bone from third one were found. Graves N 3-4 contain skeletons of one individual each. Grave N 4 is the first one to be constructed, followed by grave N 3 and the last buried remains are the ones from grave N 2. All three graves are contemporaneous, separated from each other by a strip of stones. Skeletons are situated with skulls pointing West direction. Three samples are included in this study.

- I18792/Boyanovo 2010; Mound 3, Grave 1 (molar), genetically male.

Grave is a secondary burial, dug in the soil, which covers the stone construction. The skeleton was found in a supine position. Materials associate it to a later period. The skeleton presents pronounced masculine morphological features. The age is determined according to cranial suture closure as a late stage of age group Maturus - early Senilis, 55-60 up to 65 years. The development of DJD, characteristic for determined age is recorded on the vertebrae, shoulder and elbow joints. Changes on 5th lumbar vertebra could have been a result of infection. Fragmentary preserved dentition presents one tooth (upper right first molar) lost during life. One line of linear enamel hypoplasia on premolars points to an age of three to three and a half years. A mild form of *cribra orbitalia*, rare for the individuals in the group of aged males is

ascertained. As an inborn variation can be observed the fusion of neural arches of two thoracic vertebra.

- I18793/Boyanovo 2010; Mound 3, Grave 3 (molar), genetically female.

This skeleton is in supine position, with a small ceramic vessel near the dead. Morphological features on reduced skeletal fragments determine the sex as possibly female. After cranial suture closure the individual was a young adult of about 25-30 years. Relatively completely preserved dentition presents two molars affected by caries. Lack of *cribra orbitalia* and enamel hypoplasia are ascertained. Initial degenerative joint disease changes were found on scapulae (shoulder joints) and on humeri (elbows). These changes, combined with overdeveloped deltoid tuberosity on humeral bones point to a constant overloading of individual in everyday activity. On the frontal bone two defects of button osteoma were recorded.

- I18794/Boyanovo 2010; Mound 3, Grave 4 (molar), genetically male.

It is the primary and deepest burial, situated in the approximate center of the construction. The skeleton is on its back with flexed lower limbs. Two ceramic vessels are found close to the skeleton, one near the thoracic area, the other near the foot bones. Fragments from the skeleton present pronounced masculine morphological features. The age is determined at about 30-40 years after cranial suture closure and relief of pubic symphyseal surface. Partially preserved dentition presents advanced tooth loss. The left parietal presents two defects from button osteoma. DJD changes are registered on both ulnae (wrist joint). A periosteal reaction is ascertained on both tibiae, fibulae remaining intact.

References: (273-275)

Kapitan Andreevo (South Bulgaria; Bronze Age, Iron Age)

Contact: Stanislav Iliev, Victoria Russeva

The site presents a large pit complex, uncovered by rescue excavations in 2018. About 297 archaeological structures were unearthed dating from the Late Neolithic, Early Bronze Age (EBA), to the Early and Late Iron Age (EIA and LIA). The excavations yielded two graves, one dates to the Late Neolithic (structure 123.6), the other to the Early Bronze Age (structure 38). Human skeletons found inside are highly fragmented as a result of taphonomic changes. Most of the studied structures on the site are pits from the Iron Age forming a large area. 11 of them, all dated archaeologically to the Early Iron Age (EIA), contain human bone remains. Four pits include skeletons from one individual each, one from two, and another from three individuals. These skeletons are severely disturbed due to environmental influences after deposition of the body. One pit contains the incomplete remains of two individuals; note, the absence of certain parts cannot be explained by environmental processes. Remains from incomplete skeletons were found in three more pits, each presenting one individual. In three pits only single fragments from human bones were unearthed. 12 individuals were analyzed from this site:

Early and Middle Bronze Age

- I20182/Kap. Andreevo, Kyuchuk Chair, Pit 38 (petrous bone), genetically male.

Early Iron Age

- I20180/Kap. Andreevo, Kyuchuk Chair, Pit 28, Individual 1 (petrous bone), genetically male.
- I20181/Kap. Andreevo, Kyuchuk Chair, Pit 28, Individual 2 (petrous bone), genetically male.
- I19490/Kap. Andreevo, Kyuchuk Chair, Pit 28, Individual 3 (molar tooth), genetically male.
- I20183/Kap. Andreevo, Kyuchuk Chair, Pit 91.1 (petrous bone), genetically male.
- I20184/Kap. Andreevo, Kyuchuk Chair, Pit 95 (petrous bone), genetically female.
- I19493/Kap. Andreevo, Kyuchuk Chair, Pit 199 (tibia fragment), genetically female.
- I19494/Kap. Andreevo, Kyuchuk Chair, Pit 200 (molar tooth), genetically male.
- I19495/Kap. Andreevo, Kyuchuk Chair, Pit 204 (humerus fragment), genetically male.
- I19497/Kap. Andreevo, Kyuchuk Chair, Pit 226, Individual 2 (tibia fragment), genetically female.
- I20185/Kap. Andreevo, Kyuchuk Chair, Pit 284 (petrous bone), genetically male.
- I20186/Kap. Andreevo, Kyuchuk Chair, Pit 289, Individual 1 (long bone), genetically male.

Pit 28

Bone remains from three skeletons were recorded. The anatomical position of skeletons is disturbed through natural decomposition and post-depositional natural stratification. Bones are fragmented and some parts missing as a result of taphonomical changes. Reconstruction of the skeletal remains reveals that there were three bodies placed one over another: on the top is individual 1 recorded as a 16-18 years old juvenile in supine position. The underling skeleton (individual 2) is on its right side in flexed position. Arm bones suggest that hands were tied behind the back. The individual is anthropologically identified as a male of 30-40 years at death. On the left parietal bone of the skull, near to the sagittal suture a trepanation survived by this man is noted. The styloid process of the left ulna is affected by a healed fracture. The lowest skeleton (individual 3) is on its left side considering the bones of pectoral girdle and lower limbs, while the vertebral column and rib cage are on the back. Remains from the arm bones also raises the hypothesis that the arms could have been tied behind the back. The individual is identified as a 20 to 30 year old male.

Pit 38

This grave pit, dug into a sterile layer, contains a skeleton in flexed position on its right side, with the skull pointing west-northwest. The bones, although highly damaged due to soil action, are found in primary anatomical position. Anthropological investigation points to a male individual at about 18 to 20-25 years at death. Dentition presents traces of two lines of linear enamel hypoplasia (LEH) after two unfavorable developmental periods in childhood. In front of the chest area a bronze dagger is uncovered on which traces from a textile are preserved. In front of the facial area is small ceramic vessel.

Pit 91.1

A relatively complete skeleton is found in the south sector of the pit. The body is on the back, the extremely contracted limbs are slightly twisted to the right and the skull is pointing North-Northeast. This position suggests that the body was wrapped up in a sack. Anthropological investigation indicates a male individual of 18 to 20-25 years at death.

Pit 95

A relatively complete skeleton in flexed position on its left side. Anthropological investigation indicate a female individual of 35-40 up to 45 years at death. At least six teeth are lost before death. Vertebrae present changes due to degenerative joint disease.

Pit 199 Scattered remains from an incomplete skeleton of a newborn were found.

Pit 200

A mandibular fragment, possibly from an adult individual, was retrieved from a pit which was cut by several other pits.

Pit 204

Fragments of a femur, two cervical vertebra pieces, and a long bone fragment were found. These bones point to a juvenile of 6 to 7-9 years at death.

Pit 226

Bone remains from incomplete, fragmented skeletons of two neonatals: Individual 1 is a ca. 38-40 weeks old baby and individual 2 shows a development corresponding to a smaller infant of ca. 38 weeks.

Pit 284

A relatively complete human skeleton was uncovered together with a dog skeleton in the south sector of the pit. The unusual burial position indicates that the body might have been thrown in the pit; the skull was crushed around the time of death. Sex and age determinations show that this is a possible male adolescent individual of ca. 16-18 years old.

Pit 289.1

In this pit skeletal remains of two individuals were discovered. The uppermost skeleton (Individual 1) is incomplete. The skull is oriented to south-west. Investigated bones present advanced pathological changes possibly due to a severe infectious disease. The age is estimated between 25 and 40 years. The lower skeleton (Individual 2) misses skull bones, and its postcranial skeleton was partially preserved. It is a possible adult male.

Reference: (276)

Diamandovo (South Bulgaria; Early Iron Age)

Contact: Georgi Nekhrizov, Victoria Russeva

Destroyed grave from the 8th-6th century BCE. Various bronze ornaments were found. Crushed human bones and small parts of metal finds were collected. Anthropological material presents only single fragments from which at least three individuals can be identified – two adults and a newborn at about a full term gestational development. Scarce anthropological data point to possible sex identification of one of the adults as a female. One individual is included in this study:

- I19481/Diamandovo grave 1 (molar tooth), genetically female, adult. Isolated dental find probably from one of the adults.

Svilengrad, Site 26 (Southeast Bulgaria; Early Iron Age)

Contact: Georgi Nekhrizov, Victoria Russeva

Site 26 near Svilengrad comprises a large complex of 207 pits where rescue excavations were carried out during the years 2004-2006. The chronological distribution is as follows: 9 pits from the Early Bronze Age (EBA), 133 from the Early Iron Age (EIA), 52 from the Late Iron Age (LIA) and 13 medieval pits. The major period during which the complex was in use the Iron Age, mainly its early phase. One of the most important features constitute the human remains discovered in the pits. Entire skeletons or single human bones belonging to 22 individuals were unearthed in 19 pits. In most cases these are inhumations and there are only two examples of burned bones from adults. Anthropological studies reveal that 9 pits contained the remains of small children, often new-born or prematurely born. Sex determination was possible for six individuals, most of them are males. It is concluded that 14 pits belong to the Early Iron Age and 3 to its latest phase. Samples from two burials found in pits 165 and 166 are included in this study.

- I19487/ Svilengrad, Site 26, Pit 165 (femur fragment), genetically male, infant. In this pit, a cluster of three ceramic vessels dating back to the Early Iron Age and remains of a full -term new-born baby was discovered.
- I19488/ Svilengrad, Site 26, Pit 166 (femur fragment), genetically female, adult.

The archaeological finds in this pit date it to the Late Iron Age. An adult skeleton was found in anatomical order. Skeletal remains are relatively complete. The body was placed in a sitting position with the upper part (skull, arms, chest) leaning against the western wall of the pit, while the arms were lowered at the side of the body and the legs bent. Age at death was estimated between 30 and 40 years, anthropological data about sex are controversial. Dentition is affected carious found on three teeth, while two other teeth are lost before death. Articulation surfaces point to degenerative changes on the ulna and the tibia.

References: (277-279)

Stambolovo (Eastern Rhodopes; Early Iron Age)

Contact: Georgi Nekhrizov, Victoria Russeva

The site is located in the Eastern Rhodope Mountain, 4 km SW of the village of Stambolovo in SE Bulgaria. It consists of three tumuli situated on an elevated part of a hill ridge within a deciduous forest. The archaeological excavations were carried out during 2008-2009, revealing traces of burials (inhumations and cremations) from three different periods – Early Bronze Age (mid 3rd millennium BCE), Late Bronze Age (15th–14th century BCE), and the beginning of the Early Iron Age (11th–9th century BCE). Of special interest are the attested pithos burials from the first stage of the Early Iron Age. The human remains deposited in the pithoi were not found in an anatomical order. According to the anthropological study, in none of the pithoi a complete skeleton was attested. In some cases, bones of two individuals in one and the same burial were identified. The observed peculiarities allow to suggest that the pithoi contained reburied parts of the bodies after the flesh was decomposed. Deposition of incomplete human remains, or remains

of more than one individual characterize so-called unusual burials and is an often-attested practice in the Thracian necropolis. Two individuals are included from this site:

- I15844/M2/Grave 1 in Mound 2 (long bone), genetically female, adult.

Human remains were found near the bottom of the pithos (Fig. S 16). The pithos was situated lying on its side with the rim oriented north-west. Its upper side was highly fragmented and parts were mixed. Fragments from four to five vessels were uncovered over the pithos. It is possible that they were initially placed one on another. Among human bone fragments, there were an amber bead, a small bronze fibula and an anthropomorphic terracotta figurine. These finds helped to date the grave to the 10th – first half of the 9th century BCE. Age at death is estimated around 18 years according the dental remains.

- I15848/ Stambolovo M2/Gr4, Individual 1 (femur fragment), genetically female; young adult.

Grave 4 is severely damaged due to tree roots. The mouth of the pithos, oriented to the west, was closed with a large amphora-shaped vessel. Only a few limb bones were found in the pithos.

References: (280-282)



Fig. S 16 Stambolovo, M2/Grave 1 (Bulgaria)

Kazanlak (Yasenovo, Central Bulgaria; Late Iron Age)

Contact: Georgi Nekhrizov, Victoria Russeva

A large necropolis covering an area of about 5 sq. km is situated at the foot of the Stara Planina Mountains between the rivers Gabrovnitsa and Leshnitsa. This necropolis comprises about 375 tumuli, most of them comparatively small, which are partially destroyed by land cultivation. The barrows were registered, described, and documented during systematic archaeological surface surveys carried out in the years 2010-2012 for completion of an archaeological map of the Kazanlak valley. The necropolis is linked to Seuthopolis - the capital of the Odrysian state during the early Hellenistic era. The studied anthropological material is highly fragmented. Two samples are included in this study:

- I19479/Kazanlak M 3113-Gr2 (humerus fragment), genetically undetermined sex, adult.

In the central part of the barrow a ring of larger raw stones was discovered. It encircles a grave in which a skeleton was lying on the back. Skeletal remains are highly fragmented. For age determination, only one molar tooth was available which gave a rough estimation of age at death by observing dental molar wear pattern (between 20 and 40 years). Some skeletal features indicated to a male that was observed on the field in situ.

- I19480/Kazanlak M 3114-Gr2 (femur fragment), genetically male, adult (40-50 years).

A stone construction with a circle shape and a carefully built outer side was excavated in the central part of the barrow. There were no traces of a built inner side, so this construction was probably a stone mound with the shape of a segment of a sphere or truncated cone. The second grave is in a rectangular pit, dug in the middle of the stone construction. The skeleton belongs to a man lying on his back. Two vessels were found on the right of the head - an amphorae and a black-slurry Attic kantharos. An iron spear, a bronze and an iron fibula, and traces of a coniferous tree were the other discovered objects. Analysis of the artifacts gives a possible date of the grave in the last quarter of the 4th century BCE. The dead is identified as a male (pelvic bone features). Age at death was estimated between 40-50 years. Traces of spondylosis (degeneration of the intervertebral disks) were observed on the vertebrae. Dentition presents ante-mortem tooth loss (2 molars and 1 premolar), caries and abscess (1 molar). Bony reaction occurred in the maxillary sinus due to the bad oral health.

Reference: (283)

Rozovo (Central Bulgaria, Stara Zagora, Kazanlak; Late Iron Age)

Contact: Georgi Nekhrizov, Victoria Russeva

In this treasure hunters mound a brick built tomb was discovered and partially destroyed. It consists of an antechamber and a domed burial chamber. Above the entrance of the antechamber there was a wooden shed covered with laconic type tiles. The antechamber is a narrow room with a double-faced cover and dimensions of 1.30 x 0.90 m. The grave chamber has a diameter of 2.22 m and a height of 2.17 m. It is made of different sizes of mud bricks built up in 23 courses. The top of the dome is covered with a granite slab. Only a part of the skeleton of a 40-50-year-old man was found in the tomb chamber. By analogy with the previously discovered brick tombs

in the Kazanlak valley, it can be assumed that this tomb was built in the first half of the 3rd century BCE.

- I19500/Rozovo grave 1 (molar), genetically male, adult. Reference Georgi Nekhrizov, Meglena Parvin, Angel Grigorov. 2019.

Reference: (284)

Samovodene (Veliko Tarnovo; Medieval)

Contact: Nedko Elenski

The site of Samovodene lies some 28 kilometres away from the city of Veliko in present-day Bulgaria. Excavations at this site were carried out in the 1970's and 80's by Peter Stanev. The archaeological deposits in which most human skeletons were found date to the transition from Early to Late Neolithic. The site was part of the Starčevo culture and represents early farmers in the Yantra River Valley. One individual from this site was analyzed who belonged to a horizon representing the end of Bulgaria's Early Neolithic (5700-5600 BCE):

- I2525/S1-grave 1 (petrous bone), genetically and anthropologically male.

Young adult between 17-22 years old found in flexed position, oriented SE - NW. He lay on his left side, hands folded near his face. Occlusal surface of his upper and lower first molars was heavily worn probably due to hard food consumption. His bones were large and strongly developed. His height was calculated 167.4 cm. Above his left eyebrow, a 1.5 cm healed cut mark was observed (by Alpaslan-Roodenberg).

Reference: (285)

Ryahovets (Gorna Oryahovitsa; Medieval)

Contact: Ilian Petrakiev

Ryahovets is a medieval fortress situated 7 km north of Tarnovgrad (present-day Veliko Tarnovo), the capital of Bulgaria at that time, and 3 km west of today's town of Gorna Oryahovitsa. From 1985 until 1991 archaeological excavations were conducted at the site, resumed in 2015 and continue since then. During the season of 2017 grave 1 was unearthed in the northwest corner of square LIV4, 7.70 m NW from the center of a dwelling. The grave pit was dug into a dark grey colored layer with middle-sized stones, 0.40m below the current surface. Grave 2 was discovered in front of the outer north face of a fortress wall in square XXIV7 near the northwest corner of the medieval fortress of Ryahovets. The skeleton was buried in a sterile reddish layer, mixed with small and medium-sized stones which cover the rocky surface. Fragments from undecorated wheel-made pottery found near the skull do not allow to date the grave.

- I10548/Grave 1 (petrous bone), genetically female, juvenile.

The skeleton lying in flexed position was buried on an artificial terrace or slope. Its orientation was W-E. In the east corner of the grave pit a large flat stone was placed. The dead lay on the back following the Christian funeral rite, and had no associated grave goods.

Considering the stratigraphy, the grave seems to belong to the last period the fortress was in use, which was in the first 30-60 years of the 13th century. The child's estimated age is between 10 and 12 years.

- I17980/Grave 2 (petrous bone), genetically female, juvenile.

The burial is oriented approximately SW-NE. The lower part of her legs and the feet bones were missing, probably as a result of the construction of the fortress wall. The rest of the skeleton is somewhat in a flexed position and slightly turned to its right side. The age of the child is estimated between 5 and 6 years. This burial is probably from an earlier period.

Croatia

Koprivno (Koprivno kod križa, Croatia - Dalmatian hinterland; Middle Bronze Age)

Contact: Mario Šlaus

These are two large medieval necropolises that were excavated from 2002 to 2003. The first necropolis consists of 97 graves while the second - 70 meters to the west, contains 23 graves. Based on recovered archaeological finds both necropolises were in use from the 13th to the 18th century CE. The south-eastern part of the larger necropolis (called Koprivno kod križa) goes over a prehistoric stone mound. The base of the mound is oval shaped, 19.5 meters in radius and up to 1.4 meters in height. It contains one prehistoric burial (grave 85 A) in the shape of a stone trunk whose dimensions are 90 x 40 centimeters. In it are the remains of one individual who was buried in a flexed position with no accompanying grave goods. One sample is included in this study:

- I5073/KOP1-85A (petrous bone), genetically male.

This is a reasonably well preserved skeleton, osteologically and genetically determined as male. The skeletal remains are light brown in color and have well preserved cortical bone. Based on auricular surface morphology, teeth abrasion, and the presence of degenerative bone changes age-at-death was determined at between 50 to 55 years of age. The pathological changes noted in the skeleton are consistent with this determination and consist of osteoarthritic changes, mild to moderate in expression, on the cervical and thoracic vertebrae and on the right scapula.

References: (286-288)

Matkovići (Gomila kod Matkovića, Croatia - Dalmatian hinterland; Middle Bronze Age)

Contact: Mario Šlaus

Archaeological rescue excavations of this site were conducted in 2008. This is a tumulus located on a small hill about 200 meters south-west of the hamlet of Matkovići in Ravča. It has a circular base with a diameter of 22.5 meters, while its relative height is approximately 3.2 meters. The tumulus covered an area of 360 m². Archaeological excavations revealed that the tumulus consisted of dry stone wall radial structures, a semicircular dry stone wall and two prehistoric graves with stone slabs arranged in a circle around each of them. A partially preserved stone ring was present on the outer margin of the tumulus. In the central part of the tumulus, two prehistoric graves were found. The graves were oriented in a north/northeast-south/southwest direction. The graves were constructed in the shape of a stone trunk consisting of two longer and two shorter vertically placed rectangular slabs, with an irregular cover above them. A woman and two children were buried in the northern grave (Grave 1), and one man (Grave 2) in the southern grave. All of the deceased were buried in a flexed position. The pottery found in the rock sediment and layers date the tumulus to the transition from the Middle to the Late Bronze Age, which was later confirmed by the C14 analysis (Grave 1 between 1460 and 1310 BCE, and Grave no. 2 between 1380 and 1120 BCE - personal communication by Nela Kovačević Bokarica). One sample is included in this study:

- I5074/ MAT-1B; G 1B, 12-14; (2) MAT-1C; Gr 1C (petrous bone), genetically male.

This is a well preserved skeleton, osteologically and genetically determined as male. The skeletal remains are light brown in color, robust with well preserved cortical bone. Based on auricular surface morphology, teeth abrasion, and the presence of degenerative bone changes age-at-death was determined at between 45 to 50 years of age. In terms of pathological changes this skeleton exhibits hypoplastic defects on the crowns of maxillary and mandibular canines as well as on the mandibular incisors. Mild osteoarthritis in the form of osteophytes is present on both distal femurs. This individual also has a large, 18 x 10 mm well healed depression fracture on the right side of the frontal bone located approximately 25 mm superior of nasion. The fracture has an irregular floor with rounded margins.

Reference: (289)

Zavojane-Ravča (Velika Gomila, Croatia - Dalmatian hinterland; Middle Bronze Age)
Contact: Mario Šlaus

This is a prehistoric stone tumulus called Velika gomila (Big Tumulus) located between Zavojane and Ravča by Vrgorac that was excavated as part of archaeological rescue excavations on the course of the Adriatic motorway during 2008 and 2009. The tumulus has a circular basis 26 meters in diameter with a relative height of 4.6 meters. A grave in the form of a stone cist is located in the centre of the tumulus. It was constructed of two longer and two shorter vertically placed roughly carved stone slabs with a capstone covering them. From the western side it was supported by two more parallel vertically-placed stone slabs. The grave contains the skeleton of an adult male buried in a flexed position on his right side with his head to the east. On the surface of the capstone, in the central part, a heavy bronze ring was discovered. Above, and around the grave several broken pots were found, suggesting some ritual was performed following the burial of the deceased. The vessels belong to the Bronze age Posušje culture. One sample is included in this study:

- I5080/ ZAV1; Tumulus, Central Grave (petrous bone), genetically male.

This is a moderately well preserved skeleton, osteologically and genetically determined as male. The skeletal remains are light brown in color and have well preserved cortical bone. Based on auricular surface morphology, teeth abrasion, and the absence of degenerative bone changes age-at-death was determined at between 30 to 35 years of age. The most interesting feature of this skeleton is that a small stone projectile point, swallow-tailed in shape, was found in its thoracic area. The projectile point is finely worked with small retouching on both sides. There are, however, no perimortem injuries on the available ribs or vertebrae although it should be mentioned that this part of the skeleton is poorly preserved.

Reference: (290)

Vinkovci - Jugobanka (Vinkovci – Jugobanka, continental Croatia; Medieval)
Contact: Mario Šlaus

Because of intensive urbanization in the 1970's several large rescue archaeological excavations were carried out in the town of Vinkovci on an area of approximately 332 m² in the central part of the Tržnica tell, at the position of Robna kuća "Zvijezda", and on an area of 2.100

m² in the position of Hotel "Slavonija". The western part of the Tržnica tell, separated by a natural depression, was partially explored during rescue excavations at the position of the Business Building of Cibalae Bank (formerly Jugobanka), on an area of approximately 3.660 m². In the western part of the excavation area a Starčevo settlement with a larger number of pits and several graves was excavated. Several medieval inhumations, uniformly badly preserved, were also discovered in this area. One sample from these inhumations is included in this study:

- I1879/VINJ4a, Grave 7b (tooth), genetically male.

This is a very fragmented and poorly preserved skeleton genetically determined as male recovered from Grave 7b. Based on cranial suture and palatine suture obliteration, and teeth abrasion, age-at-death is determined as older than 45 years.

References: (291, 292)

Vinkovci – Zablaće (Middle Neolithic)

Contact: Maja Krznarić Škrivanko

Rescue archaeological excavations at the location by the Vinka factory, north of Vinkovci, at Vinkovačko Novo Selo - Zablaće were conducted in the period between 2014 and 2016. The largest lowland settlement of Sopot culture in the Vinkovci was discovered which stretched across an area of about 40 ha, testifying to the long standing habitation in one place, planned construction and maintenance of the settlement, building of dugout and above ground residential structures with furnaces and storage spaces. The central part of the large Sopot village that consisted of semi-dugout features and huts. Two large dugout structures located in the central and north-east parts of the excavated area were investigated.

Smaller dugout features gravitated toward these large dugouts. The discovery of two parallel canals in the north-south direction was important for gaining insight into the infrastructure of the settlement. Given that the canals were buried in the already earth-covered large working dugout, they were most probably later date structures that could be linked to above ground houses. For the time being, two aboveground features can be defined – the houses were oriented in a regular pattern with rectangular floor plans. The aboveground house that was fully uncovered measured 7 x 13 m and was positioned in the north-south direction. The second rectangular aboveground house was 7.14 m wide and only 8.58 m of its length was uncovered due to the fact that it extended outside the excavated surface. This house too had an almost symmetrically north-south orientation.

Intensive pottery production took place in the settlement given that there were at least 4 kilns in which pottery could be baked. Pottery material is most abundant category of finds. Although more than 40 Sopot settlements have been located to date in the Vinkovci region, the one at the site of Vinka is the largest and the only one where graves were discovered. This testifies to the density of the population in this area during the 5th millennium BCE. For now, mention can be made of a few Bronze Age and medieval pits. While surveying the area south of the excavated zone shards of medieval pottery were found. Three medieval waste pits and one hearth/kiln were investigated at the Vinka site which probably belonged to the periphery of the medieval settlement mentioned in medieval sources as Zablaće.

Graves were found for the first time on Sopot sites in the Vinkovci area. The graves were located between the houses in the area of trench 2. Grave 1 was buried in the already deserted dugout, grave 2 in the pothole and grave 3 in the working pit. All the deceased were in bent positions laying either on their left or right hips. The graves were without offerings, additionally confirming the assumption that there were no burial rituals.

- I7398/ VVINKA GR 1; Vinka, SII, Kv. C, grave nr. 3 (phalanx), genetically male.

A complete skeleton of an adult male (35-45 y). Sutural ossicles in the lambdoid suture. An additional cusp, a parastyle, on the buccal side of the mesiobuccal cusp of the second left maxillary molar. Two carious lesions and two abscesses on maxillary teeth and linear enamel hypoplasia on mandibular tooth. Marginal osteophytes on thoracic and lumbar vertebral bodies. Supracondylar processes on anteromedial surfaces of distal third of both humeri. Hyperplasia of the third rib, bifid fourth rib and flaring of the eighth rib.

- I7538/ VVINKA GR 3; Vinka, SII, Kv. A, grave nr. 2 (petrous bone), genetically female.

Mandible and postcranial remains of an adult female (35-50 y). Bilateral septal aperture. Osteoarthritic changes on both patellae and distal end of the left femur.

- I7399/ VVINKA GR 2; Vinka, SII, Kv. D, grave nr. 1 (petrous bone), genetically female.

A complete skeleton of a child (0-5 y). Metopic suture on the frontal bone and ectocranial porosity on parietal bone. *Cribrra orbitalia* in the right orbit.

References: (293-296)

Gornja Vrba – Savsko polje (Middle Neolithic)

Contact: Mario Bodružić

The archaeological site of Gornja Vrba – Savsko polje is located on the northern bank of the Sava River, about 2 km east of the center of Slavonski Brod. During several campaigns of archaeological excavations conducted from 2015 to 2017, about 80,000 square metres were explored, with remains dating from the Middle Neolithic to the Late Medieval period. Most of the archeological deposits represent the remains of a Middle Neolithic settlement, preliminary attributed to the Sopot culture (5500–4500 BCE), but this has not yet been confirmed through AMS dating. Furthermore, excavations revealed the existence of rectangular and trapezoidal structures, aligned north–south. These comprised evenly distributed post-pits, outer walls in the form of narrow channels containing preserved postholes and elongated side pits flanking the structures on their western and eastern sides. The dimensions of these structures (likely houses) varied from 10–18 m in length and 6–9 m wide. Structures of identical spatial distribution, size and assumed appearance formed the basis of the LBK settlements in the Transdanubian area, and so this site is particularly interesting in the context of further study of LBK influence on the formation of Middle Neolithic cultural complexes in the area bounded by Sava and Drava rivers.

A total of nine Neolithic burials were found during excavations at the site. All graves were located within the Neolithic settlement, as part of stratigraphic units such as side pits flanking the

houses or in pits that (in the absence of human remains) would be interpreted exclusively as waste pits.

- I18827/3864, grave 5 (petrous bone), genetically male.

Burial 5 was found in the northeastern part of the investigated Neolithic settlement (Fig. S 17). The grave-fill was defined after the removal of a larger filling or layer located northeast of one above-ground structure / house. The deceased was laid in a shallow cut, oval-shaped in plan, with slightly concave bottom, oriented in NE-SW direction. The skeleton of younger adult individual (18-20 y) was well-preserved, although fragmented, and laid in a crouched position, turned on his left side, with the head and chest facing east. His arms were crossed over his chest, next to his body, and his legs were bent at the knees and bent along his body. In addition to the remains of the deceased (as in other burials at the site), no other remains of funeral practices such as grave goods have been found. Linear enamel hypoplasia on the anterior teeth.



Fig. S 17 Grave 5.

References: (297-300)

Đakovo – Franjevac (Chalcolithic)

Contact: Jacqueline Balen

The Đakovo-Franjevac site is located on the route of the A5 motorway, at an elevated position of about 106 m above sea level. The terrain descends from the west and south sides of the investigated plateau towards Franjevački rit, a tributary of the river Jošava that is only

occasionally flooded. The Archaeological Museum in Zagreb conducted protective excavations at the site during 2007. The highest concentration of movable archeological finds attributed to the Copper Age and the Middle Ages were found on the southeastern slope. The analysis of movable material established that the position was used by the bearers of the Kostolac culture during prehistory, and such an attribution was confirmed by 14C dates falling in the range from 3340 to 2840 BCE.

Archaeological research has defined a longer settlement of the bearers of the Kostolac culture at the site. Waste pits of various shapes and sizes, bell-shaped pits used to store food, narrow long canals that probably served as the foundations of fences, and several workspaces were found. No concrete remains of above-ground structures have been found, but a large number of pillars and a considerable amount of wattle and daub fragments suggest the existence of these types of structures as well.

The largest number of movable finds at the Đakovo-Franjevac site consisted of fragments of pottery – different types of bowls and pots as well as cups. In addition to the standard forms of vessels, there are square vessels and a number of objects possibly attributed to the cult purpose. Based on the remains found, the existence of a fertility cult is assumed. In addition to pottery, a significant amount of chipped and polished stone tools was found at the Đakovo-Franjevac site. The results of the analysis suggests that the processing of raw materials did not take place on site. Six copper finds were also found at the site: three awls, two fragments that were probably also parts of an awl, and one fragment in the shape of a plate with three rivets that was probably part of a dagger. Analysis of the composition of copper objects showed that they contained arsenic.

The economy and everyday life of the Kostolac population at the site is evidenced by the large amount of animal bones and plant remains. Among animal remains, the largest percentage is occupied by pigs (33.76%) and cattle (21.6%) and small ruminants such as sheep, goats and deer. Paleobotanical analyzes showed that the Eneolithic population consumed single-grain wheat, barley, millet, flax, blackberry, lentils, black elderberry, etc., or a wide range of cultivated and wild plant species.

- I20502/ P6575; SJ 939, U-639/2 (petrous bone), genetically male.

A complete skeleton of an adult male (20-35 y) was found in a pit, together with the remains of two pigs. The formation of periostitis was recorded on the long bones. Metopic suture on the frontal bone and additional ossicle on either side of the lambdoid suture. Spondylolysis in the fifth lumbar vertebra. Striation along the medial side of the shaft of both tibiae, on the frontal side of both fibulae and along the shafts of both femora. Healed *cribra orbitalia* and new bone formation in the left orbit. Ectocranial porosity on the frontal bone, on both parietal bones and the occipital. Bipartite left patella.

Reference: (301)

Donja Ostrvica – Pasičine (Bronze Age)

Contact: Mario Novak

These excavations were carried out in 1982 in Donja Ostrvica – Pasičine near Omiš at the location of the Velika gomila stone barrow (T-1). The barrow is oval-shaped with a diameter of

19.4 m and up to 2.4 m in height. During the excavation six graves were registered and studied: graves 1 and 2 are dated to the Bronze Age, while other burials (graves 3-6) are dated to the Middle Ages/Early Modern Period.

- I18712/ 3772; Velika Gomila T. 1 Gr.1 (petrous bone), genetically male.

Grave 1 was located nearest to the center of the barrow; it was in the shape of a stone chest and covered by a massive stone slab. There were no grave goods within the burial chamber. The skeleton was found in crouched position lying on its right side with the head to the west. The complete cranium without the maxilla (but including the mandible) of an adult individual (45+ y) was available for the analysis. Linear enamel hypoplasia is present on the mandibular canines, two carious lesions on mandibular teeth.

Reference: (302)

Bogomolje (Bronze Age)

Contact: Mario Novak

The excavations conducted in 1981 near the village of Bogomolje on the island of Hvar revealed the presence of the stone barrow at the Glava maslinova site (T-3). The barrow was elliptic in shape with a diameter of 15.9 m and was situated on the top of the hill. Three graves were excavated in the barrow (graves 1, 2, and 3), one older (grave 2) and two younger ones (graves 1 and 3).

- I18748/3822, T-3, grave 1 (petrous bone), genetically male, adult.

This grave was later dug in the very barrow, first by moving the stones aside and then building sides without mortar, and was finally covered by stone slabs. The bottom of the grave was filled with pebbles. There were no grave goods within the burial chamber. The partially preserved skeleton of a robust adult individual was lying on its left side in crouched position (only the skull and the trunk have been registered). Most of the neurocranium was available for the analysis. Antemortem healed blunt force trauma is present on the right side of the frontal bone, healed porotic hyperostosis on both parietal and the occipital bones.

Reference: (303)

Cetina Valley (Early Bronze Age)

Contact: Mario Novak, Mario Carić

Systematic archaeological excavation of numerous prehistoric sites located around the source of the Cetina River were conducted between 1953 and 1968. All presented graves/skeletons are dated to the Early Bronze Age, i.e. the Cetina culture (ca 2200-1600 BCE).

During the campaign carried out at the Rudine site in 1958 stone barrows 19 (T-19) and 21 (T-21) were completely excavated (among several others). T-19 was oval-shaped with a diameter of 17.1 m reaching in height up to 2.4 m. It contained four burials: three in graves and one in the stone deposit. Numerous pottery fragments were found in and around the barrow suggesting

some kind of ritual feasts. T-21 was also oval-shaped with a diameter of 13.6 m reaching in height up to 1.2 m. The tumulus contained a central grave in the shape of a stone chest.

Nine stone barrows were completely excavated during the campaign conducted at the Preočani site including the Luića gomila or barrow 93 (T-93). This is an oval-shaped stone barrow with a diameter of 12.5 m reaching in height up to 1.1 m. The barrow contained one grave in the shape of a stone chest covered with a large square stone slab. The grave contained the remains of two individuals lying in crouched position with some bones belonging to the third individual moved out of the grave (primary skeleton). Three pottery fragments were found inside the grave.

- I18747/3821, Rudine, T-19, grave 1 (petrous bone), genetically male, old adult.

This burial was located on south-western side of the barrow. The skeleton of an older adult individual was found in the stone deposit lying on its back with the arms and legs stretched. The bones are very fragmented due to soil/stone pressure. There were no grave-goods associated with this skeleton. Only the partially preserved neurocranium was available for the analysis. Healed trepanation aperture on the right side of the frontal bone, healed porotic hyperostosis on the frontal and the right parietal bones.

- I18746/3820, Rudine, T-19, grave 4 (petrous bone), genetically male.

Grave 4 was found in the middle of the barrow, eastern of grave 3. Based on the position it seems that this is the earliest burial at this site. It was in the shape of a stone chest and covered by two stone slabs. The skeleton was nicely preserved, in crouched position lying on its right side with the head to the south-east. This grave was used at least twice with the presented individual being its last user. Linear enamel hypoplasia on the anterior teeth.

- I18088/3946, Rudine, T-21, central grave (tooth), genetically male.

The skeleton of a very robust adult individual (25-35 y) was found in crouched position on its side. Only the facial region (including the mandible) was available for the analysis. Healed *cribra orbitalia* is present in the right orbit, linear enamel hypoplasia on the anterior teeth.

- I18752/3826, Preočani, T-93, individual A (petrous bone), genetically male.

This is an adult individual found lying on the right side. Very few cranial fragments were available for the analysis.

- I18745/3819, Preočani, T-93, individual B (petrous bone), genetically female.
Very few cranial fragments were available for the analysis.

Contact: Anna Osterholtz

- I11843/u-25, grave 1; u-28, grave 1 (tooth), genetically male.
- I19016/u-37b (tooth), genetically female.
- I19017/u-37c (tooth), genetically female.

- I19019/u-37e (tooth), genetically female.
- I19020/u-37f (tooth), genetically female.
- I19021/u-62 (tooth), genetically female.
- I19022/u-64 (tooth), genetically female.
- I19025/u-61c (tooth), genetically male.
- I19026/u-61d (tooth), genetically male.
- I1907/u-61e (tooth), genetically female.
- I19029/u-61g (tooth), genetically male.
- I19030/u-61h (tooth), genetically male.
- I19031/u-61i (tooth), genetically male.
- I19032/u-61j (tooth), genetically male.
- I19035/u-15 (bone), genetically male.

Reference: (302)

Bezdanjača Cave (Middle/Late Bronze Age; 1500-800 BCE)

Contact: Siniša Radović

Bezdanjača Cave is located on the Vatinovac hill, near Vrhovine, in the Lika region of Croatia. The cave was first recognized as a prehistoric site in 1964 and the archaeological excavations began in 1965. In total, 1176 m of the cave system has been explored, of which only the first 190 m are of archaeological interest. The difference in height between the highest and the lowest point of the cave is around 200 m. The entrance to the cave is located at 740 m above sea level, and measures 31 m tall. At its base, the entrance bifurcates into two main branches, namely the western channel and the eastern channel. The cave is naturally hidden and difficult to access, which suggests that it has lain undisturbed since the cessation of its use by prehistoric communities.

Just over 70 m from the entrance of the eastern channel, archaeologists excavated the greatest number of archaeological deposits, which revealed the presence of several rather well-preserved human skeletons. Architectural remains including numerous drystone wall and wooden structures that could have elaborated the entrance to the cave or formed platforms functioning as working surfaces or beds. Traces of hearths, pottery and bronze artefacts, as well as bracken and hay, were found both on the stone structures and on the floor of the channel, and were used in some cases to assess the chronology of the site.

Two cultural horizons can be distinguished at Bezdanjača: an older one, dating to the Middle Bronze Age (BrC/D, 1500–1200 BCE), and a more recent one, dating to the Late Bronze Age (BrD/HaA, 1200–1000 BCE). Radiocarbon analysis of several wood samples from the site yielded dates of 1350–1100 BCE. Recent radiocarbon dates published by Zavodny *et al.* for several individuals from Bezdanjača align with the previous radiocarbon dates from the same site.

- I18736/3801, BzV 30b (petrous bone), genetically female.

Complete neurocranium of an adult individual. Small button osteoma on the left parietal bone. Wormian bones along the lambdoid and sagittal sutures.

- I18718/3778, BzV 37b (petrous bone), genetically female.

A complete cranium of an adult (25-40y) individual (without the mandible). Two small button osteoma on the left parietal bone, healed porotic hyperostosis on the parietal bones. Wormian bones along the lambdoid suture.

- I18728/3788, BzV 28a (petrous bone), genetically female.

Direct radiocarbon dated (UCIAMS233513, PSU6017; 3090±25 BP, 1422-1281 calBCE). A complete cranium of an adult (40-50y) individual (without the mandible). Small button osteoma on the frontal bone, healed porotic hyperostosis on the parietal and the occipital bones, antemortem healed blunt-force trauma on the frontal bone. Wormian bones along the lambdoid suture.

- I18733/3793, BzV 33d (petrous bone), genetically female.

A complete cranium of an adult (45+ y) individual. Small button osteoma on the right parietal bone, healed porotic hyperostosis on the parietal and the occipital bones, four carious lesions and three alveolar abscesses.

- I18735/3800, BzV 37a (petrous bone), genetically female.

A complete cranium of an adult (*maturus*) individual (without the mandible). Three alveolar abscesses on the maxilla.

- I18722/3782, BzV 27a (petrous bone), genetically female.

A complete cranium of an adult (50+ y) individual. Healed porotic hyperostosis on the parietal and the occipital bones, antemortem healed blunt-force trauma on the right parietal bone, degenerative osteoarthritis on the right TMJ. Wormian bones along the lambdoid suture. Two alveolar abscesses on the maxilla.

- I18414/3796, BzV Inv. br. ZPGK 45 (petrous bone), genetically female.

Partially preserved cranium of an adult (40-50 y) individual. One alveolar abscess on the maxilla.

- I18413/ 3795; AL33 Sk. Gr. 5 (petrous bone), genetically female.

Partially preserved cranium of an adult (25-35 y) individual. Healed *cribra orbitalia* in both orbits.

- I18734/3794, BzV 26a (petrous bone), genetically female.

A complete cranium of an adult (*maturus*) individual (without the mandible). Healed porotic hyperostosis on the parietal and the occipital bones, healed *cribra orbitalia* in both orbits. One alveolar abscess on the maxilla.

- I18727/3787, BzV Inv. br. ZPGK 40 (petrous), genetically female.

A complete cranium of an adult (20-30 y) individual (without the mandible). Two small button osteoma on the frontal bone, healed *cribra orbitalia* in the left orbit. Wormian bones along the lambdoid suture.

- I18720/3780, BzV 27d (petrous bone), genetically female.

A complete cranium of an adult (45+ y) individual (without the mandible). Small button osteoma on the left parietal bone. Wormian bones along the lambdoid suture.

- I18739/3804, BzV 34a (petrous bone), genetically female.

A complete cranium of an adult (40-50 y) individual (without the mandible). Healed porotic hyperostosis on the parietal bones, antemortem healed blunt-force trauma on the right parietal bone, two carious lesions and one alveolar abscess on the maxilla.

- I18717/3777, BzV 33a (petrous bone), genetically male.

A complete cranium of an adult (40+ y) individual (without the mandible). Small button osteoma on the frontal bone, two carious lesions and two alveolar abscesses on the maxilla.

- I18737/3802, BzV 21d (petrous bone), genetically male.

Partially preserved cranium of a subadult (10-12 y) individual. Wormian bones along the lambdoid suture.

- I18730/3790, BzV 37f (petrous), genetically female.

Complete neurocranium of an adult individual.

- I18738/3803, BzV 39a (petrous bone), genetically female.

A complete cranium of an adult (25-35 y) individual (without the mandible). Healed porotic hyperostosis on the parietal bones, healed *cribra orbitalia* in both orbits, oval-shaped trepanation aperture on the frontal bone. Wormian bones along the lambdoid suture.

- I18723/3783, BzV Blok 9/1, 1088 (petrous bone), genetically male.

Complete neurocranium of an adult individual. Healed porotic hyperostosis on the parietal bones. Wormian bones along the lambdoid suture.

- I18729/3789, BzV 22a (petrous bone), genetically male.

A complete cranium of an adult (*maturus*) individual (without the mandible). Small button osteoma on the right parietal bone, healed porotic hyperostosis on the frontal, parietal and the occipital bones, antemortem healed blunt-force trauma on the right parietal bone, healed *cribra orbitalia* in both orbits.

- I18732/3792, BzV 33b (petrous bone), genetically male.

A complete cranium of an adult (20-30 y) individual (without the mandible).

- I18721/3781, BzV 11a (petrous bone), genetically male.
Complete neurocranium of an adult individual. Healed porotic hyperostosis on the frontal, parietal and the occipital bones, perimortem blunt force trauma on the right parietal bone. Wormian bones along the lambdoid suture.
- I18724/3784, BzV 33c (petrous bone), genetically female.
A complete cranium of an adult individual (without the mandible). Wormian bones along the lambdoid suture.
- I18725/3785, BzV 18a (petrous bone), genetically male.
Direct radiocarbon dated (UCIAMS233512, PSU6016; 3090±25 BP, 1422-1281 calBCE). A complete cranium of an adult (20-30 y) individual (without the mandible). Small button osteoma on the left parietal bone, healed *cribra orbitalia* in both orbits.
- I18417/3799, BzV 33o (petrous bone), genetically male.
A complete cranium of an adult (40+ y) individual (without the mandible). Small button osteoma on the frontal bone, two carious lesions and two alveolar abscesses on the maxilla.
- I18416/3798, BzV 18b (petrous bone), genetically female.
Partially preserved cranium of a subadult (7-8 y) individual. Healed *cribra orbitalia* in both orbits.
- I18415/3797, BzV 33e (petrous bone), genetically male.
A complete cranium of a subadult (10-11 y) individual (without the mandible).
- I18085/3943, BzV 30d (premolar), genetically male.
Only the facial region of a subadult (8-10 y) individual is preserved.
- I18086/3944, BzV 33l (molar), genetically female.
Only the mandible of a young adult individual is preserved.
- I18075/3855, BzV 33r (premolar), genetically male.
Only the mandible of an adolescent/young adult (15-20 y) individual is preserved. Linear enamel hypoplasia on the anterior teeth.
- I18074/3854, BzV 33t (premolar), genetically female.
Only the mandible of an adult individual is preserved.
- I18073/3853, BzV 33p (canine), genetically female.
Only the mandible of an adolescent (12-18 y) individual is preserved.
- I18071/3851, BzV 21c (ossicle), genetically male.
Only the facial region of a subadult (8-10 y) individual is preserved. Healed *cribra orbitalia* in both orbits.

- I18079/3858, BzV 12a (molar), genetically female.
Only the mandible of an adult (25-35 y) individual is preserved.
- I18087/3945, BzV 33u (molar), genetically female.
Only the left side of the mandible of an adolescent individual is preserved.
- I18078/3857, BzV 24 (premolar), genetically female.
Only the mandible of an adult (20-30 y) individual is preserved. Linear enamel hypoplasia on the anterior teeth.
- I18072/3852, BzV 4 (premolar), genetically male.
Only the facial region of an adult (18-25 y) individual is preserved. Linear enamel hypoplasia on the anterior teeth.
- I18082/3861, BzV 33j (molar), genetically female.
Only the mandible of an adult individual is preserved.
- I18077/3856, BzV 33f (molar), genetically female.
Only the mandible of an adult (25-35 y) individual is preserved.

References: (304-309)

Velim – Kosa (Bronze/Iron Age)

Contact: Natalija Čondić

In 2013 and 2014, Archaeological Museum Zadar carried out a rescue excavation at the construction site of Stankovci Photovoltaic Power Station (Zadar County, northern Dalmatia). Four Liburnian culture tumuli (stone burial mounds), located relatively close to each other (c. 20 m away on average), were investigated. Most were well-preserved and were predominantly constructed of rubble and, to a lesser extent, of earth. The only exception is Tumulus 4, which was damaged by machines when the road along the southern edge of the future construction site was being created. Although the tumuli are well-preserved, the grave structures within them are rather damaged.

Grave 1 in Tumulus 2 (diameter: 9 m; height: 95 cm) yielded the remains of two adult individuals based on the presence of two left temporal bones. Tumulus 2 contained a single grave which had been severely damaged, with only the northern liming and shorter western side remaining in situ. Disarticulated human bones were found throughout the 30 cm-thick layer of grave fill and were scattered across an area measuring c. 100 cm x 60 cm, both within and outside the confines of the grave. The positions of the bones indicate that the individual's head had originally faced west. A bronze ring was found inside the grave and numerous pottery sherds were distributed across the tumulus. Based on the few grave goods and the pottery sherds recovered, tumuli date to between the Middle/Late Bronze Age and the end of the Early Iron Age (15th–5th c. BCE). The only available direct radiocarbon date so far (Tumulus 3, grave 1) puts this burial to the end of the Middle Bronze Age (UCIAMS 233623, 3180±25 BP, 1521-1421 calBCE).

- I18830/3867, Tumulus 2, grave 1, individual A (petrous), genetically male. Very fragmented and partially preserved remains of an adult individual.

- I18831/3868, Tumulus 2, grave 1, individual B (petrous), genetically male.

Very fragmented and partially preserved remains of an adult individual.

Reference: (310)

Sv. Križ Brdovečki (Early Iron Age)

Contact: Hrvoje Potrebica, Ian Armit

The remains of an Early Iron Age tumulus were excavated in 2001 in the vicinity of Sv. Križ Brdovečki, a hillfort overlooking the Sava Valley around 30 km west of Zagreb. This grave contained a single male individual accompanied by the remains of a horse and numerous objects including an axe, spear and horse-riding equipment (Cvitković, I. and Škoberne, Ž. 2003; Škoberne 2004: 161-170). This princely grave has been radiocarbon dated to 737-383 calBCE (2371±40 BP, SUERC-69418).

A series of flat inhumation graves excavated close to the tumulus have yielded a range of radiocarbon dates, some contemporary with the princely burial and some rather later, suggesting a longevity of funerary ritual in the vicinity. Petrous bones from six of these individuals were successfully analysed for aDNA and are listed here in chronological order from earliest to latest:

- I5727/CR05; Grob 10; Sonda 1 (petrous bone), genetically female.
- I5725/CR03; Grob 6 (petrous bone), genetically male.
- I5726/CR04; Grob 9; Sonda 1 (petrous bone), genetically female.
- I5723/CR01; Grob 1; Sonda 1 (petrous bone), genetically male.
- I5724/CR02; Grob 3; Sonda D (petrous bone), genetically male.
- I5728/CR06; Grob 11 (petrous bone), genetically female.

References: (311, 312)

Sv. Petar Ludbreški, Staro Groblje (Late Bronze Age)

Contact: Saša Kovačević, Ian Armit

The site of Sv. Petar Ludbreški is a lowland settlement located near the River Drava in northwestern Croatia. Inside the settlement, the well-preserved remains of a bronze foundry belonging to the end of the Late Bronze Age was found (pit 1/1977), as well as two separate, isolated human burials deposited in waste pits from the same period. One of these burials (in pit 20/1960 in trench IV) was excavated in 1960 by K. Vinski Gasparini of the Arheološki Muzej u Zagrebu. Although little information survives regarding the context of the burial, it appears that this individual had been deposited vertically in a crouched (almost sitting) position within a very deep pit that also contained charcoal, pottery from the end of the Late Bronze Age, a clay brazier

and several clay weights. The bones of this individual were partly charred and exhibited a healed fracture to the right femur (Nicholls 2017, 89).

- I5729/CR07; 1960 (petrous bone), genetically male.

Reference: (313)

Trogir (Split; Byzantine)

Contact: Lujana Paraman, Marina Ugarković, Martin Steskal

Osteological study is done by Paul Klostermann, Michaela Binder

In 2018 the small central Adriatic town of Trogir/Croatia was the subject of a field archaeological investigation of the Croatian-Austrian cooperation in the study of ancient Tragurion/Tragurium. The objective of this research was a better understanding of the settlement stratigraphy and the history of use of a place whose Early Medieval and pre-Medieval history is still poorly known. Due to its privileged location in the fertile Kaštela bay region, Trogir's history can be traced back to the Late Copper or Early Bronze Age. The foundation of the settlement can be connected with the communities of livestock herders of nomadic and afterward transhumant type that populated Middle Dalmatia from the late Copper Age and at the beginning of the Bronze Age. Archaeological data from the Early Iron Age period suggests Trogir was an important commercial port already in that period, with trade connections to southern Italy and Greece. The commercial trade intensified especially after the establishment of the Greek settlements Issa and Pharos on the Middle Adriatic islands Vis and Hvar at the beginning of the 4th c. BCE. The increasing Greek influence in the area is preserved in Trogir's street layout: Archaeological excavations confirmed that the city was renewed by the same urbanistic principles as the town of Issa, with elongated 13 m wide residential blocks typical for the Hellenistic period. The last two centuries BCE are marked by the complete transformation of the communities in the Kaštela bay under both local and Greek influence, as well as the rising presence and influence of Romans in Dalmatia. With the loss of Issa's domination in the course of the Adriatic war operations in the civil war between Caesar and Pompey in 47 BCE, both ancient Trogir and Issa lost their autonomy and were soon integrated into Roman Illyricum, as one of the settlements within the territory of the colony Salona. With the Roman administration came organized trade, quarrying and intensive agriculture. The area was densely populated and organized as a system of agronomical countryside estates (*villae rusticae*). Although scarce, the data from the Trogir hinterland suggests that the native settlements were abandoned and the karst fields were also occupied by the Roman *villae rusticae*. The Late Antique period of the 5th and 6th century is marked by the abandoning of the *villae rusticae* in the area around Trogir and the withdrawal of the population into the fortified town, as well as into the Prehistoric hillforts in its vicinity.

Since the old town of Trogir, today located on a little island between the mainland and the island of Čiovo and a UNESCO World Heritage site since 1997, is densely covered with buildings, the Croatian-Austrian team took advantage of a substantial renovation of a basement in one of the oldest houses (12th/13th c.) still preserved in the Romanesque/Gothic city fabric. It is located on the south-west side of the crossroads of modern Ulica Matije Gupca and Lučićeva Ulica street. The Lučićeva street is located along the 3rd western *cardo* (*stenopos*), while Matije Gupca street is located on the main city *decumanus* (*plateia*) stretching from the city square

(*agora, forum*) on the east to the assumed line of the western Hellenistic-Roman defense wall in modern Mornarska street. The trench in the basement of Ulica Matije Gupca 15 initially unveiled a sequence of recent layers and layers indicating construction activities as well as processes of sedimentation. These layers covered parts of a cemetery with at least eight graves (one of them not excavated) including mostly well-preserved skeletal remains of eight non-adult individuals. Almost all the individuals (7 out of 8) died during infancy. The remaining individual was the only adolescent who died at an age between 16–18 years. The cemetery dates from the late 7th to the first half of the 10th century CE, although it should be noted that this is only a frame for the actual period of use since only a part of it has been excavated. These graves are to date the earliest among the rare funerary evidence of the Early Medieval period in the cities of Dalmatia.

- I15743/2652, grave 5, MG15 2018 (petrous bone), genetically female, infant.

The remains of this burial were well preserved and belonged to a 12–18 month-old. Early life stresses and deficiencies were visible in the form enamel hypoplasia, protruding cribra orbitalia, scurvy as well as growth inhibition – shown by the discrepancy between dental development and long bone length.

- I15741/2654, grave 7, SU170, MG15 2018 (petrous bone), genetically female, neonate.

The individual died within three months after birth. The endocranial lesions, heightened porosity on the maxilla and the bloated sternal rib ends and long bone ends with rough epiphyseal surfaces indicate a generalized metabolic disorder which likely already affected the individual in utero.

- I15463/2649, grave 2, MG15 2018 (petrous bone), genetically female, neonate.

The neonate died in the 38th – 40th gestational week. The extensive new bone formation within the cranial vault and the porosities on the facial bones, the mandible and the pelvis suggest that the individual suffered from a non-specific infectious disease and/or intrauterine metabolic disease.

- I15462/2647, grave 1, ind. 1, SU 135, MG 15 2018 (petrous bone), genetically female, infant.

Grave 1 contained the remains of two infants buried in superposition to each other in stone box burials. The aDNA sample taken from the older burial was successful. There was active endocranial new bone formation on the occipital bone and vessel impressions on one parietal suggesting the infant was affected by an infectious or metabolic disease.

- I15744/2651, grave 4, SU148, MG15 2018 (petrous bone), genetically female, infant.

The age-at-death was approximately 2 years. Pitted enamel defects and short diaphyseal length of the long bones in comparison with dental maturation age reflected possible metabolic disruption due to stresses intrauterine or early life. The aDNA analysis showed that the individuals in grave 2 and grave 4 were sisters.

- I15742/2653, grave 6, SU 160, MG 15 2018 (petrous bone), genetically female, adolescent.

The remains belonged to a 16–18-year-old individual. Developmental malformations in the pelvis and femora were noted, which might have affected locomotion. There were stress indicators in form of linear enamel hypoplasia on the teeth as well as hyperostosis of the occipital and parietal bones. Additionally, there were signs of well-healed blunt force trauma to

the skull and ribs as well as potential perimortem trauma indicating that the individual had sustained multiple incidents of traumatic events.

Reference: (314)

Cyprus

Kissonerga-Mylouthkia (Cypro-Pre-Pottery Neolithic B; Cypro-PPNB)

Contact: Kirsi O. Lorentz

Commingled, incomplete and fragmentary human remains of a minimum of six individuals (MNI 6) were recovered from the oldest known water wells in the world, at Kissonerga-Mylouthkia, Cyprus. These wells date to Cypro-Pre-Pottery Neolithic B (c. 8,200-7,200 BCE; Period 1A, Cypro-PPNB, c. 9,100-9,300 BP, c. 8,200-8,600 Cal BC; Period 1B, Cypro-LPPNB, c. 8,000-8,200 BP, c. 6,800-7,200 Cal BC; (315)). The two Cypro-PPNB water wells (Wells 116 and 133) were discovered at Kissonerga-Mylouthkia along the Southwestern coast of Cyprus. The wells would have been not more than a few minutes walk from the coast, provided that the then coastline of Kissonerga-Mylouthkia was the same, or close to the current coastline (316). Evidence suggests that the site was not a residential site, but involved only a restricted set of activities: water acquisition, stone vessel manufacture, flint working, and disposal of some human remains at well 133, and obsidian working, preparation and consumption of marine molluscs, and disposal of foetal remains at Well 116 (*ibid.*). The possible existence of a nearby contemporary settlement is only an inference, based on the botanical evidence for crop processing and weeds of cultivation recovered from the wells.

Both wells contained some cranial and post-cranial fragments (317). MNI was determined by duplication of skeletal elements, together with additional data on age at death and sex when possible. Age at death estimates for foetal, subadult, and adult remains relied on long bone growth, dental development, epiphyseal fusion, and cranial suture closure, respectively, when relevant diagnostic regions were present. The fragmentary and incomplete nature of remains precluded use of other methods. When no diagnostic regions were present, age estimation as 'adult' or 'sub-adult' relied on general morphological appearance and size. Sex estimates were based on morphology of the commingled remains.

One of the six individuals is of late foetal age (c. 7 1/2+ foetal months; (317)), recovered from the Cypro-EPPNB Well 116 (contexts 116.124 and 116.191). The partial remains of five individuals were recovered from the Cypro-LPPNB Well 133 (contexts 133.260, 133.264, 133.282, 133.329, 133.331, and 133.332), including a child of c. 6–10 years, and an adolescent of c. 14–19 years of age at death. At least three separate adults are represented within these commingled human remains deriving from Well 133 fills.

The find context of these PPNB individuals is unusual – rather than formal burial their remains were disposed of in disused and filled-in water wells, within a short walking distance from the sea shore, with refuse and artefacts such as a macehead. This atypical disposal may indicate that these individuals are not representative of the general PPNB population in Cyprus at the time. It may even be consistent with a hypothesis that they came from elsewhere. Interestingly, the two males for whom the auditory canals are present display external auditory exostoses (EAEs), indicative of repetitive aquatic activity over a substantial time period (318). Further research is required as to local/non-local origin of these individuals at the southern coast of Cyprus. Four samples are included in this study.

- I4208/KMY8; KMYL 1197, B200.211B (petrous bone), genetically male.
- I4207/KMY1; KMYL 1181, F133.260A, Skull 1 (petrous bone), genetically male.

- I4209/KMYL2; KMYL 1181 F133.260 B, Skull1, !2! (petrous bone), genetically male.
- I4210/KMYL3; KMYL F133,282 !3! (petrous bone), genetically male.

References: (315-318)

Greece

Kastrouli (Desfina, Phokis, near Delphi; Mycenaean and Archaic)

Contact: Ioannis Liritzis, Athanasios Sideris, Thomas E. Levy, Andreas Bertsatos, Maria-Eleni Chovalopoulou

The archaeological site of Kastrouli near the town of Desfina (Phokis) has been systematically investigated since 2016 until 2020 through an interdisciplinary and multi-scientific integrated approach (319-322). The archaeological excavation employed amongst others, cyber-archaeology tools, archaeometric investigations concerning luminescence dating, spectroscopic and mineralogical analyses for the characterization and provenance of ceramic fabric, and geophysical prospection (www.kastrouli.org). Major results include the discovery of a Late Bronze Age prestige mortuary complex; petrographic evidence for the use of local clay sources; dating by ceramic typology, C-14 and OSL to the Late Helladic/ Late Mycenaean III and reuse in the Geometric, and later periods. The successful application of terrestrial geophysical prospection and accurate positioning of the excavated finds, features via cyber-archaeology tools linked to photogrammetry, the archaeometric results, and the biological anthropological study of human remains have produced important new data that begin to complete the puzzle of Kastrouli settlement in the Phokis periphery of the Mycenaean World. The concept of methodology, implementation and interpretation of the processed data and work in progress have been reviewed (322).

Kastrouli's Late Mycenaean (Late Helladic IIIB-C) settlement is situated ca. 4 kilometers east of Desfina and southeast of Delphi, one of the most important shrines of Greek antiquity (coordinates: N 38° 23' 56.7'', E 22° 34' 30'', 550 m asl Google Earth). Kastrouli site lies at an altitude of 550 m from sea level, on a rocky hill with a strategic location that dominates the Mesokampos plateau, this peripheral Mycenaean site is certainly linked to other contemporary settlements in the vicinity. A timeless checkpoint for contact between the two main harbors of Kirrha and Antikyra and probably a seaport at Steno, was the Kastrouli fort (319, 321). It has been suggested that Kastrouli may have been listed in Homer's Catalogue of Ships as Anemoreia's Homeric site, when the stature of the Phokis region was founded when it was said that 40 ships had joined the naval campaign under the leadership of Agamemnon against Troy (*Iliad*. 2.521,(323)).

According to this view, the Mycenaean transliterated word from Linear B mentions the Anemoreia, which may be connected to the god of winds (Anemoi - attested through as Anemohiereia or Anemon Hiereia, "Priestess of the Winds" (Linear B: a-ne-mo-i-je-re-ja, a-ne-mo,i-je-re-ja) (322). This is supported by the strong prevailing northern winds from mount Kirphis across from Kastrouli. The southern Phokis has been historically "defined", but it has largely been neglected by researchers concerning the Bronze Age and subsequent periods; until our research it was committed to relative obscurity and essentially neglected from contributing more substantively to the overall understanding of Classical and Mediterranean antiquity. This makes an archaeological and scientific approach essential to bring to light the rich past of southern Phokis starting from Kastrouli and expanded southward to the coastal sites of Sykia, Steno, Vroulia, Antikyra, and Medeon, which serves as a necessary supplement to the present textual narrative (324, 325).

Excavations at Kastrouli were enriched with the transdisciplinary work that integrated spatial/context recording and artifact collection, aerial Photography from helium balloon and drone, photogrammetry, CAVEcam Stereo Photography for 3D visualization, ¹⁴C and OSL dating; XRF, XRD, as well as mineralogy of ceramics. Additionally, an exhaustive bone analysis (biological anthropology, collagen extraction and preservation, isotopes and collagen degradation and evaluation with FTIR bone diagenesis) was made, prior to aDNA extraction and initial palaeo-genetic and palaeoproteomic research, for conservation and interpretation (326-329).

The three excavation seasons (2016 - 2018) at Kastrouli brought to light significant finds including phi (Φ) and psi (Ψ) figurines, gold jewelry pieces, lead and bronze pieces, animal bones and numerous commingled human bones, pottery sherds, pithoi sherds with chevron motif, a banded rim cup, stone mortars and grinders, clay and stone spindle whorls, stone beads, as well as, sea-shells. While two well-preserved tombs were looted in the early 1970s, the looters failed to disturb the main burial remains in Tomb A containing commingled human and non-human skeletal remains and the two individuals in the adjacent Tomb B, also found with ceramics. Other excavation areas revealed: three buildings (1-3) and two fortified entrance gates (east and west). The vast quantity of pottery discovered, containing fragments of stirrup jars, amphorae, deep and shallow cups as well as alabastra, is of particular interest. The pottery is dated from the Late Helladic III A2 till the LH III C Middle periods, on the basis of typology and decoration (319-321, 323, 330).

The XRF analysis, the mineralogical determination and the microstructure examination of a selective number of ancient ceramics from the Late Mycenaean settlement of Kastrouli enabled us to characterize them in terms of technological and provenance issues. The high skillfulness of Kastrouli people, evident from the use of various local clay sources exploited in their environment, makes this peripheral Mycenaean settlement of particular importance. (331-333).

OSL and TL dating of ceramics and surface luminescence dating of the Tomb A and stone foundation reconfirms the Late Mycenaean age and reuse of the tombs in later periods (334, 335). The luminescence dating: (a) produced ages from the Late Mycenaean/Helladic to Hellenistic times indicating that the site was reused by later people (i.e. following the 9th c BCE, the fortified settlement was still in use in the Archaic, Classical and Hellenistic times), and (b) provided a definite LBA destruction of the site, corroborated as well by the fire-destruction layers found in both buildings, 1 and 2. Moreover, the sample dated in the Archaic period from the Tomb B, which is Mycenaean according to the archaeological material, as well as the similar dates of the prenatal samples from the Building 2, are proofs of later reuse of both the tomb and the building, and a strong indication of the post-Mycenaean continuity of the site, eluding thus far the archaeological record. The obtained ages and the excavated finds provide valuable information revealing the life-span of Kastrouli and together with current analytical work demonstrate its place as a small but of major importance settlement in the periphery of the Mycenaean World of mainland Greece.

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Sino-Hellenic Academic Project (www.huaxiahellas.com). TEL thanks the Phokion Potamianos family for their support.

Delphi, Kastrouli-Desfina Tomb A (BA Mycenaean)

9 samples are included in this study, excavated in 2016.

- I13532/KAS4; comingled burial Tomb A (femur), genetically female. Locus L121 Tomb A, dense concentration of human remains (possible secondary burial) in southern chamber of tomb.
- I13580/KAS-10; comingled burial Tomb A (femur), genetically male. L112 Tomb A, dense concentration of human remains (possible secondary burial) in eastern end of tomb (locus L112).
- I13536/KAS-9; comingled burial Tomb A (femur), genetically female. L121 Tomb A.
- I13531/KAS-3; comingled burial Tomb A (femur), genetically female. L121 Tomb A. Inside Tomb. Dense collection of human remains, probably secondary burial, in Square 6/19, L121.
- I13433/KS-T1-8; comingled burial Tomb A (tooth), genetically female. Crate 11, Tomb A, L120, fill in southern chamber of tomb.
- I13577-KS-T2A; comingled burial Tomb A (tooth), genetically male. Year of excavation 2016, sq.6/19, L112, dense concentration of human remains (possible secondary burial) in eastern end of tomb.
- I13579/ KS-T2C; comingled burial Tomb A (tooth), genetically male. L121, inside tomb. Dense concentration of human remains (possible secondary burial) in southern chamber of tomb.
- I13428/ KS-T1-4; comingled burial Tomb A (tooth), genetically male. Crate11, L119 Excavating fill to the south of the tomb in Squares 5/19 and 6/19.
- I13578/ KS-T2B; comingled burial Tomb A (tooth), genetically female. Sq.6/19, L112 dense concentration of human remains (possible secondary burial) in eastern end of tomb.

Delphi, Kastrouli-Desfina Tomb B (Archaic)

1 sample is included in this study, excavated in 2018.

- I17962/ 11, Tomb B, Bag B10; 15, Tomb B, Bag B6 (femur), genetically male.

Delphi, Kastrouli-Desfina Building 2 (Archaic)

2 samples are included in this study, excavated in 2018.

- I17960/(3) Room A; Bag A1 (ulna), genetically male.
- I17959/ (1) Room A; Bag A14 (5) (ulna), genetically male, prenatal.

Crete, Zakros, Karaviadaina (Middle Minoan)

Contact: Stella Chryssoulaki and Panagiotis Karkanias

The tomb of Karaviadaina was excavated by Dr Stella Chryssoulaki in the year 1994. The site is situated in the hinterland of Zakros, one of the major urban and palatial centers of Crete during the 2nd millennium BCE, at an inland cultivable enclave that has yielded evidence of Minoan habitation. The tomb is located on a gentle slope, in a cavity of the limestone bedrock. The side facing the hillside, which was most probably partly closed by a wall, has been destroyed by the construction of the modern road leading to the bay of Kato Zakros. Within the intact part of the tomb the remains of six individuals were found. These were most probably female, and of varying age. Besides, the tomb yielded 37 whole or largely preserved pots and fragments of others, as well as some stone vases. According to the finds the tomb was in use during the earlier part of the Protopalatial period, that is, in Middle Minoan IB and Middle Minoan IIA. The site is unpublished. One sample is included in the study.

- I14916/KRV.BxV.B.1106 (petrous bone), genetically female.

Reference: (336) [mention of Karaviadaina in the site catalogue, as an area where traces of occupation are found].

Attica, Kolikrepi-Spata (BA_Mycenaean)

Contact: Sevi Triantaphyllou, Niki Papakonstantinou, Maria Stathi

The site of Kolikrepi is located 3 km west of the modern town of Spata (eastern part of Attica region) and lies in the area between two partly excavated mortuary sites of Magouleza hill and Velanideza. A large-scale rescue excavation conducted by the Ephorate of Antiquities of east Attica from 2009 to 2013, under the direction of Maria Stathi, revealed one of the largest unlooted Mycenaean cemeteries excavated to date in Attica. The cemetery was in use for nearly five centuries, covering the entire time span between Late Helladic I/IIA and early Late Helladic IIIC. Its cemetery covered an area of 5.5 acres extending on the southern slope of a hill and consisted of at least 65 tombs cut into the natural bedrock (soft limestone rock, *kimilia*). The vast majority of the tombs (53) belonged to the architectural form of chamber tomb, most of which were equipped with dromoi, leading through securely blocked doorways (stomion) to cave-shaped chambers. In 14 out of 53 chamber tombs the dromos was replaced by a rectangular or circular pit leading to the stomion. Most of the dromoi accommodated small side niches with artefacts and more rarely human bones. The chambers varied in size and shape and had been used for multiple, collective burials. Pits dug into the floor level, covered in some cases with stone slabs, were filled with skeletal remains and artefacts. The cemetery included also 8 pit graves of variable layout (pit-caves, double pits, pit with short dromos) dug in areas between the chamber tombs, as well as, 4 graves which could not be attributed to a

specific architectural type due to destruction during earlier road construction works. The tombs held a significant number of findings, including a remarkable variety of pottery, jewellery, sealstones, bronze tools, weapons, clay figurines and spindle whorls (337, 338). Skeletal material was discovered in 55 of the 65 tombs. With the exception of a few disturbed primary burials in pit graves and chamber tombs, it consisted mainly of disarticulated and commingled bones resulting from the intense and continuous use of the chamber tombs, the successive deposition of bodies, multiple funerary episodes and the secondary manipulation of both the skeletal and the cultural remains. The secondary practices included, among others, disturbance, disarticulation and clearance of earlier remains, body dispersal and selective or random relocation of bones in piles placed alongside the walls of the chambers, or within pits dug in the floor or in side niches (337, 339). The overall human bone sample, thoroughly studied and recorded to date, includes 43.950 identifiable bone fragments (making up 25.027 elements) from 19 chamber tombs and 2 pit graves (1 pit-cave and 1 pit with dromos). The studied remains comprised a Minimum Number of 304 Individuals, including all ages and both sexes (340). Four samples from three chamber tombs are included in this study.

Tomb 29

Tomb 29 is a chamber tomb located at the south-east part of the cemetery. The tomb's contents testify to a long period of continuous use from the Late Helladic IIA to the Late Helladic IIIA2. The chamber did not include primary burials, but it comprised various secondary assemblages. A large pile of commingled bones and artefacts occupied the entire north-east part. Two pits (Pit 1 and 2) dug in the floor of the chamber contained disarticulated skeletal remains. A Minimum Number of 23 Individuals was identified for all contexts, including 8 subadults and 15 adults.

- I15582/ Sample 18; Tomb 29-Pit 1-K10-KOL 657 (petrous bone), genetically female.

Sample I15582 belongs to a skull (K10) found in the lower layer of Pit 1 clustered with three more skulls in its south side. The pit contained the remains from at least 5 subadults and 6 adults. Papakonstantinou assessed this individual as a mature adult male, based on cranial suture closure and morphological traits of the skull (mastoid process, supraorbital ridge, nuchal crest). The skull was generally well preserved showing only localized traces of surface erosion, and a perforation (boring) associated with insect activity, probably by dermestid beetle (*Coleoptera: Dermestidea*), that indicates that the individual was initially placed freely on the floor of the chamber without any soil covering before being redeposited in the pit (340). This clue is further reinforced by the results of histological analysis conducted on samples from the pit which exhibited no microbial bioerosion consistent with sub-aerial exposure (341). A spherical jar associated with the skulls date the deposit to Late Helladic IIA period, which is confirmed by the C14 analysis (1610-1448 calBCE (3255±25 BP, PSUAMS-7850).

Tomb 45

Chamber tomb 45 was located in the central cluster of tombs of the cemetery and presented evidence of use from Late Helladic IIA until the Late Helladic IIIB period. The human remains found in the tomb comprised a minimum number of 17 individuals (7 subadults and 10 adults), secondarily deposited on the floor of the chamber, close to the north wall, as well as within two pits.

- I15571/ Sample 8; Tomb 45-Pit 1-K2-KOL 1128 (petrous bone), genetically female.

The skull found on the top layer of Pit 1 belongs to the skeleton of a child (c. 8-9 years), which was re-individuated during the laboratory analysis. Most of the elements attributed to the skeleton were collected from a small bone concentration on the upper layer of the pit, placed at the south-west corner. The preservation of the skull was fairly good with moderate erosion and traces of insect activity. It has directly been AMS-dated to the Late Helladic IIA period (1505-1429 calBCE (3200±20 BP, PSUAMS-6939), which is quite interesting given the fact that pottery recovered from the lower deposit of the pit was dated in Late Helladic IIB and LH IIIA period.

- I14872/ Sample 7; Tomb 45-Pit 2-K5-KOL 800 (molar), genetically female.

Tooth sample derived from the well preserved mandible of a skull (K5) found in the southern part of the eight-shaped Pit 2, used for the relocation of the skeletal remains from 10 individuals. Bones had been deposited under a dense layer of sherds dating in Late Helladic IIA, IIB and IIIB periods. The age assessment of the skull indicated a range between 40-45 years (mature adult) based on ectocranial vault suture closure and dental attrition, and cranial morphology (glabella, mental protuberance) suggested female sex, also confirmed by aDNA results. Regarding the state of health, dentition presented linear enamel hypoplasia, carious lesions and calculus deposition. The calibrated span of dates is 1497-1316 calBCE (3145±25 BP, PSUAMS-7813), namely in Late Helladic IIB-III A2.

Tomb 46

Chamber tomb situated in the central section of the cemetery, dating from Late Helladic IIA until Late Helladic IIIB. Skeletal remains were found at the west part of the chamber as a large pile of disarticulated bones along the west wall, while a significant quantity of commingled human bones was recovered from four pits. The Minimum number of Individuals was estimated at 16 individuals (4 subadults-12 adults of both sexes) was estimated.

- I16709/24; Tomb 46-pit 1-K2-KOL 321 (petrous bone), genetically male.

Sample I16709 was selected from a nearly complete skull found in the secondary deposit of at least 3 adult individuals within Pit 1. It was well preserved in terms of surface condition with slight and patchy erosion, slight sediment concretion and black or dark brown staining probably due to increased moisture and organic minerals in the surrounding soil. The stage of cranial suture obliteration suggested an age at death between 30 and 40 years (prime adult), while the morphology of the skull (mastoid process, nuchal crest) indicated male sex which was confirmed by the aDNA analysis. The parietal and occipital bones, and the left orbital roof presented porous lesions (porotic hyperostosis and cribra orbitalia) (340). The ceramic material, as well as, radiocarbon dating results date the skeletal assemblage of the pit to Late Helladic IIA period (1505-1429 calBCE (3200±20 BP, PSUAMS-6939).

References: (337-343)

Palace of Nestor excavation (BA Mycenaean and EIA)

Contact: Sharon R. Stocker, Jack L. Davis, Lynne Schepartz

Ancient DNA was recovered from 11 individuals in five different burial contexts at Pylos (Fig. S 18); forms of burial included a shaft grave (the grave of the so-called “Griffin Warrior”), two chamber tombs with multiple burials, a cist grave with two burials, and a small tholos tomb with multiple burials. Four of the five burial contexts were excavated in the 1950s by a University of Cincinnati team under the direction of Carl W. Blegen, and the grave of the “Griffin Warrior” was excavated by the current University of Cincinnati team working at the Palace of Nestor under the direction of Sharon R. Stocker and Jack L. Davis.¹ The samples range in date from the Late Helladic period to the Early Iron Age. All skeletal biological observations are by Lynne A. Schepartz and Sari Miller-Antonio. With the exception of the grave of the Griffin Warrior, relative dates are based on those provided by Joanne Murphy in her forthcoming re-publication of the tombs excavated under Blegen’s supervision.²

- Griffin Warrior

Excavated by Sharon R. Stocker and Jack L. Davis, 2015

- I13519/ 1479; Trench N-CO2, Level 30, SN20-0168, GRIFFIN WARRIOR, DNA26 (petrous bone), genetically male.

The Griffin Warrior was buried alone in a stone-lined shaft grave of Late Helladic IIA date located northeast of the Palace of Nestor (Fig. S 18). The Warrior was interred on his back in an extended position within a wooden coffin. Schepartz estimates that he was an adult male, ca. 30–35 years old. His skeleton was robust, with an estimated stature of 1.60-1.70 m, and displayed no significant pathologies or signs of trauma. His skull was crushed, but it was possible to make a virtual facial reconstruction using forensic imaging procedures.

¹ Samples were chosen for DNA analysis in the spring of 2018 under terms of a permit granted by the Ministry of Culture and Sports of Greece. Skeletal elements were selected by Stocker, on the recommendation of Schepartz. Samples were taken by Daniel Fernandes, representing the laboratory of Ron Pinhasi in Vienna.

² J.M. Murphy, *The Legacy of Death at Pylos: A Restudy of the Bronze Age Tombs Excavated by Blegen* (INSTAP Academic Press, in press).

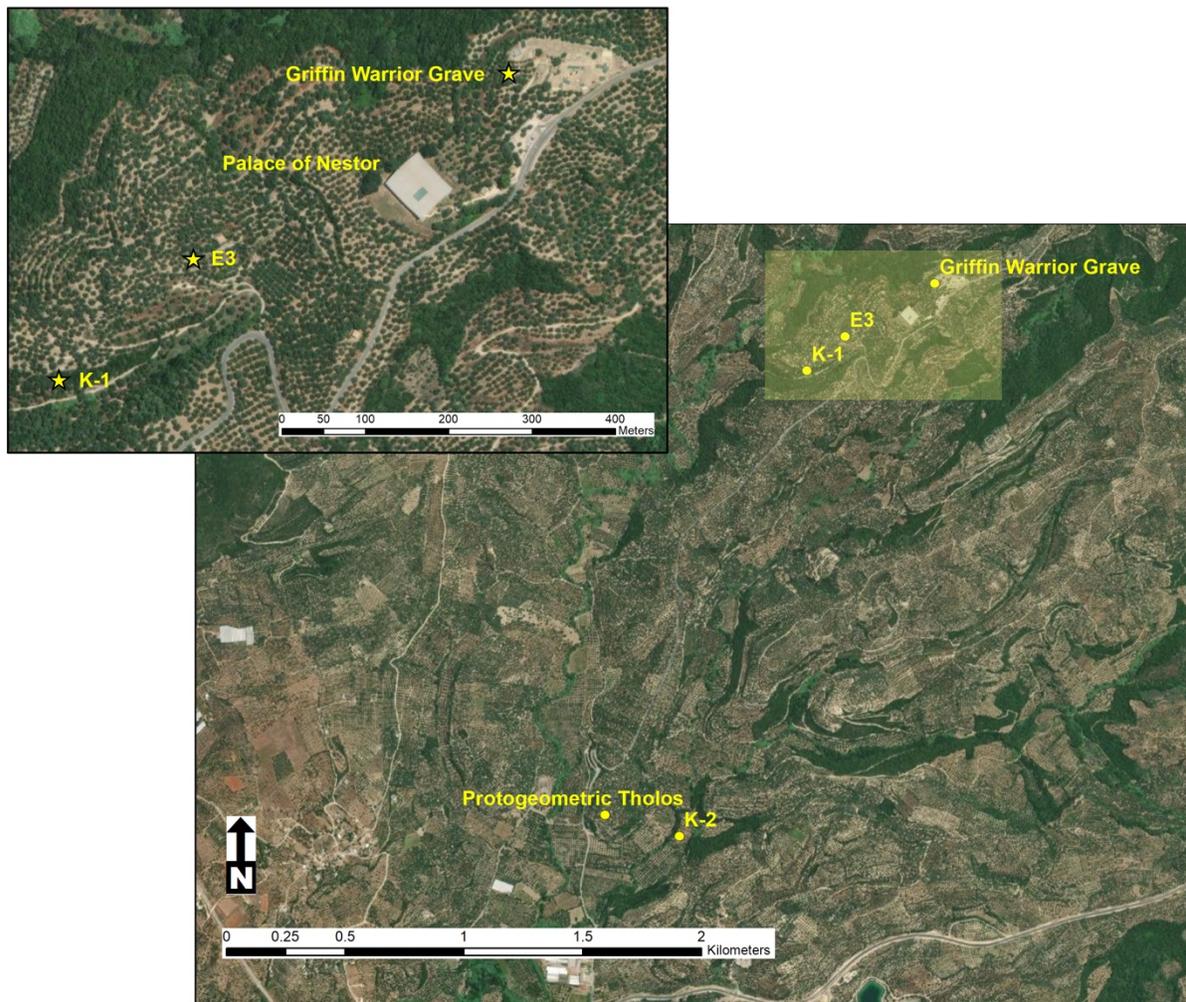


Fig. S 18 Relative location and distance scale of tombs of studied ancient individuals. Image credit: Michael Loy, courtesy of the Department of Classics, University of Cincinnati. The base image was exported from Google Earth.

- K-1 Kondou

Excavated by Lord William Taylour, 1957

K-1 is a chamber tomb located southwest of the Palace of Nestor. Schepartz and Miller-Antonio identified a minimum of 9 individuals in the tomb, which was used in two distinct periods, LH IIIA2 and LH IIIB–LH IIIC.

Ancient DNA has been recovered from two male skulls in the chamber, and from a tooth found in a pit at the outer end of the (*dromos*) entry passage.

- I13510/ 1433, Kondou, Tomb K-1, PY31 (Kontos), Skull, 1957 DNA7 (petrous bone), genetically male. First-degree relative of I13517.

I13510 is one of the individuals from the chamber. Schepartz and Miller-Antonio assessed this individual as an adult female aged 35-45 years, because several of the cranial features are not so strongly developed as might be expected in a male in the Pylos population. He had poor oral health with many teeth lost during life, including all of the maxillary teeth. This would have

limited his ability to chew normally and would have altered aspects of his facial and cranial vault morphology. The left orbital roof shows evidence of remodeled porosity, indicative of stress from infection or poor nutrition during childhood. Aside from these conditions, the cranium has two clear areas of healed blunt force trauma on the left and right parietal bones. The injuries could be the result of either inter-personal violence or accidents such as falls.

- I13517/ 1477, Kondou, Tomb K-1, PY32 (Kontos), Skull, 1957, DNA8 (petrous bone), genetically male. First-degree relative of I13510

I13517 is another burial found in the chamber, estimated to be an adult male and older than I13510 based on cranial suture closure. Obliteration of the posterior sagittal suture is significant, and there is closure of the mid-lambdoidal and lateral coronal sutures. Endocranially all these sutures are closed. This evidence suggests an older age than most individuals observed at Pylos (40-50 years), and he was one of the most robust males.

- I19366/P6187; 2/7/57, Kondou I, [7], Pit in dromos, DNA9 (tooth), genetically female. 2nd or 3rd degree relationship with I13510 and I13517

This sample, a slightly worn, isolated left maxillary second molar, is from a pit in the entry passage of the tomb. Among the skull fragments, bone fragments, and teeth found in the pit, Schepartz and Miller-Antonio identified the remains of an adult and a subadult of indeterminate sex. Given the degree of wear on the tooth, it should be from the subadult. We cannot rule out the possibility that this tooth and other fragmentary skeletal material in the entrance passage was swept out of the burial chamber after decomposition of the constituent corpses.

The two males in the chamber were identified as first-degree relatives (I13510 and I13517) and as 2nd or 3rd degree relatives of I19366 in the dromos. The presence of an LH IIIA2 kylix associated with the pit in the dromos likely dates I19366, I13510, and I13517 to LH IIIA2.

- K-2 Kokkevis

Excavated by Lord William Taylour and Mabel L. Lang, 1958 and 1959

Schepartz and Miller-Antonio determined that there were at least 19 burials in this chamber tomb. Murphy dates the earliest burial to LH IIIA2 and the tomb was used in LH IIIB, but most of the burials are of LH IIIC Middle and Late, later than the destruction of the Palace of Nestor.

I13506/1429, Kokkevis, Tomb V, KK1a, 1959, KK1+KK4 DNA17 (petrous bone), genetically male.

I13506 is a fragmentary cranium that is not overly muscular, but the basic morphology and the broad and blunt mastoid processes suggest it is the skull of a male, as confirmed by the DNA results. The age estimate is 35-40 years.

- I13513/ 1473, Kokkevis, Tomb V, KK3a, 7/7/59, 3 skulls from s.part of tomb (1st layer), 11A, DNA22 (petrous bone), sex undetermined.
- I13514/1474, Kokkevis, Tomb V, KK3d, 1959, KK2 (4), Skull 3d, DNA23 (petrous bone), genetically female.

Both samples I13513 and I13514 are from a cranial vault and associated maxilla of the same individual. The cranium features moderate muscular development. Of note are the open basal synchondrosis and large deep glenoid fossae. The associated maxilla has the left palate preserved, along with eight teeth and an M3 socket. The nasal aperture is narrow and tall with a

prominent anterior spine. The maxilla is short with a slight palatine torus. Based on cranial morphology and dimensions, the open basal synchondrosis, and the dental development, this individual was estimated to be a possible male adolescent aged 15 +/- 3 years.

- I13518/ 1478, 1478, Kokkevis, Tomb V, KK1b, 1959, DNA18 (petrous bone), genetically male.

This adult individual is characterized by strong male cranial and facial features, with an age estimate of 30-35 years.

- I19364 /P6185; 7/7/59, Kokkevis, Tomb V, 3 skulls from s.part of tomb (1st layer), (11A) (tooth), genetically male.

This is an isolated adult maxillary molar that cannot be associated with any specific individual.

I13506 and I13518 are father and son, and I19364 is a second or third degree relative of both. I13506 and I19364 were found in the south part of the tomb in an upper layer (Taylour's Group IV); this family group is likely to be LH IIIC Middle-Late in date. I13518 is almost certainly the product of a union between first cousins.

- E-3, Tsakalis

Excavated by William P. Donovan, 1956

- I13516/1476, Tsakalis, PY2, Dromos/Tomb E3, Cist grave, 8/11/56, DNA6 (petrous bone), genetically female.

E-3 is an unusual grave in an extensive cemetery of chamber tombs just outside the maximum limits of the town surrounding the Palace of Nestor. The grave is a long cist containing two extended burials, one set on top of the other. Schepartz and Miller-Antonio concluded that one of the two was a male, the other a female. This skull to which this petrous bone comes belongs to the lower of the two burials, and displays clear female levels of muscular development, sharp orbital borders and a pointed chin. Some teeth were lost to decay early in life. The postcranial bones are slender but show notable development of the upper arms and thick cortical bone in the legs. The age is estimated to be that of a young adult, 20-25 years.

- Kokkevis α

Excavated by Lord William Taylour, 1958

- I19368/ P6189; 18/7/58, Kokkevis Alpha, S. half (2), Kokkevis alpha, human bone [9], DNA16 (tooth), genetically female.

Kokkevis α is a very small tholos tomb near the modern village of Koryfasion, south of the asphalt road leading from the coast to the Palace of Nestor. A single skull and other human remains were recovered on the tomb floor, associated with pottery of the Early Iron Age (Protogeometric). One individual skull and a fragmentary skeleton belong to a younger adult, considered possibly to be female. In addition to that individual, there were commingled dental remains of other adult individuals based on tooth identification, size, and degree of dental attrition. These include a smaller and older female, another individual whose teeth are larger and have less dental attrition, and a third individual who is possibly a mid-aged to older adult. The sampled tooth is associated with the younger individual previously not given a sex estimate. This suggests that at least two of the three individuals in the tomb were female.

General Observations

This initial program of DNA analysis at Pylos points to the great potential that further work can have, but even the small number of samples so far examined has yielded informative results. The difficulties of working with disarticulated and disturbed burials in chamber tombs are challenging, since crania are often unlinked to postcranial information. DNA has clarified the sex of a male affected by severe tooth decay and associated cranio-facial bone remodeling, and determined the sex of an adolescent that was undeterminable from the skeletal remains.

Of special interest are the familial relationships established within two chamber tombs. It has generally been assumed that chamber tombs were “family tombs,” although little direct evidence for familial relationships exists.³ DNA results constitute the first concrete proof of this at Pylos. In one case, remains of an individual redeposited in the entrance passageway of the tomb can be dated by associated pottery, and that allows her two relatives, whose remains were found mixed with those of others inside the chamber of the tomb, also to be dated. In another chamber tomb, two of three relatives were interred in the same part of the chamber and in the same stratum, permitting the third sample to be more closely dated.

Fthiotis, Lokris, Proskynas (Late Bronze Age)

Contact: Anastasia Papathanasiou

Proskynas is located in central Greece and was excavated from 1996 to 2000 by the 14th Ephorate of Prehistoric and Classical Antiquities, under the direction of Eleni Zachou. On a flat hilltop four habitation phases were uncovered, ranging from Late Neolithic I to the Mycenaean period, approximately 5000–1300 B.C. The major habitation period, dates to the Early Bronze Age. 14 burials were uncovered in flexed position and with no offerings. Six burials belong to the Middle Helladic or the Early Mycenaean period, and come from a burial circle of 11 m in diameter, defined by large stones. The rest belong to the earlier phases of the site and they are individual pit burials uncovered in the foundations of the Early Bronze Age (MH) buildings or in coeval open spaces.

- I6420/ Proskynas IV (long bone). Middle Helladic. Genetically male, 14–15years.

Vranas Marathon (Roman)

Contact: Sevi Triantaphyllou, Anna Touchais, Gilles Touchais, Nikolas Papadimitriou, Maria Pantelidou-Gofa

Vranas Marathon is located 1.5 km to the NW from the spectacular Marathon tumulus where the Athenian warriors of the famous battle of Marathon (490 BCE) were buried. The site

³ On Mycenaean burial customs and grave types see W. Cavanagh, “Death and the Mycenaeans,” in C.W. Shelmerdine, ed., *The Cambridge Handbook to the Aegean Bronze Age* (Cambridge: Cambridge University Press, 2008) 327-341; C. Mee, “Death and Burial,” in E. Cline, ed., *The Oxford Handbook of the Bronze Age Aegean* (Oxford: Oxford University Press, 2010) 277-290.

consists of four prehistoric tumuli excavated by S Marinatos in 1970 (344) with funerary features emerging from the early Middle Helladic to the Late Helladic period although a significant Late Roman use is also considered. A new project which aimed at the examination and publication of the prehistoric tumuli lasted between 2014 and 2018 (345-349) and involved also the study and publication of the human remains (346): 48-52; (348): 49-54. The latter mission included two stages: 1) the investigation of the human remains laid *in situ* in tumulus I, and 2) the study and recording of the disarticulated remains derived from tumuli II-IV. Apart from the macroscopic work, a number of analytical methods were applied with limited results. 17 samples of petrous bones and teeth were selected from the human remains out of which only one sample (48) provided recoverable aDNA and surprisingly, the individual where the sample was derived from is dated to the Roman period.

- I7833/ Sample 48 - Tumulus IV, Tumulus IV-IV.4.57; (2) Sample 46 - Tumulus IV, Tumulus IV-IV.4.119 (petrous bone), genetically male.

Iran

Hasanlu and Dinkha Tepe (Iran; BA-IA)

Contact: Janet Monge

The Hasanlu Archaeological Project was undertaken by a joint venture between the University of Pennsylvania Museum, the Metropolitan Museum of Art, and the Archaeological Service of Iran with continued reconnaissance, survey and excavations between 1956 and 1974 (12 excavations seasons) under the direction of Dr. Robert Dyson. The major rationale for the long exploration was to understand the prehistory of northwestern Iran from the Pottery Neolithic continuously to the Medieval Period. The main field effort was directed to the excavation of the site of Hasanlu but several other regional sites were also explored including Dinkha Tepe. The human remains sampled here are all housed at the Penn Museum (Philadelphia, PA, USA) and derive from the Bronze Age or Iron Age.

These sites are located on a high plateau southwest of Lake Urmia, an intermountain (Zagros) basin in Western Azerbaijan in northwestern Iran. Hasanlu lies within the Soldūz Valley and Dinkha Tepe, the Ošnū Valley, approximately 25km west of Hasanlu. The area today is rich in agricultural resources, well watered by the various streams and rivers that flow into Lake Urmia, and serves as an overland route of communication/transport/population movement between adjacent mountain passes. This was most likely the case in the past as well.

The relationship between the population centers of Hasanlu and Dinkha Tepe remains unknown. Dinkha Tepe is often referred to as a satellite center to Hasanlu but more recently, the site has come to be considered as an independent urban city-state. Historically the greatest effort was expended on the excavations and analysis of Hasanlu and as a consequence less is known about Dinkha Tepe.

Burials were excavated at both Dinkha Tepe and Hasanlu from Low and High Mound contexts. Burial context between the sites is distinctive. All burials from Hasanlu are either simple interments or urn burials. At Dinkha Tepe, an array of burial types have been excavated: urn, pit, simple interments, stone lined interments and interments from brick tombs. In addition, human remains recovered from the Iron Age II (Hasanlu level IVb) on the High Mound (Citadel), represents a catastrophic death event when the city was sacked by an unknown invasion force.

Excavations on the north side of the Dinkha Tepe uncovered a cemetery used during both the Bronze and Iron Ages (Dinkha II and III). At Hasanlu, burials were exposed on both the Low and High Mounds and correspond to Hasanlu periods IV and V.

Dinkha Tepe (BA IA)

14 samples are included in this study.

- I3915/DT389, 66-23-389 (petrous bone), genetically male. (MA)
- I4237/66-23-374 (Box 82) (petrous bone), genetically female. (OA)

- I4273/66-23-387 (Box 86) (petrous bone), genetically female. (OA)
- I3914/ DT377, 66-23-377 (petrous bone), genetically female. (MA)
- I4238/66-23-393(Box 90) (petrous bone), genetically male. (MA)
- I4239/66-23-396(Box 94) (petrous bone), genetically female. (YA)
- I4340/66-23-400 (Box 99) (petrous bone), genetically female. (MA)
- I4236/66-23-370 (Box 80) (petrous bone), genetically female. (OA)
- I3911/DT1; 69-33-1 (petrous bone), genetically male. (IN)
- I3912/DT3, 69-33-3 (petrous bone), genetically male. (YA)
- I4274/66-23-404 (Box 102) (petrous bone); genetically male. (YA)
- I4272/66-23-381(Box 84) (petrous bone), genetically female. (MA)
- I4341/69-33-2 (Box 108) (petrous bone), genetically female. (MA)
- I3913/ DT4, 69-33-4 (petrous bone), genetically female. (YA)

Hasanlu (MBA IA)

21 samples are included in this study.

- I4338/65-31-768 (Box 60) (petrous bone), genetically female. (YA)
- I4280/ W31 E5 B8* (Hasanlu lover 2) (petrous bone), genetically male. (SA)
- I4269/ W31 E5 B7* (Hasanlu lover 1) (petrous bone), genetically male. (MA)
- I4233/75-29-534* (Box 123) (petrous bone), genetically male. (MA)
- I4357/60-20-231* (Box 21) (petrous bone), genetically female. (MA)
- I4232/65-31-792 (Box 71) (petrous bone), genetically male. (YA)
- I6430/ HSNL_753; 65-31-753 (petrous bone), genetically male. (OA)
- I4355/71-23-545* (Box 119) (petrous bone), genetically male. (YA)
- I6429/ HSNL_739, 65-31-739 (petrous bone), genetically male. (CH)
- I4353/60-20-232* (petrous bone), genetically male. (OA)
- 14100/HSNL302; 63-5-302* (petrous bone), genetically female. (YA)
- I4356/65-31-765 (petrous bone), genetically male. (CH)
- I6428/HSNL_730, 65-31-730 (petrous bone), genetically male. (IN)
- I6388/HSNL_103; 58-4-103 (petrous bone), genetically male. (YA)
- I6431/HSNL_754, 65-31-754 (petrous bone), genetically male. (MA)
- I6432/HSNL_780, 65-31-780 (petrous bone), genetically female. (IN)
- I4099/HSNL 749; 65-31-749 (petrous bone), genetically female. (OA)
- I6426/ HSNL_235, 60-20-235 (petrous bone), genetically male. (SA)
- I4097/HSNL 773; 65-31-773 (petrous bone), genetically male. (OA)
- I4098/HSNL 758; 65-31-758 (Box 56) (petrous bone), genetically female. (SA)
- I4354/65-31-756 (petrous bone), genetically male. (MA)

Age of individuals: IN: Birth to 3; CH: 4 to 11; SA: 12 to 19; YA: 20 to 34; MA: 35-49; OA: 50-64

* Recovery from the Citadel at Hasanlu IVb (catastrophic event)

References: (350, 351)

Iraq

Bestansur (PPN)

Contact: Roger Matthews

Within the scope of the Central Zagros Archaeological Project (CZAP), excavations have been conducted since 2012 at Early Neolithic Bestansur. The project investigates the nature of neolithisation during the Early Holocene, by fieldwork and research at sites in the higher and lower Zagros, including Sheikh-e Abad and Jani in Iran, and Zarzi, Bestansur and Shimshara in Iraq. The importance of these sites lies in their very early dates and long occupations, spanning ~9,800-6,000 BCE, and their location on the most important route-ways through the Zagros mountains, including the later Silk Road, enabling study of movements of people, animals, materials, practices and ideas during this critical period of change. The sites are part of a cluster of important Neolithic sites in this region, including Asiab, Sarab, Ganj Dareh, and Abdul Hosein in Iran, and Karim Shahir and Jarmo in Iraq. The Central Zagros Project is a joint UK, Iran, Iraq Research Project.

The Neolithic site at Bestansur is located on the fertile Shahrizor Plain in the western foothills of the north-central Zagros mountains, in Sulaimaniyah province in the Kurdistan Region of Iraq (352). Bestansur lies close to a perennial spring and comprises extensive Early Neolithic occupation and later levels, which form much of the 7.5m high central mound. Bestansur represents an early stage in the transition to sedentary, farming life, where the inhabitants pursued a mixed strategy of hunting, foraging, herding and cultivating, and constructed substantial buildings of mudbrick, including a major building with more than 72 individuals buried under its floors in association with hundreds of beads (353). These human remains provide new insights into mortuary practices, demography, diet and disease during the early stages of sedentarisation.

Excavations in Trench 10 on the eastern flank of the mound revealed a sequence of two large, well-preserved buildings, Building 5 which overlies Building 8, in a neighbourhood of smaller structures.

These buildings have provided significant new insights into Early Neolithic lifeways and mortuary practices. The rectilinear mudbrick structures were constructed with an open portico, facing southeast. Space 50 in Building 5 is a large room, ca. 8 x 4.5 m, which contains multiple deposits of disarticulated human remains, including many skulls. There are several major phases of deposition of human remains. Phase 1a) comprises burials inserted into the packing of the underlying Building 8 prior to the construction of Building 5. In Phase 1b)-1c) burials were cut through the floors of Building 5. Phase 2 human remains consist of scatters of small bones on floor surfaces of Space 50, while in Phase 3 a single adult inhumation was placed within the fill of the abandoned Building 5. The sequences of burial cuts into the packing and the later floors are sealed below multiple replasterings

The human remains assemblage from Trench 10 to date comprises >79 individuals, 72 of which come from Space 50 with more to be excavated. The floors of Space 50 consist of multiple layers of thin brown, green and white plasters in at least two phases. Ongoing

excavation of Buildings 5 and 8 is providing high-resolution insight into Early Neolithic activity in and around large buildings which clearly had a special character and hosted multi-staged human burial activities through significant periods, radiocarbon dated to 7677-7356 BCE (calibrated BCE 1σ). Excavations in Trench 7, to the west of the mound, revealed the double burial of an adult male and an adolescent female which were placed in an external area to Building 3.

The recovery of more than 81 individuals in total from Bestansur provides an important new assemblage for analysis of the impact of more sedentary agricultural human populations, lifeways and health. At Bestansur the human osteological assemblage provides insights into health across all age groups from perinatal infants to older adults. Pathological skeletal and dental indicators were observed across a significant proportion (ca. 30%) of the population, many of whom demonstrated multiple pathologies. Most frequently occurring were enamel hypoplasia, cribra orbitalia, porotic hyperostosis, and periostitic bone, all of which are indications of physiological stress or malnutrition. Evidence of healed fractures is also attested at Bestansur in an individual with a badly healed lower leg fracture which would have inhibited their mobility.

Excavations at Bestansur, whose global importance is recognised by its inscription on the UNESCO World Heritage Tentative List, are shedding new light on some of the early stages in the transition to settled village life in the Early Neolithic of the Eastern Fertile Crescent. The sophisticated nature of the mudbrick architecture is attested in large-scale multi-roomed rectilinear buildings, at least one of which is richly associated with the burial of the human dead. The community living at Neolithic Bestansur was sustained by a biodiverse diet with potentially less reliance on a Neolithic plant package and significant exploitation, including some degree of management, of animals including domesticated goat, wild sheep and pig alongside hunting of a range of large and small mammals. Consumption of fish, fowl and land snail was also a significant component of their diet. The material culture of Bestansur is rich in imported items such as obsidian, carnelian and seashells, indicating the extent to which Early Neolithic communities interacted with each other across the Eastern Fertile Crescent and beyond. Their material culture attests highly developed networks of engagements reaching far and wide as well as being locally embedded. The corpus of human remains from Bestansur Building 5 is one of the most substantial and most richly contextualised Neolithic assemblages from the Eastern Fertile Crescent. It is providing unique insights into the challenges faced by human communities through the Neolithic transition, with considerable evidence for malnutrition and dietary stress early in life in many of the individuals.

- I8936/ B TSR_284; 1781; 284 (petrous bone), genetically male.

This sample from Phase 1a), a petrous portion belonging to an infant in Context 1781 is from a packing layer throughout Space 50, which contained numerous disarticulated small bone fragments and teeth. A radiocarbon date of 7735-7586 calBCE from another sample in this context (8640 \pm 40 BP, Beta-533614) indicates that at least some of these remains are from earlier disturbed contexts or are the remains left behind after secondary burial.

- I8959/ B TSR_292, 1812 SK9, 292; B TSR_369, 1812 SK9, 369 (petrous bone), genetically male.

C1812 SK9 from Phase 1c) is a juvenile aged between 5 to 7 years and is from an area of juvenile burials in between the south-east corner of Building 5 and the underlying Wall 47 of Building 8. These burials are mostly disarticulated crania and post-crania. A total of 17 individuals aged from pre-natal to 7 years have been recovered from this area so far, this individual being the oldest. Some individuals in this area were also associated with red ochre or beads of shell and carnelian.

- I8843/ B TSR_58; 1228 SK1; 58 (petrous bone), genetically female.

C1228 SK1 is an adolescent female individual aged from 14 to 20, with evidence of mild calculus and linear enamel hyperplasia. During life she was around 5'4" or 154 cm in stature. This individual was one of two articulated burials from Trench 7, the other individual is an adult male aged 30 to 40+. These two individuals were placed in a flexed position on the left side, positioned closely but facing away from each other. Both were poorly preserved, though all skeletal parts are represented. It is possible that the deposition of SK1 disturbed that of SK2.

- I8955/ B TSR_287; 1812 SK3; 287 (petrous bone), genetically female.

C1812 SK3 is a juvenile aged around 1.5 to 3 years and is also from the area of juvenile burials described above, in Phase 1c). This individual was represented by a partial skull, a mandible, teeth, and some post-cranial bones.

References: (352-354)

Nemrik 9 (PPN and Middle Assyrian)

Contact: Arkadiusz Sołtysiak

The site Nemrik 9 is a Pre-Pottery Neolithic site (dated to c. 10.000-8.000 BP) covering up to 2 ha and located close to the contemporary Mosul Dam in Northern Iraq. It has been excavated in 1985-1989 by the team from the University of Warsaw, Poland, directed by Stefan Kozłowski (355). In total, the skeletons of at least 96 individuals were unearthed, mainly in the deposits of commingled bones under the floors of the houses dated to c. 9100-8900 BP and at a regular cemetery dated to the second half of the 9th millennium BP (356). Moreover, three poorly preserved skeletons were dated to the historical periods, including one representing the Middle Assyrian period (356).

The PPN individuals from Nemrik were farmers who cultivated already domesticated wheat and barley (357). There is also archaeozoological evidence of ongoing cattle domestication at the site (358). At some point between c. 8900 and 8600 BP a major cultural transition occurred at the site, with complete shift of the burial custom from burying disarticulated and commingled bones of many individuals under the floors of the houses to a regular outdoor cemetery where only single skeletons of adults were inhumated (356). There is a striking difference between Nemrik 9 and Zawi Chemi in terms of trauma: there was no single case of trauma to the skull at Nemrik (356). There is also no evidence of artificial cranial modification that was common at the PPN sites in Iran (359).

4 samples are included in this study.

- I6443/NMRK-2734; NK/2734 (petrous bone), genetically female, adolescent ? (house 3, layer 5).
- I6457/NMRK-3401; NK/3401 (petrous bone), genetically male, adult 30-35 years* (house 4a, grave cluster a, layer IIIb).
- I6445/NMRK-2802; NK/2802 (petrous bone), genetically female, young adult** (house 2a, grave 39, layer IIIb).
- I6441/NMRK-2701; NK/2701 (petrous bone), genetically male, mature adult*** (grave D, layer MA).

* IIIb = 9100-8900 BP V = after 8400 BP MA = Middle Assyrian (Late Bronze Age)

Shanidar Cave (Proto-Neolithic period)

Contact: Anagnostis Agelarakis

In Shanidar valley of the Baradost Mountains, at the Zagros highland complex of northeastern Iraqi Kurdistan, surrounded by mountains over 1,800 meters high and near the bank of the Greater Zab river (a tributary to Tigris River) is the site of the Proto-Neolithic village, Zawi Chemi Shanidar. The Village site is situated in the immediate vicinity of the contemporary small Kurdish village of Shanidar. Four kilometers away from the Village site is the location of the large cave of Shanidar, at an elevation of 747 meters toward the rugged highland terrain in the Baradost Mountains. Shanidar Cave has been the scene of extensive archeological investigations by my late doctoral advisor, Dr. Ralph. S. Solecki, since 1951 (360). The archeological research enabled the documentation of the Zagros Mousterian (Middle Palaeolithic), the Baradostian (Upper Palaeolithic), and the Zarzian (Epipalaeolithic) cultures of the region.

Results of the archeological record, including the cultural materials and structures, the palaeoenvironmental indicators, as well as narratives and comparative settlement pattern observations of the local Kurdish population, were implying that the Zawi Chemi village site had not functioned as a permanent village. Hence, the inhabitants of the Village site could have been changing their habitation site seasonally, yet not as nomadic hunters and gatherers, seeking shelter especially during winter in the protected environment of Shanidar Cave (361). Nonetheless, the Cave site could have been inhabited more often and even for longer yearly periods by the membership of a select Zawi Chemi subgroup.

Unlike the Baradostian Upper Palaeolithic and Zarzian Epipalaeolithic horizons, the Proto-Neolithic horizon of the Cave site, or Layer B1 (the Zawi Chemi cultural horizon of the Cave site), revealed the presence of a burial ground. The burial ground, comprised much occupational debris, charcoal flecks and ashes as well as snail shells. Notably, the clearly defined allocation of the burial ground had been separated from the living areas in the Cave site by distinctive stone constructions. The gray sediments of B1b were superimposed over the area of the excavated burial ground by sedimentological deposits of a 40.0 to 55.0 cm thick layer of yellow loam (a stratigraphic subdivision of Layer B1, namely B1a), apparently the result of cultural stratigraphy, brought into the Cave site by the Proto-Neolithic people to shield and demarcate the precise location of the funerary activity area. Superimposing the yellow loam materials (B1a), was the

well-delimited stratigraphic Layer A, representing a very dense occupational zone during a local ceramic Neolithic cultural tradition; indicative that the Cave site had not been occupied since the Proto-Neolithic for some period of time, while the Village site was to be reoccupied only in the 6th century CE.

Regarding the contextual associations of the burial ground, a total number of 26 graves were excavated by Solecki, R. S., in 1960, involving 31 individuals (361). This was a demographic sample comprising both genders and a wide range of age subgroups, from the Perinatal to the *Maturus* cohort (Ibid. p. 164-166). The burial features occupied an ovate area, of approximately 24 square meters toward the back of the cave floor, at axonometric stratigraphic levels of a relatively uniform depth of approximately 1.0 meter from the present ground surface, or approximately 0.5 meter from the contact line between the pottery Neolithic and the Proto-Neolithic horizon; indicative of the comparatively shallow intra-site deposits of the Proto-Neolithic component (personal communication with Solecki, R. S. since 1985; (361)).

The vast majority of the adult individuals in the Proto-Neolithic burial ground had been interred in flexed or tightly flexed positions with limestone blocks or slabs, broken or whole mortars covering their crania and/or trunks. A number of the burials were accompanied by luxury grave offerings, while there was a clear emphasis on the type and numbers of burial goods that had been offered for the adornment of the very young individuals. Less than half of the burials were associated with features, which revealed primary associations with wood charcoal and ashes, indicative of extensive firing activities; suggested to reflect elements of the burial customs, however, with no thermal alterations detected on the skeletal bodies. Further, stone concentrations and stone pavements were associated with the activity area allotted for the burial of the dead.

Archaeologically, both the Proto-Neolithic occupation of the Zawi Chemi Shanidar open village site and the coeval Zawi Chemi cultural horizon of the Shanidar Cave Site, resembled (based on the cultural materials) patterns observed at the roughly coeval sites of Karim Shahir, Tell M/lefaat, and Gird Chai, in the Zagros region (362, 363). Furthermore, based on the artifactual assemblages, the burial customs, and the associated architectural remains, the Zawi Chemi cultural horizon, considered as it may be within the roughly coeval horizon of the Late Levantine Natufian, exhibiting similarities with the mortuary practices of the Natufians, yet also revealing different traditions, aspects of its own local heritage, with great innovation, variability of materials used and exchanged, and the development of new technologies for a new way of life, reflected on a transitional cultural component between the Epipaleolithic Zarzian and the fully settled Early Neolithic and Neolithic villages of the region.

Three samples are included in this study.

- I3882/SH2; Homo 356-384-A (tooth), genetically male.

Inspectional evaluations of anatomic morphology of Homo 356-384-A revealed a relatively gracile cranial and infracranial skeletal build with an overall absence of emphasized manifestations of muscular imprints. Limitations imposed by the incomplete preservation of the skeletal body, similarly with the limitations to retrieve more than just a few mensurational evaluations, which ranged between the upper limits of female and lower limits of male indicia,

resulted to an assessment of indeterminate gender for the individual involved. The age assessment of this individual indicated a range between 40 to 50 years at death. Despite the limitations imposed by preservation, all cranial fragments revealed pathological changes of diploic component expansion, with thinning of the ectocranial table coupled by porotic hyperostotic manifestations at the occipital and parietal fragments. Endocranially there were focal changes, particularly at the squamous region of the occipital indicative of meningeal inflammatory conditions. Additionally, the ectocranial surface of the left parietal fragment was manifesting at the external acoustic meatus mild hyperostotic conditions whereas an auditory (4.69 x 3.19 mm) osteoma pedunculated at the superior wall of the auditory canal. On the intracranial skeleton, a vertebral Schmörl's node indicated the event of an axially oriented stress overload, most probably due to trauma impact.

- I3883/SH3; 381-A (tooth), genetically male.

Although incompletely preserved, Homo 381-A revealed anatomic features and morphometrics that were indicative of emphasized robustness in skeletal build with moderate skeleto-muscular origin and insertion imprints, representing an individual of male gender and age at death within the cohorts of late SubAdulthood to early Young Adulthood (17-20 years of age); histological analysis of osteon counts (collaboration Agelarakis, A., Armelagos, G., and Paine, R., in 1986-88) provided an age assessment of 20 years at the incidence of death. A healed focus of pulled deltoid muscle fibers in their origin *locus* at the left acromial extremity of the clavicle, along with the muchemphasized muscular imprints of the lower diaphyseal end of the right humerus and forearm bones, indicated an *in vivo* commanding abduction, extension and rotation ability of the arm, with powerful flexion - extension of the elbow combined with strength in forearm supination - pronation as well as abduction and extension of the hand.

- I2516/SH5; Homo 371-298-A (bone), genetically female.

The individual Homo 371-298-A was of female gender, and of 25 to less than 35 years at the incidence of death; hence ranging from the terminal year of young adulthood to the earlier second half years of middle adulthood. There were cranial and intracranial axial traumata, which had been life threatening and had required the support of her cultural context through medical intervention and subsequently in prolonged healing regimens. In brief, she had sustained two head injuries at the vault area presenting smooth and shallow depressions nearly circular in shape. All the vertebrae were marked by moderate Schmörl's nodes, the most severe documented at the lower thoracic vertebrae. Similarly, a Schmörl's node was documented on the superior surface of the first sacral vertebra (the *basis ossis sacri*, of the ossified *os sacrum*) by compression of the fifth lumbar vertebra. A linear enamel hypoplastic defect had marked the early infancy ring of the right maxillary central incisor (R.I¹); an incident of arrested and improved biological growth at 2.8 years of life. Both incisal, and premolar occlusal surfaces revealed slight to moderate wear patterns, whereas the first molars exhibited heavier wear compared to the seconds with just flattened cusps.

References: (360-367)

Jordan

'Ain Ghazal (Amman; PPNB and PPNC)

Contact: Gary Rollefson, Michelle Bonogofsky

'Ain Ghazal began as a moderately-sized village (ca. 2 hectares) at the beginning the Middle PPNB period, but it grew to enormous proportions as immigrants poured into the settlement at the beginning of the Late PPNB, reaching megasite extent (ca. 14 hectares) by about 7,500 calBCE. Occupied through an unbroken sequence of 2,500 years, cultural changes can be clearly monitored in terms of economy, architecture, social and religious ritual, and social organization from the MPPNB through the LPPNB, PPNC, and well into the Yarmoukian culture of the Pottery Neolithic period. 'Ain Ghazal was finally abandoned around 5,775 calBC (368).

The earliest phase of occupation enjoyed a mixed subsistence economy of hunting, cereal and pulse agriculture, and domesticated goats. Architecture was rectangular and sheltered single family units. In Phase 2, due to the sudden doubling of population, architecture included two-story "apartment complexes" that sheltered extended families; the economy now included domestic sheep as well as goats, and hunting was relegated to a generally opportunistic exercise. Little changed in Phase 3 except for the sudden departure of 90% of the inhabitants, although architecture reverted to single-family households. Little changed again in Phase 4 except for the emergence of a ceramic industry; farming, herding, and architecture continued as in Phase 3.

Phase 1: 8,300-7,500 calBCE, Middle Pre-Pottery Neolithic B (MPPNB)

The settlement was founded around 8,300 calBCE (Pre-Pottery Neolithic B) as a small village (2 hectares?, just outside Amman, Jordan) and grew persistently at a rate of c. 0.17/annum until c. 7,500 calBCE,

Phase 2: 7,500-7,000/6,900 calBCE, Late Pre-Pottery Neolithic B (LPPNB)

At the beginning of the Late Pre-Pottery Neolithic B, the site's population doubled as people who had abandoned all of the farming villages in the Jordan Valley and the rest of Palestine, migrating en masse to the Jordanian highlands. The general birth rate continued to between 0.16-0.17 % per year, reaching a maximum of 15 hectares in size and a population of around 3,000 by 7,000 calBCE,

Phase 3: 7,000/6,900-6,500 calBCE, Pre-Pottery Neolithic C (PPNC)

At the start of the Pre-Pottery Neolithic C, when a sudden collapse caused a population implosion to about 10% (c. 300 people) within a generation or two. Population began to grow again slowly.

Phase 4: 6,500-5,500 calBCE, Yarmoukian Pottery Neolithic

By the emergence of the Pottery Neolithic beginning at c. 6,500 calBCE, the population may have reached 750 people. 2 samples are included in this study:

- I8554/AG88 3681 027 B 5-88 (petrous bone), genetically male, Juvenile.

This severely damaged PPNC burial consisted of incomplete calvaria fragments and an ulna of an infant less than one year old, excavated from a corner of a wall, directly under a plaster floor. No facial bones, mandible, teeth, or additional postcranial elements were recovered. Faunal bone

fragments were in the fill. The infant appeared to have been interred facing the southwest, without any observable pathologies; see Ain Ghazal(369-371).

- I1708/ AG84_7; AG 4453 048, middle skeleton (petrous bone), genetically female; 14 years old.

Montenegro

Vrbička Cave (Mesolithic_EN, Montenegro)

Contact: Dušan Borić, Nikola Borovinić, Emanuela Cristiani

Vrbička Cave (N42° 53' 27.2", E18° 52' 14.3", c. 948 m asl) is located in the Duga ravine in the village of Presjeka, at the distance of c. 18 km northwest of the present-day town of Nikšić in Montenegro. Excavations at the site took place in 2012–2013, 2015–2017, and 2020. The site contains finds dated to the Upper Palaeolithic, Mesolithic, Early Neolithic, Late Neolithic, and Bronze Age (372). Two analyzed isolated human teeth from this site were identified in the collection of faunal remains. The lower left canine (tooth 33) (I16994/3428) found in the lower levels of the Holocene strata in context (51) in spit 4 in Trench 1/2015, quad. 102/100/D (11/13/2015) has directly been AMS-dated to the Early Neolithic by OxA-39673 (5890–5740 calBCE at 95% confidence) and this individual would represent one of the earliest Neolithic occupants of the area. The other specimen is first upper incisor (tooth 11) and comes from the upper levels of the site, found in context (25), spit 1, quad. 106.5/100 (08/08/2013), located in the part of the cave where there is a very thin palimpsest of Holocene strata above the Pleistocene deposits. The stratigraphic position of this specimen makes its chronological attribution difficult. Attempts to directly date this specimen at the Oxford Radiocarbon Accelerator Unit have failed due to no yield (P-48725). The fact that the results of its genetic modelling could fit well the Iron Gates Mesolithic hunter-gatherer population as a source could tentatively suggest that this specimen is of a Mesolithic date. Two samples are included in this study.

- I16995/3429; no number, 1/2013, (25), spit 1, quad. 106.5/100 (tooth), genetically male.
- I16994/3428 (tooth) Trench 1/2015, context (51), spit 4, quad. 102/100/D (tooth), genetically male.

Velika Gruda (MLBA_IA)

Contact: Dušan Borić, Gojko Andriješević, Nikola Borovinić

Velika Gruda is a large burial mound situated in the Tivat coastal plain. It was excavated by the University of Zurich and the Opštinski zavod za zaštitu spomenika kulture in Kotor from 1988 to 1990(373). The tumulus is 6 m high and measures 26 m in diameter. The top stone covering is 1 m thick with four identified superposed clay mounds underneath. The primary central slab cist grave 1 belongs to the lowermost clay mound 1. This first mound is dated to the Late Copper Age (374). On top of this clay mound a much smaller clay mound consisted of Burial 2, placed in a pit and covered by a heap of rocks as well as subsequent clay mound coverings, the top stone covering, and associated burials are all dated to the Late Bronze Age – Reinecke's Bz D based on typological characteristics of the associated material culture along with several conventional charcoal dates that gave calibrated ranges ca. 1500–1058 calBCE ((375): Table 4), but might have been affected by the old wood effect. This general dating is also now confirmed with five new AMS dates made for the first time directly on five different individuals studied for aDNA. All five dates are relatively homogenous and indicate a span between 1414 and 1052 calBCE at 95% confidence. Associated $\delta^{13}\text{C}$ isotope values from AMS burns that range between -17.0‰

and –18.6 ‰ are slightly elevated compared to a purely terrestrial diet and considering the proximity of the sea coast likely indicate a moderate consumption of foods from the marine ecosystem. This fact likely suggests that the obtained dates need a slight correction for the existence of a marine reservoir effect, which would likely make them younger by several hundred years. The global marine reservoir age (ΔR) is assumed to be around 400 ^{14}C years but the needed correction factor based on the obtained isotope values is likely smaller, possibly placing them at the end of the second millennium BCE. In the Bronze Age levels, there were in total 125 individuals identified on the basis of physical anthropology analyses, found deposited in 10 collective tombs and more than 33 pot burials. Burial 2 (1990) is a collective burial, which, based on osteological analyses, contained five individuals (one old adult female, one adult male, one of unknown sex, and two children). Burial 3 (1990) is a collective burial, which, based on osteological analyses, contained two individuals, both possible adult males. Burial 6 (1989) contained the remains of one 18-month-old individual in a large jar. Burial 7 (1990) contained the remains of two child individuals placed in a pot. Burial 10 (1989) represents a collective burial that contained the remains of five individuals (a child, a subadult, one adult female, and two adult males). Burial 11 (1990) represents a collective burial that contained the remains of 17 individuals (seven children and 10 adults, of which the sex identification was possible for three males and one female). Burial 22 (1990). Burial 26 (1989); 27 (1990). Genomic analyses have identified three different family groups among the analyzed individuals:

Family A encompasses six members: I13777 in burial 2-locus 1 and I13169/PSUAMS-7923 in Burial 5 are brothers. Both are either sons of or brothers of I13776 in Burial 2-locus 1 (who is a 2nd or 3rd degree relative of I13168 in Burial 7/PSUAMS-7834). Both are also 2nd or 3rd degree relatives of I13775 in Burial 2-locus 1, I13168 in Burial 8, and I14499 in Burial 10 (who is also a 1st degree relative of I13168 in Burial 7/PSUAMS-7834); *Family B* encompasses four members: female individual I14497 is a 1st degree relative of I14500 in Burial 22 and a 2nd or 3rd degree relative of I13167 in Burial 6/PSUAMS-7922 (who is a 2nd or 3rd degree relative of I14498 in Burial 26-27); *Family C* encompasses 2 members: individual I13172 in Burial 3a/PSUAMS-7925 and I131710/RISE595 in Burial 2 are 2nd or 3rd degree relatives. Among the analyzed individuals, five specimens have no relatives detected: I14501 (Burial 11), I13778 (Burial 3, no. 1/PSUAMS-7882), I13171 (Burial 3a), and two neonates I13166 (FK Berich IV1), and I13165 (FK Berich IV).

- I13170/877; 2, Box D; Velika Gruda, Grave 2 (petrous), genetically female.
- I13167/874; Burial 6 (petrous bone), genetically male.
- I14497/1725; 1989, 10/9, FK9, Koord D26, sch. 2 niv. 182 (tooth), genetically female.
- I14500/1728; 1988, datum 8/9, G. 22, horizont. Sch. 2 (tooth), genetically female.
- I14498/1726; 1988, FK10, G. 26-27, datum 19/9, niv. 213, UGN (tooth), genetically male.
- I13165/872; Box E, FK Berich IV (petrous bone), genetically female, neonate.
- I13166/873; Box E, FK 23 Berich IV1 (petrous bone), genetically male, neonate.
- I14501/1729; 1990, burial 11; Box D, excavated in 1990 (tooth), genetically female.
- I13171/878; 3a, Box E, Schicht 3 (petrous bone), genetically female.
- I13172/879; 879; 3a, Box E, Schicht 3 (petrous bone), genetically female.
- I13778/841; Burial 3, nr. 1, Box D (petrous bone), genetically male.
- I13169/876; Burial 5, Box G (petrous bone), genetically male.
- I13168/875; Burial 7 Box G; (petrous bone), genetically female.
- I14499/1727; Box D; 1990, Burial 10 (tooth), genetically male.
- I13776/838; Burial 2, Box C, locus 1 (petrous bone), genetically female.

- I13775/837; Burial 2, Box C, locus 1 (petrous bone), genetically male.
- I13777/839; Burial 2, Box C, locus 1 (petrous bone), genetically male.

North Macedonia

Contact: Fanica Veljanovska, Zlatko Videvski, Milos Bilbija, Strahil Temov, Dragi Mitrevski, Lence Jovanova, Pasko Kuzman and Nada Pocuca Kuzman

Neolithic

Pista Novo Selo

1 sample is included in this study.

The site Pista near Novo Selo is a Neolithic settlement mound with material culture showing affinities with the Anzabegovo-Vrisnik group. Its 4m thick deposit of accumulated dwelling layers represents a roughly two millennia long occupation (6000 – 4000 BCE).

- I3881/Mace 4; Skeleton1 (molar), genetically female, adult.

Late Bronze Age, XIII-XII century BCE

Dimov Grob, V. Ulanci-Gradsko

1 sample is included in this study.

Excavated from 1992 to 1994 respectively by Dragi Mitrevski and Zlatko Videski under the auspices of the Museum of Macedonia, Skopje, this flat necropolis yielded 135 stone cists and rectangular pits. The dead were inhumated in contracted posture, males on their right side, female on their left.

- I7231/UL-VE-75/1 (petrous bone), genetically male. Adult of 30-35 years old.

Skupi Skopje, East Necropolis

1 sample. is included in this study.

The Ancient City of Skupi was built during the late 1st Century A.D. by the Romans and served as the Roman capital of Dardania until an earthquake destroyed the city. Excavations starting in the thirties of the 20th century have uncovered among other things the remains of a military camp, a large theatre, street plans, a basilica, and two necropoles.

- I10168/SKU-SK-5139 (tooth), genetically male. Adult between 35-40 years.

This human sample stems from a Late Bronze Age grave emerging from beneath the Roman occupation layers.

Vodovrati Veles

1 sample is included in this study.

- I10171/Vod-Ve-19a (tooth), genetically female. Adult between 40-45 years.

Vodovrati is a Late Bronze Age site located in near Veles. It is part of a series of cist grave necropoles along the Vardar belonging to the Ulanci group (14th – 12th century BCE).

Iron Age, VII-VI century BCE

Vodovratski Pat, V. Vodovrati-Gradsko

1 sample is included in this study.

Flat necropolis with stone cist graves of which 24 were investigated in 1954 and 1992. The inhumated deceased were buried in contracted position. The males were laid on the right side, and the females on their left side.

- I7233/VOD-VE-16 (petrous bone), genetically female. Adult between 50 and 55 years old.

Bucinci Skopje

3 samples are included in this study.

- I10377/BUC-SK-26 (tooth), genetically male. Adult between 50 and 55 years.
- I10378/BUC-SK-27 (tooth), genetically female. Adult between 19 and 21 years.
- I10379/BUC-SK-27C (tooth), genetically female. Adult between 40 and 45 years.

Plaosnik-Ohrid

5 samples are included in this study.

A complex archaeological site with a chronological continuity from Prehistory to the end of the Late Middle Ages after Christ's era. Within this area there are dominant remains of monumental Christian basilicas with mosaic floors and remains of the medieval monastery of St. Clement "St. Panteleimon". The archaeological research at this site had begun in 1942, and with longer or shorter breaks, they continue until today, being performed by the Institute and Museum – Ohrid.

- I10384/PLA-OH-2 (2009) (petrous bone), genetically male. Adult between 40 and 45 years old.
- I10385/PLA-OH-7(2009) (petrous bone), genetically female. Adult between 25 and 30.
- I10387/PLA-OH-87 (2008) (tooth), genetically female. Adult between 40 and 45.
- I10388/PLA-OH-170(2008) (petrous bone), genetically male. Juvenile ca. 8-10 years old.
- I10389/PLA-OH-286(2008) (tooth), genetically female. Adult between 40 and 45.

Lisicin Dol-Marvinci, Valandovo

Lisicin Dol is a flat necropolis investigated between 1997 and 2013. The number of unearthed graves is 403 and includes stone cist tombs, pithoi and rectangular pits. The deceased were buried in flat, supine position.

- I10383/LIS-VAL-222 (petrous bone), genetically female. Adult between 35 and 40.
- I8112/LIS-VAL-193 (petrous bone), genetically male. Adult between 40 and 45 years old.

Govrlevo-Skopje

Govrlevo, known as a Neolithic site, also includes layers of later periods. The samples were taken from skeletons buried in an Iron Age occupation deposit.

- I10381/GOV-SK-bb2(2008) (tooth), genetically male. Adult between 40 and 45.
- I10382/GOV-SK-bb3(2008) (tooth), genetically female. Adult between 40 and 45.
- I10380/GOV-SK-bb1 (tooth), genetically female. Adult between 30-35 years.

Classical and Hellenistic period, V-I century BCE

Isar Marvinci, V. Marvinci-Valandovo, Southwest Necropolis

Excavations were carried out from 2008 to 2012 under the auspices of the Cultural Heritage Protection Office and the Museum of Macedonia. Due to its long-term use stretching over several periods this necropolis comprised both inhumation and cremation graves of which 3500 were investigated. They were of different manufacture such as stone cist tombs, simple rectangular pits, burials under small tumuli, burials in rock chambers, in urns, and free cremation burials (Fig. S 19).

- I10166/MAR-VA-1340 (tooth), genetically male. Adult between 40 and 45 years.
- I10390/MAR-VA-1417 (petrous bone), genetically male. Adult between 50 and 55 years.
- I10391/MAR-VA-2466 (petrous bone), genetically female. Adult between 50 and 55 years.
- I10167/MAR-VA-2841 (tooth), genetically male. Adult between 50 and 55 years.
- I10392/MAR-VA-2863 (petrous bone), genetically male. Adult between 35 and 40 years.



Fig. S 19 A view from Marvinci Valandovo

High Medieval Period, VIII-XI century

Tumba S. Opticari Bitola

- I2530/Grave 1-Macats (petrous bone). Genetically female. 30-35 years old adult.

Republic of Moldova

Contact: Ion Ciobanu, Marta Krenz-Niedbała, Sylwia Łukasik, Sergei Lysenko, Alexey G. Nikitin, Evgenii Pascari, Sergei Razumov, Henry M. Shephard, Angela Simalcsik, Vitalii Sinika, Nikolai Telnov⁴

Transnistria, Slobodzeya district, Glinoe/Hlinaia, left bank of the Lower Dniester (Late EN_EBA_Kvitianskaia_PostMariupol)

Contact: Shephard, Henry M.; Nikitin, Alexey; Razumov, Sergei; Lysenko, Sergei; Sinika, Vitalii; Telnov, Nikolai; Pascari, Evgenii; Łukasik, Sylwia; Krenz-Niedbała, Marta

The Glinoe site is located on the left bank of the lower Dniester river in the Slobodzeya (Slobozia) region in south-eastern Moldova (N 46°40'40.6", E 29°47'57.7", height above sea level - 11.37 m). Kurgan 110 contains 10 burials, dated from late Eneolithic (the last third of the 4th Millennium BCE) to the medieval times (10th-11th centuries CE). Burial 1 (Glinoe K110B1), from which the sample originates, was attributed to the Catacomb culture. Burial 1 is the main grave of the kurgan, located on the ancient horizon in the kurgan (376). Fragments of Trypillian ceramics were found nearby this grave. Burial 1 was found at a depth of 0.4 m in the 1st northern trench, 2 m to the south and 4 m to the west of the northern edge. The contours of the burial structure in the embankment were not traced. The skeleton was found at the depth of 0.5 m, laying in an extended position on his back with his head to the west, and arms extended along the body. The burial had no grave goods.

- I20086/Glinoe (Hlinaia) K110-B1 (tooth), genetically male.

Adult 20-30 years (age-at-death was estimated based on tooth wear; Fig. S 20). Morphological traits of the skull (mastoid process, supraorbital ridge, zygomatic bone, gonial angle, and nuchal crest) have indicated male sex, as confirmed by the aDNA results. The skeletal remains were poorly preserved and highly fragmented (Figure S14). Fragments of the cranial bones (frontal, occipital, parietals, zygomatic, maxillae, and mandible with teeth), clavicles, scapulae, right patella, illia, ribs, and long bones of upper and lower extremities (humeri, ulnas, radii, femurs, tibiae, fibulae, hand and foot bones) were recovered from the grave. On both lower canines, enamel hypoplasia is present. Other paleopathological changes were not noticed.

⁴ We list the names alphabetically.



Fig. S 20 Glinoe (Hlinaia) Kurgan 110, burial 1.

Tiraspol, Transnistria

Kurgan 3 was excavated in 1983. It was located 500 m to the south of the Tiraspol-Odessa highway. The kurgan consisted of four horizons. A total of 31 burials were discovered in the kurgan, six belonging to a local Usatovo group, ten belonging to the Yamnaya culture, five to the Catacomb culture, and seven to the middle and late Bronze Age. One Sarmatian and two late nomadic burials were also discovered in the kurgan.

Burial 11 was discovered in the SE sector of the kurgan at a depth of 4.15 m. The burial contained three skeletons in supine extended position with the skulls facing SE.

Burial 17 was discovered in the E sector of the kurgan, at a depth of 4.32 m. The burial pit was oval in shape. The skeleton laid in extended supine position with the skull oriented to S. A biconical vessel, filled to 1/3 with food remnants, was located to the right of the skull.

- I20082/ TiK3.11, Tiraspol Kurgan 3, Burial 11. Catacomb culture (tooth), genetically male.
- I20083/ TiK3.17, Tiraspol Kurgan 3, burial 17. Catacomb culture (tooth), genetically male.

Dănceni, Ialoveni District

The ground burial cemetery at Dănceni II was located on the edge of a low (5-6 m) above-floodplain terrace on the right bank of the Ishnovets River, approximately 1.5 km NW from the village. The cemetery was researched by I.A. Rafalovič and V.A. Dergachev in 1976. The cemetery consisted of four or five burials, arranged in a semicircle with a radius of 6-7 m. To the east of the hypothetical center of the circle were the burials of adults. One child's burial was located to the south. One or two destroyed children's burials was located to the north. The distance between burials was 1.5-4 m.

Graves 93 and 308 were of the catacomb type. Some scholars attribute them to the Thraco-Getae period (4th-3rd centuries BCE (377)).

I20071/ DIIGB308, grave 308. Catacomb or Thraco-Getaean (tooth), genetically female.

Sărăteni, Hîncești District

A group of seven kurgans was located to the NE, E and SE of the villages Sărăteni and Obileni, on a steep promontory of a high plateau. Six kurgans were investigated by T. I. Demchenko in 1988. Four kurgans (1-3, 6) were built during the Chalcolithic era. Kurgan 4 was erected in the late Trypillian time. Kurgan 5 is associated with a Sarmatian burial.

Kurgan 3 (4 m in height, 50 m in diameter) was located 670 m to SSE from Kurgan 2 and occupied the extreme southern position in the group. 15 burials were discovered in the kurgan. The first embankment (H. 2.65 m, D. 27 m) was built above the Eneolithic burial 15. It was surrounded by a ring 32 m in diameter, made up of stones laid in one row. Burials of the Yamnaya culture were lowered into the first embankment.

- I20077/ SK3.9, Kurgan 3, burial 9. Catacomb culture (tooth), genetically male, adult.

Burial 9 was discovered in the SE sector of the kurgan, at a depth of 5.47 m. The burial chamber was quasi-rectangular shaped with rounded corners and was oriented along the SW-NE axis. The dimensions of the pit: length 2 m, height 1.2 m, depth 0.15 m. The skeleton of a mature male laid in extended supine position, oriented 67° NE, facing SE. Right leg was extended, left leg was slightly bent and laid over the right leg at the knee.

References: (376-381)

Transnistria, Camenca district, Katerinovka, (Middle Bronze Age)

Contact: Sinika, Vitalii; Łukasik, Sylwia; Krenz-Niedbała, Marta

Katerinovka site is located in the Camenca region in the north-eastern part of Moldova (N 47°55'9.39", E 28°51'13.51"). Kurgan 1 at this site contains 4 single burials and four anthropomorphic stelae. The sample for ancient DNA research was taken from individuals buried in grave 1 (Katerinovka K1B1), attributed to the Yamnaya culture ((382)). This burial was found at a depth of 0.6 m. The contour was in the form of an oval, measuring 7.5 × 6 m, oriented on a long axis in the NE-SW direction. The burial was partially destroyed and robbed. The filling at a depth of 0.45-0.6 m contained scattered human bones and displaced stones of the lining of the primary embankment – the position of the individual in the grave was undeterminable. The bones found in this grave were not colored with ochre.

- I12510/Katerinovka K1B1 (tooth), genetically female.

Adult older than 50 years (age-at death was estimated based on cranial suture closure and tooth wear). Morphological traits of the skull (cranial vault, supraorbital ridge, zygomatic bone, anterior mandible, gonial angle) have indicated female sex, as confirmed by the aDNA results.

The skeletal remains were well-preserved, but incomplete. Cranial bones (frontal, sphenoid, mandible, parietals, left zygomatic, left maxilla with teeth), right clavicle, scapula, vertebrae, ribs, and long bones of the extremities (humerus, right radius, femur, hand and feet bones) were recovered from the grave. The external surface of the mandibular body above the left second premolar, exhibited a fistula. Upper left second incisor, upper left first molar, lower right second molar, lower right premolars, lower right second incisor, lower left first and second molars were lost ante-mortem. There is a significant reduction of the alveolar bone in maxillae and mandible. Degenerative changes were observed on cervical vertebrae. Osteoarthritic changes were noticed on the 3rd metacarpal, 5th metatarsal, phalanx, ribs, and head of the humerus.

Ciumai (Bronze Age)

Contact: Angela Simalcsik, Ion Ciobanu

Burial mound no. 1 (T1) in Ciumai (com. Vinogradovca, Taraclia district, Republic of Moldova) was investigated by rescue excavation in 2015. The mound was located in the south of the Republic of Moldova, on the first terrace of the Salcia River that flows into the Ialpu River. Geographical coordinates: N 45°47'40.09" / E 28°34'12.39". The mantle of mound underwent interventions both during the construction of the Ialpu Lake – Taraclia artificial Lake Canal in the '80s of the 20th century, and during the rehabilitation period of the M3 national road. This archaeological objective provided at least 40 archaeological complexes, of which 14 graves. The burial mound was built in three stages, in different epochs, first by the late Eneolithic communities of the post-Mariupol (primary grave), the early Yamnaya communities (four

graves), the late Yamnaya communities (six graves), the Sarmatian communities of the first centuries of the Christian era (a grave), 21 pits, four hearths and a ditch from the late Middle Ages or the modern period.

- I10397/CIUM-T1G1 (phalanx), genetically male, adult.

Grave 1 from burial mound no. 1 in Ciumai, assigned to the Bronze Age, was found in the south-eastern sector of the tumulus, 7.5 m away from the central landmark, at a depth of 0.52 m. The grave and the skeleton was destroyed, from the skeleton being preserved only the bones of the lower limbs, after the position of which, we deduced that the deceased was facing north. All the preserved bones bear intense traces of red ochre. In the immediate vicinity of the skeleton and under it were reported traces of dark brown rot from vegetable bedding. To the left of the deceased, in the lower part of the left tibia, was discovered a fragmentary ceramic vessel. The skeleton is incomplete, in poor preservation state. It comes from a male individual, with biological age at the time of death between 20-40 years (young adult), with a robust skeleton.

Reference: (383)

Crihana Veche (Early, Middle and Late Bronze Age)

Contact: Angela Simalcsik, Ion Ciobanu

Burial mound no. 9 (T9) in Crihana Veche (Cahul district, Republic of Moldova) was investigated in 2015 by preventive excavations. The mound was located on the northern edge of the locality, 15 m west of the national road R34, A283 Cahul-Giurgiulesti, on the first terrace of the Prut River. Geographical coordinates: N 45°51'47.53" / E 28°11'29.76". At the beginning of the research, the height of the mound was about 1.25 m, and the diameter was about 24x27 m. 20 burial graves and other features dating from different epochs have been discovered. Three major cultural-chronological phases were captured in the construction of the mound. The first is the late Eneolithic, through the Hadžider-Cernavodă I culture (grave 10 and two semicircular trenches that flanked the grave in the north-northeast – south-southwest). The next horizon is represented by a group of four graves belonging to the early Yamnaya communities, followed by another group of six Yamnaya graves, but from the late phase, made in the same mantle. Related to the third mantle is the group of eight graves from the late Bronze Age, which form a specific group, merged in the south-eastern sector of the mantle. The last chronological horizon is represented by a Sarmatian grave from the first centuries of the new era.

- I7862/CRIV-T9G5 (petrous bone). Genetically undetermined sex, adult.

Grave 5 from mound no. 9 (T9) in Crihana Veche, assigned to the late Yamnaya communities, was reported in the south-eastern sector of the mound, 9 m away from the central landmark and at a depth of 0.83 m. The grave pit could not be identified. The deceased was placed in a crouched position on his back, with his head facing east. The skull was face up. The left upper limb (only the humerus has been preserved) was extended along the trunk, and the right was bent at the elbow, with the palm placed in the lumbar region of the spine. The legs were bent to the left. The degree of crunching of the legs is medium. The skeleton, which is partially represented and poorly preserved, comes from a male of about 40-45 years (middle-aged adult). The bones are robust, with extremely pronounced muscle insertions, including the limbs, girdle bones and occipital. Dental health is very good. Enthesopathic changes in the bones

of the lower limbs and degenerative changes in the spine betray his terrestrial/land mobility and physical overload.

- I10420/CRIV-T9G13 (petrous bone), genetically female, adult.

Grave 13 from burial mound no. 9 in Crihana Veche, assigned to the late Bronze Age, were discovered in the south-south-western sector of the mound, at 9.2 m from the central landmark, at a depth of 1.43 m. The funeral chamber could not be identified. Judging by the preserved skeletal remains, the deceased was placed in a crouched position on the right side, with the skull to the east. The skull was placed on the right side, facing north. The hands were bent at the elbows, the left one being placed perpendicular to the torso. Only the humerus was preserved from the left hand. The lower limbs were crouched tightly on the right side. The skeleton, which is gracile, moderate to poorly represented and poorly preserved, comes from a female of biological age at the time of death in the range of 40-45 years (middle-aged adult). Her state of dental health is precarious (numerous antemortem tooth losses, almost total edentulation - periodontitis).

- I10421/CRIV-T9G14 (petrous bone), genetically male, adult.

Grave 14 from mound no. 9 in Crihana Veche assigned to the late Bronze Age was discovered in the south-eastern sector of the mound, at 12.3 m from the central landmark, at a depth of 1.80 m. The funeral chamber could not be identified. The deceased was placed in a crouched position on the left side, with the skull to the east. The skull was placed on the left side, facing south. The hands were bent at the elbows, placed in front of the rib cage, the lower limbs being squatted strongly, on the left side, with the feet outstretched. In the immediate vicinity of the skeleton and below it, traces of brown rot from vegetable bedding were reported. The skeleton, which is well represented and good preserved, comes from a male of biological age at the time of death in the range of 50-60 years (old adult). On dentition it has advanced wear, some antemortem tooth losses and massive deposits of supragingival calculus. The skeleton is very massive, at the extreme limit of robustness. The muscle insertions are very well developed, both on the bones of the limbs and on those of the girdles. The skeletal stature is very high, about 180 cm. At the postcranial level there is ample evidence of degenerative osteoarthritis, but also of extreme physical activities, including riding.

Burial mound no. 5A (T5A) from Crihana Veche (Cahul district, Republic of Moldova) is part of the tumular necropolis named *La Pietricei*, located on an upper terrace of the Prut River (170-180 m). At the beginning of research (in 2014) the necropolis numbered over 20 mounds. Geographical coordinates: N 45°50'45" / E 28°11'41". The mound was investigated in 2016 by preventive excavation. The mantle of mound no. 5A was fused with the mantle of a neighbouring mound (mound no. 5), located just 2 m south of it, so that at the start of the research they formed the "eight" in the plan. Burial mound no. 5A was built in two stages. The first mantle was built in the middle Bronze Age, above grave 2, assigned to the Multi-cordoned Ware culture. The second mantle is directly related to grave 1 (Scythian culture), disturbed / robbed in antiquity.

- I10412/ CRIV-T5AG2 (petrous bone), genetically female; juvenile/adolescent.

Grave 2 from mound no. 5A in Crihana Veche, assigned to the Multi-cordoned Ware culture, was discovered in the eastern sector of the mound, 5.9 m east of the central landmark and at a depth of 0.83 m. The pit of the grave was approximately rectangular, with rounded corners. The funeral chamber was provided in the southern, eastern and northern part with a step

(width - 0.1 m in the southern part, 0.16 m in the eastern part, 0.45 m in the northern part), located at a depth of 0.43 m from the level of contour capture. The chamber had a trapezoidal shape (1.45x1.2 m), with slightly arched sides and rounded corners, being oriented in the south-southwest-north-northeast direction; the depth at the level of the step was 0.3 m. At the bottom, the pit was up to 1.30 m wide. The deceased was placed on the bottom of the pit, in a crouched position on the right side, with his head to south. The skull was on the right side, facing east. The hands were bent at the elbows, placed in front of the chest, slightly displaced, the lower limbs being crouched in the middle, on the right side. In front of the rib cage, at 0.10 m from the eastern wall of the pit, was placed a ceramic vessel - a bitronconic pot, with a flat bottom and a shoulder highlighted in the upper part of the vessel, with a slightly highlighted and cut lip. The skeleton, which is complete and very well preserved, comes from a juvenile individual, with a biological age at the time of death in the range of 16-18 years, with masculine morphological characteristics - robust, with large joint surfaces, accentuated muscle insertions, skeletal stature of 167 cm.

Burial mound no. 12 (T12) from Crihana Veche (Cahul district, Republic of Moldova) it was located on the second terrace of the Prut River (120-130 m). Geographical coordinates: N 45°50'45" / E 28°11'41". The mound was investigated in 2016 by preventive excavation. At the start of archaeological investigations, the mound was about 1.25 m high and about 28 m in diameter. 23 graves and three ritual features (?) were discovered. The burial mound was built in four stages, at different times. The first mantle was built above grave 10, assigned to the late Eneolithic communities of the Hadjider-Cernavodă I, two pits (of worship?) being connected to this complex, in one of them a vessel was discovered. The second mantle was raised above grave 6 assigned to the early Yamnaya communities, the mantle in which four other Yamnaya graves were later dug. The third mantle was raised above grave 5 (Yamnaya, middle phase), afterwards five other Yamnaya graves were arranged. The next layer of the mound (fourth) was built above grave 13, which belongs to the Multi-cordoned Ware communities, and later five other graves of Multi-cordoned Ware culture and Sabatinovka culture were dug in this mantle. The Antiquity layer is represented by two Sarmatian graves from the 2nd-3rd centuries CE. The last chronological phase of mound is represented by a grave belonging to the migrant communities from the Middle Age.

- I10436/ CRIV-T12G13 (tooth), genetically male, adult.

Grave 13 from mound no. 12 in Crihana Veche assigned to the Multi-cordoned Ware culture was reported in the southern sector of the mound, at 11.5 m from the central landmark, at a depth of 1.82 m. The pit had a rectangular shape (2.65x2.20 m), with rounded corners and a slightly arched south side and was provided with a step, oriented east-west, located at a depth of 0.50 m from the contour. The funeral chamber had a quadrilateral shape (2.05x1.60 m), with rounded corners, and a depth from the step of 0.45 m. The skeleton was identified at the bottom of the pit, in a crouched position on the left, with his head to the east. The skull was facing south. His hands were bent at the elbows and brought to the chest. The legs were placed on the left side. The degree of crouching of the legs was medium. In the immediate vicinity of the skeleton and below it, traces of brown rot were reported from the vegetable bedding. In front of the rib cage, above the lower part of the hands, a ceramic vessel was discovered - a truncated cone-shaped pot, with a slightly highlighted flat bottom and slightly bulging walls at the top. Between the anatomically connected tibiae of the deceased was discovered a buckle made of bone, provided

with a hole. The skeleton, which is complete and very well preserved, comes from a male with a biological age of about 50-60 years (old adult), with a robust bones, extremely accentuated muscle insertions, a skeletal stature of about 175-182 cm. The skull has post-coronal depression associated with a slight intentional cranial deformation. Regarding the state of health, we mention a series of dental pathologies (calculus, severe gingival infection on jaws, antemortem tooth losses, periodontitis), linear enamel hypoplasia as an indicator of physiological stress produced in childhood), and generalized degenerative osteoarthritis. The enthesopathic changes on all the bones of the limbs and belts, together with the characteristics of “rider's syndrome” and “archer's syndrome” are excellent indicators of intense physical activities. In addition, three perimortem fractures were identified - on the diaphyses of the right humerus and right ulna and on the diaphysis of the left tibia. Reddish marks from ochre were identified on the cranial and postcranial skeletal components.

References: (383, 384)

Tantăreni (Middle Bronze Age)

Contact: Angela Simalcsik, Ion Ciobanu

- I10449/TANT-G1 (phalanx), genetically male, adult.

The grave 1 from Tântăreni (Telenesti district, Republic of Moldova) was discovered accidentally in 2016, as a result of the collapse of the bank of a ravine, where several human bones appeared at the surface. Geographical coordinates: N 46°54'11" / E 29°8'20". Only the bones of the lower limbs of the skeleton were preserved *in situ*; according to their position, it was deduced that the deceased was in a crouched position, on his left side, the degree of crouching being medium to high. A bone buckle with a hole in the centre was found between the tibiae. The grave is assigned to the Multi-cordoned Ware culture. The skeleton, which is almost complete and well preserved, comes from a male individual with biological age at the time of death in the range of 30-35 years (young adult), with robust bones, high skeletal stature. Enthesopathic changes frequently associated with both terrestrial mobility and equestrian activities are highlighted in the lower limbs of these individual. Several reddish marks from ochre were identified on the right femur, right tibia and left orbit (unpublished).

- I10438/CRIV-T12G18 (petrous bone), genetically male, adult.

Grave 18 from mound no. 12 in Crihana Veche assigned to the Bronze Age was reported in the south-eastern sector of the mound, at 10.6 m southeast of the central landmark and a depth of 1.58 m. The funeral chamber was not detected. Due to the fact that only the lower limbs were preserved *in situ*, it was not possible to elucidate several aspects related to the funeral ritual. The deceased was placed in a crouched position, with his head to the north. The lower limbs had a maximum level of crouching, on the right side. The skeleton, represented only by extremely poorly preserved postcranial remains, comes from a male of about 20-25 years (young adult), with a robust bones, accentuated muscle insertions, a high skeletal stature (probably). Reddish traces of ochre were identified on the bones.

- I10439/ CRIV-T12G20 (tooth), genetically male, adult.

Grave 20 from mound no. 12 in Crihana Veche, assigned probably to the late Yamnaya communities, was reported in the southern sector of the mound, 9.7 m south of the central

landmark and at a depth of 1.52 m. The funeral chamber could not be detected. The skeleton was partially disturbed, probably by the plough blade. The deceased was placed in a crouched position on the right side, with his head to the east. The skull was placed facing north. Only part of the skull, fragments of the ribs and a few long bones of the upper and lower limbs have been preserved *in situ*. The hands were bent at the elbows, placed in front of the rib cage. The lower limbs being crouched, on the right side, the right femur displaced to the west. The skeleton, which is incomplete, extremely fragmentary and poorly preserved, comes from an adult male with a biological age of over 20 years. On some fragments from the cranial and postcranial bones reddish marks have been identified, probably from ochre.

References: (384, 385)

Purcari (Stefan Voda district, right bank of the Lower Dniester; Middle Bronze Age)

Contact: Henry M. Shephard

Kurgan 1 was located on the right bank of the Lower Dniester. Burial 9 was located in the southeast section of the kurgan, at a depth of 4.6 m. A female (25-35) skeleton was laying in an extended position on the back, head to the SW. The skeleton was lightly covered in red ochre: "*Beneath it is marked brown ashes from the mat. The buried woman laid among the stones of the lining of the Usatovo kurgan, and one of the slabs partially covered her legs (378)*". A naviform vessel was found 0.1 m from the left temple. 1 sample is included in the study.

- I20088/Pr/K1/B9, Kurgan 1, Burial 9. Catacomb culture (Ingul) (tooth), genetically female.

Romania

Popesti-Vasilati (Neolithic)

Contact: Angela Simalcsik, Catalin Lazar

During 1971-1972, on the occasion of excavation on that site, a prehistoric necropolis was identified, which contained 17 tombs, of which 16 belong to the Boian culture, Vidra phase (c. 5000-4500 BCE). The necropolis, mostly disturbed by various works and constructions, was researched in 1971-1972 by M. Sânpetru and D. Șerbănescu and assigned to the Boian civilization. 16 Neolithic graves and a Bronze Age grave have been discovered. Regarding the Neolithic complexes, 10 skeletons were oriented west-east, the rest being oriented in a close direction (southwest - northeast). Regarding the position of the deceased, 15 were deposited on the left side and only one (grave 5) crouched on the right side, the latter being also oriented west-east. Some skeletons had the upper limbs bent at the elbows and brought forward, and others had the left upper limb bent at the elbow and turned forward, with the palm resting under the head, and the right upper limb directed to the right femur. Only in seven graves was discovered a grave goods, consisting mainly of ornaments (beads from seashells, bone or copper shells, a bone ring, stone tools). The anthropological analysis of the skeletal series revealed a high infant mortality and a life expectancy at birth of 25.8 years. No individual in this group was over 60 years of age. Mortality among female is higher than in male. The skeleton discovered in grave 10 is poorly preserved, but well represented. They come from a male individual, aged 20-30 years (young adult). The cemetery was located 800 m north of the village of Popești (Călărași county, Romania), on the high terrace of the Dâmbovița River(386).

- I0739/ROM37, grave 10 (petrous bone), genetically male.

Grave 10 (I0739/ROM37) contain an individual laid in a crouched position, on the left side, oriented on directions close to east. In the neck area, four beads from the Spondylus valve were identified. From an anthropological point of view, the individual from grave 10 belongs to an adult male (386, 387). Based on the radiocarbon dating of the skeleton from grave 10, it belongs to 4895-4686 calBCE (5900±40 BP, Poz-82187).

Cârcea, Viaduct (Dolj County; Neolithic)

Contact: Mihai Constantinescu, Dusan Boric

The sites of Cârcea-*La Viaduct* and Cârcea-*La Hanuri* (Dolj County), are situated on the banks of Cârcea river, and were excavated between 1971-1975. Most of the bones are coming from the first site and they were discovered in a ditch and they were found with ceramics or animal bones; the human bones are fragmentary, and they displayed traces of breakages or fire, perimortem lesions or postmortem manipulation.

- I17835/ S XVI C2, G9, -2.6m; tooth 11b (tooth), genetically male.
- I6661/CIRC_794; F794, Neolithic timpurin, S XVII square7 C2 (molar), genetically female.

Gârlești (Dolj County; Neolithic)

Contact: Mihai Constantinescu

The cemetery from Gârlești (Dolj County) was found during a river erosion and salvage excavations from 1989 unearthed 15 skeletons, mostly from adults (only three non-adults). The individuals were buried crouched on the left side with NNW-SSE orientation (eight skeletons) and on the right side with SE-NW orientation (four skeletons); for three graves position of the skeletons is unknown. The inventory consists in two copper beads were found in two graves.

- I6662/GIRL-4; F796, Neolithic miglorin, M4 (barbat gracil) (molar), genetically female. 35-45 years old individual, crouched on the left side with NNW-SSE orientation.
- I6663/GIRL-14; F798, neolithic miglorin, M14 (barbat gracil) (molar), genetically male. 35-45 years old individual, crouched on the left side with NNW-SSE orientation. Based on the radiocarbon dating of the skeleton from grave 14, it belongs to 5613-5385 calBCE (6539±41 BP, RoAMS:326.53).

Urziceni (Bodrogkeresztur; Chalcolithic)

Contact: Cristian Virag

The Eneolithic necropolis from Urziceni is located in the free zone of the Romanian-Hungarian border at Urziceni – Vállaj, on a small terrace in the marshy valley of the Negru Brook. The necropolis was discovered in 2003 and is dated between 4300-4000 BCE, in Eneolithic period. At present, in Urziceni necropolis was excavated so far 130 graves with numerous grave goods, among which gold objects and other artefacts of special value made of copper, shell, horn and stone.

For this cultural horizon the inhumation is practiced, the deceased being placed in a crouched position, oriented E-W, lying on the left or the right side, with the head facing W or E. A general-valid observation (but there are exceptions) is that the position of the deceased on one side or the other is determined by the sex of the deceased, respectively women are seated on the left and men on the right side. Differences between sexes continue with the funeral inventory. In the graves of women, the number of vessels is bigger, 5 to 7 vessels, placed around the dead. In the area of the basin are found in many cases strings of shell beads, probably used in the ornamentation of clothing. As for men, the number of vessels is significantly smaller, 1-2 vessels, usually located near the legs, alongside with stone or copper tools, namely arrowheads, knives, scrapers, borers. The necropolis is remarkable due to its spectacular inventory: numerous ceramic pots, copper pieces (ornaments and weapons), *Spondylus* and marble adornments, lithic pieces (arrowheads, blades, axes), 8 pieces of gold, bone pieces (tools and ornaments). Thirty-nine samples are included in this study.

- I7134/URZ152; Grave 52. Genetically male (petrous bone). Adult between 50-54 years. Brother of I11906. Typical inventory for Bodrogkeresztur culture.
- I18154/E.0127; Grave 17. Genetically female (molar). Adult 20-30 years. Eneolithic period.

- I18117 (dup. I20807)/E.0061; Grave 17. Genetically female (molar). Adult 20-30 years. I18117 and I7137 are 1st degree relatives. Eneolithic period.
- I18113/E.0057 (E.0123); Grave 6. Genetically male (molar). Adolescent 14-16 years. Eneolithic period.
- I15622/1738; Grave 24. Genetically female (petrous bone). Adult 23-29 years. Sister of I7133. Eneolithic period.
- I14158/1146; Grave 9A. Genetically female (molar). Adult 25-30 years. Grave with two buried individuals, mother with child. Eneolithic period.
- I15623/1739; Grave 68. Genetically male (petrous bone). Adult 30-40 years. Eneolithic period.
- I15621/1737; Grave 25. Genetically male (petrous bone). Child 2-6 years. Eneolithic period.
- I15618/1734; Grave 43. Genetically female (petrous bone). Adolescent 15-16 years. Eneolithic period.
- I14164/1152; Grave 70. Genetically female (petrous bone). Adult 35-45 years. Eneolithic period.
- I15619/1735; Grave 65/2. Genetically male (petrous bone). Adult 18-25 years. Grave with two buried individuals. Eneolithic period.
- I15617/1733; Grave 67. Genetically male (petrous bone). Adult 23-59 years. Brother. I18114. Brother. I7135. Eneolithic period.
- I7131/URZ137; Grave 37. Genetically female (petrous bone). Adult 25-35 years. Eneolithic period.
- I14163/1151; Grave 21. Genetically male (petrous bone). Adult 24-27 years. Eneolithic period.
- I14166/1154; Grave 26. Genetically female (petrous bone). Adult 30-35 years. Eneolithic period.
- I14161/1149; Grave 60. Genetically male (petrous bone). Adult 22-27 years. Eneolithic period.
- I14157/1145; Grave 10. Genetically female (petrous bone). Adult 35-45 years. Eneolithic period.
- I14162/1150; Grave 28. Genetically female (petrous bone). Adult 39-45 years. Eneolithic period.
- I14160/1148; Grave 41. Genetically female (petrous bone). Adult 30-35 years. Eneolithic period.
- I14165/1153; Grave 51. Genetically female (petrous bone). Adult 30-40 years. Eneolithic period.
- I14159/1147; Grave 65/1. Genetically male (petrous bone). Adult 35-45 years. Grave with two buried individuals. Eneolithic period

- I15616/1732 (E.0128; E.0129); Grave 71. Genetically male (petrous bone). Young adult 17-19 years. Eneolithic period, belonging to the Bodrogkeresztúr culture.
- I20810/P6239; Grave 42. Genetically female (petrous bone). Child 4-5 years. Eneolithic period
- I18114/3151; E.0058 E.0124; P6240); Grave 2. Genetically male (molar). Adult 25-30 years. Brother I15617, Brother I7135. Eneolithic period.
- I20809/P6238; Grave 35. Genetically female (petrous bone). Adult 25-50 years. Eneolithic period.
- I20806/P6235; Grave 11. Genetically male (petrous bone). Child 6-12 years. Eneolithic period, belonging to the Bodrogkeresztúr culture.
- I7135/URZI153; Grave 53. Genetically male (petrous bone). Adult 18-22 years. Eneolithic period.
- I18116/E.0060 (E.0126; P6241); Grave 73. Genetically male (molar). Adult 30 40 years. Eneolithic period.
- I15620/1736 (P7331, 32); Grave 32. Genetically male (petrous bone). Adult 23-39 years. Eneolithic period.
- I18115 (dup. I20808)/E.0059 (P6237; E.0125); Grave 23. Genetically female (molar) Adult 23-29 years. Eneolithic period.
- I7137/URZI75; Grave 75. Genetically male (petrous bone). Child 9-12 years. Eneolithic period.
- I7127/URZI_12; Grave 12. Genetically male (petrous bone) Adult 35-45 years. Eneolithic period.
- I7128/URZI_13; Grave 13. Genetically female (petrous bone). Adult 25-35 years. Eneolithic period.
- I7136/URZI58; Grave 58. Genetically male (petrous bone). Adult 35-50 years. Eneolithic period.
- I7133/URZI44; Grave 44. Genetically female (petrous bone). Adult 35-45 years. Eneolithic period.
- I7130/URZI31; Grave 31. Genetically female (petrous bone). Adult 30-40 years. Eneolithic period.
- I7132/URZI39; Grave 39. Genetically female (petrous bone). Adult 35-45 years. Eneolithic period.
- I7129/URZI29; Grave 29. Genetically female (petrous bone). Adult 26-30 years. Eneolithic period.
- I7126/URZI_5; Grave 5. Genetically male (petrous bone). Adult 19-20 years. Middle Neolithic, Pişcolt Group.

References: (388-392)

Trestiana (Neolithic, Middle and Late Bronze Age)

Contact: Angela Simalcsik, Catalin Lazar

In 1960, the Neolithic settlement Starčevo-Criș was discovered in the point “Trestiana” (Grivița commune, Vaslui County, Romania), on the low terrace of the Bârlad River. Geographical coordinates: N 46°11'26" / E 27°40'22". The rescue excavations started in 1964, being coordinated by E. Popușoi and continued, with interruptions, until 2001. Numerous houses, hearths, ovens were unveiled. 42 graves were discovered on the surface of the settlement. Of these, according to the authors of the discovery, 11 belong to the Starčevo-Criș culture, five - to the Noua culture, three - to the Hallstatt culture, one - to the migration era, another 21 remained with uncertain cultural attribution.

- I6184/ROM23, Grave 18 (premolar), genetically male.

This grave belongs to Starčevo-Criș communities, and it was identified 1t 10 m west from house 11. There was identified a single individual, in a crouched position, on the left side, oriented on directions close to east. Funerary inventory was not found in this grave. Instead, numerous ceramic fragments have been identified over and under the body of the deceased, which represent a type of funeral treatment specific to the Starčevo-Criș communities. The skeleton belongs to a mature male, 40-50 years old (Popușoi 2005; Lazar 2021).

- I6185/ROM31, Grave 34 (incisor), genetically male.

This grave belonged to an adult and were identified not far from the A/L13 house, at 0.85 m depth, in the yellow layer with calcareous concretions. In a crouched position, the skeleton is relatively well preserved, sitting on the left side and facing north. No inventory. In the absence of any funerary goods, this grave was not attributed to a historical period but based on radiocarbon dating (3430±25 BP, PSUAMS-3982 / 1873-1630 calBCE), it belongs to the Bronze Age.

- I6186/ROM33, Grave 17 (molar), genetically female.

The grave was identified 1 m south from the A/L 17 house, at a depth of 0.50 m, in the yellow layer with calcareous concretions. The skeleton is very poorly preserved, and it belongs to a baby. The deposition position was crouched, with the head oriented to the north. The grave does not contain inventory. Initially, this grave was not attributed to a historical period, but based on radiocarbon dating (3290±25 BP, PSUAMS-3873 / 1615-1506 calBCE), it belongs to the Bronze Age.

References: Trestiana(393-397)

Ploiești Triaj (Prahova County; Bronze Age)

Contact: Andrei Soficaru

In 1941-1943 at Ploiești-Triaj (Prahova County) were excavated two mounds with burials dated in Bronze Age. The second one had 47 m diameter and 1.50 m height, and a number of 21 burials were found (one from Medieval period, three from 4th century CE and 16 from Bronze Age).

- I10494/ PLOI-8; Tumul 2, M8 (petrous bone), genetically female.

Adult individual, laid on lateral left decubitus, with the legs crouched and arms in front of the skeleton, orientated 340°NNW-160°SSE. It was buried in a mound with ochre on the left elbow.

Cârlomănești Arman (Bronze Age)

Contact: Mihai Constantinescu

The site of Cârlomănești, County Buzău, consists of a multilayered settlement covering the entire period of evolution of the Bronze Age Monteoru culture (2300-1500 BCE) and, on the adjacent hill *Arman*, there is a cemetery of which, up to the present, 143 graves were investigated. The excavations in the cemetery started in 2001 and continues to this day. The archaeological inventory and the radiocarbon dates suggest that the bulk of the graves are dated in the early/middle stages of the Monteoru culture (2280-1750 BCE). The vast majority of the graves have their pits filled up with river stones, brought from the nearby valley, being buried at shallow depths (0,05-1 m), which suggests that in the Bronze Age, most of these structures were visible on the soil surface. Five graves have catacombs as a funeral structure, a construction typical for the populations which wandered the nearby plain. Most of the deceased are inhumated, six graves (8.58%) having cremated human remains. In contrast to the other Monteoru culture cemeteries, more than half of the graves have multiple burials (2-5 individuals), the individuals being buried in different stages, in many cases the bones of the older burials being gathered and deposited with their inventory on different sides of the funeral pit. The common position of the deceased is lateral decubitus with the legs crouched on the left side (rarely on the right side) with their skulls-oriented westwards. More than 90% of the graves have funeral inventory, consisting in ceramic, bronze, gold, and silver objects, amber, faience and kaolin objects, almost exclusively female adornments.

- I10561/CARM-46A; M46A (petrous bone), genetically male.

30-50 years old individual, laid on lateral decubitus with the legs crouched on the right side, oriented 270° V - 90° E. He was buried in a rectangular pit with stones deposited on the corners with two ceramic vessels as funerary inventory.

- I10480/CARM-44; M44 (petrous bone), genetically male.

30-40 years old individual, laid on lateral decubitus with the legs crouched on the left side, oriented 239° VSV - 59° ENE. The skeleton was buried in a complex funeral structure, with a rectangular shaft filled with rivers stones, which had a hearth (on which a fire was made after the

burial) towards the bottom and a catacomb on its south side where the individual was buried. Only two ceramic fragments were found among the stones from the shaft.

- I10482/CARM-55; M55 (petrous bone), genetically female.

30-50 years old individual, laid on dorsal decubitus with the legs crouched on the left side, oriented 263° VSV - 83° ENE. She was buried in a rectangular pit with river stones marking off its bottom and outer limits and had a rich inventory consisting in three ceramic vessels, one bronze bracelet, three bronze loop rings, two bronze needles, and six tubular kaolin pearls.

- I10559/CARM_26A; M26A (petrous bone), genetically male.

6-7 years old individual, laid possibly crouched on the left side, oriented towards SSW. Buried together with another sub-adult, in an oval structure made of river stones with four ceramic vessels deposited near the skeletons.

- I10481/CARM-51A (petrous bone), genetically male.

9-13 years old individual, laid on lateral decubitus with the legs crouched on the left side, oriented 270° V - 90° E. Buried together with another sub-adult, in a rectangular pit filled with river stones and had a rich inventory consisting in five ceramic vessels.

- I10562/CARM-80A (petrous bone), genetically female.

30-40 years old individual, laid on lateral decubitus with the legs crouched on the left side, oriented 266° VSV - 86° ENE. She was buried in a simple oval shape pit, being placed face to face with a subadult, with two vessels, a loop ring and a ceramic spindle whorl as funeral inventory.

- I10483/CARM-58 (petrous bone), genetically female.

8-9 years old individual, laid on lateral decubitus with the legs crouched on the left side, oriented 241° VSV - 61° ENE. The skeleton was buried in a pit grave, with a rectangular shaft filled with river stones and a catacomb on its northern side, where the individual was buried, with two vessels deposited near its tibiae.

- I10479/CARM-33B (petrous bone), genetically male.

18-25 years old individual, laid on lateral decubitus with the legs crouched on the right side, oriented 219° SSV-39° NNE. He was buried in an oval shape pit, underneath another adult individual, with no funeral inventory.

- I10558/CARM-19 (petrous bone), genetically female.

40-50 years old individual laid on lateral decubitus with the legs crouched on the left side, oriented 264° VSV-84° ENE. He was buried in a rectangular pit filled with river stones with two ceramic vessels as funerary inventory.

Târgșoru Vechi (Bronze Age)

Contact: Alin Frînculeasa and Bianca Preda-Bălănică

Grave 1, dated to the Early Bronze Age, was discovered in 2014 during the preventive archaeological research carried out at Târgșoru Vechi, Prahova County, in Southern Romania.

The burial was located within the ruins of the ‘Biserica Albă’ (‘White Church’), in the space destined for the altar. It was partly disturbed by medieval inhumation and re-inhumation burials. The deceased was laid crouched on the left side, the arms were bent and seem to have been brought to the chin, the legs were strongly flexed. The orientation was on the ENE-WSW direction. The grave goods consisted of a vessel placed near the upper limbs, and a copper artefact found about 0.15 m south of the bones of the lower limbs. The pot was partially destroyed by medieval burials, however the truncated shape with slightly arched body walls could be reconstructed. The thickened lip marked by a horizontal incision, below which four elongated buttons were applied symmetrically, assign it to the local Early Bronze Age pottery traditions (Glina culture). The copper artefact had a length of 33 mm and a maximum thickness of 8 mm, it was square in section, with thinned ends. The bio-anthropological assessment of the human remains determined the individual was a female. The synostosis of cranial sutures indicated 34.7 - 41.10 years; the right auricular surface indicated 35 - 39 years. No pathological changes were observed. The ¹⁴C date of the burial indicated: PSUAMS-3996 = 3980±25 (BP/2574-2459 calBCE, sigma 2, 95.4% probability).

- I7152/TARGV-1, Târgșoru Vechi M.1 (petrous bone), genetically female.

References: (398, 399)

Smeeni (Bronze Age)

Contact: Alin Frînculeasa and Bianca Preda-Bălănică

The burial mound from *Smeeni Movila Mare*, located in Buzău County, Southern Romania, was investigated in 1959 in order to rescue this archaeological site already partially destroyed in the southern and the south-western area, and endangered by unauthorized excavations. It was about 4 m high and had a diameter of 55×49 m (NS-EW). Older habitation layers were identified under the mound, one dated to the Eneolithic period, the Boian culture (first half of the 5th millennium BCE), and another subsequent one contained habitation structures assigned to the Horodișteștea-Foltești horizon (second half of the 4th millennium BCE). These first two levels were almost entirely destroyed during the building of the mound, as a consequence of land use. Thirty burials were unearthed, to which are added four more that were destroyed by excavations performed prior to the beginning of the archaeological research, but which could be recorded by the archaeologist. All of them were inhumation burials. Six phases of burials were identified according to the stratigraphic observations, to some characteristics of the burial ritual (the type of grave pit, the position and orientation of the deceased), as well as to the items placed as grave goods. The first two were assigned to the Yamnaya communities, the third to the catacomb burials, the fourth to the Middle Bronze Age (the Tei culture), while the last two were attributed to the Sarmatians (2nd-3rd centuries CE) and to the Late Middle Ages (18th century CE).

The burials of the first phase were covered with small mounds, with diameters ranging between 7-11 m and heights between 0.9-1.30 m. Subsequently, over these mounds was raised an additional layer that covered and integrated them into a single structure that reached a diameter of 38×32 m and a maximum height of 3.5 m. The burials of the second phase, divided into two sub-phases, pierced through this mantle. Due to the destruction of a segment of the mound, the chronological relation between the burials of the second and third phases could not be established. However, they were considered stratigraphically subsequent to those of the first

phase. As regards the burials of the fourth phase, several criteria were taken into account, such as the grave goods closely related to Tei culture (Middle Bronze Age) as well as the oval shape of the burial pit. The other two phases (Sarmatian and Medieval) were identified based on specific grave goods and burial rituals.

Grave 25 was discovered in sector III of the mound, towards its margins, in trench 8a. The pit was oval in shape, 1.38 m long and 0.68 m wide. The maximum depth reached -1.37 m from the mound and -0.95 m from the excavation level. The deceased was placed in a crouched position on the left side, oriented on the NE 51° - SW 231° direction. The upper limbs seem to have been disturbed, the lower limbs were flexed and oriented to the left. No traces of ochre were identified, nor any grave goods, but among the osteological remains two ovicaprine bones (tibia and talus) were identified, probably resulting from a food offering. Stratigraphically the grave was assigned to the fourth phase of mound use, and chronologically to the Middle Bronze Age (Tei culture). The bio-anthropological assessment of the human remains indicated the deceased was a young adult, about 30 years. In the absence of the pelvic girdle, reservations were expressed regarding the secure attribution of sex, however inclining to the female sex. Genetically, the individual was a male. The stature was calculated to 169 cm. The ¹⁴C date of the burial indicated: DeA-14448 = 3651±28 BP (2135-1941 calBCE, sigma 2, 95.4% probability).

- I12828/M25, Smeeni, Gr 25 (molar), genetically male.

References: (400, 401)

Brăilița (Medieval)

Contact: Andrei Soficaru

- I17642/2702; M10A (molar), genetically male.

The skeleton is a male, 30-45 year-old, with osteoarthritis and three trephinations on the skull

Ploiești Triaj (Medieval)

Contact: Andrei Soficaru

In 1941-1943 at Ploiești-Triaj (Prahova County) were excavated two mounds with burials dated in Bronze Age. The second one had 47 m diameter and 1.50 m height, and a number of 21 burials were found (one from Medieval period, three from 4th century CE and 16 from Bronze Age).

- I10495/PLO1_9, Tumulus 2, Grave 9 (petrous bones), genetically male.

Adult individual, laid on dorsal decubitus with upper limbs along the body and lower limbs stretched and parallel, orientated W-E, no inventory.

Serbia

Podlokanj; The Južne bašte necropolis (C_BA)

Contact: Lidija Milasinovic

The Južne bašte necropolis is situated in the village Podlokanj in the north part of Banat, Serbia. The necropolis was excavated in the period from 1996 to 2001. Total of 54 graves were found. Based on the material from graves it is concluded that the necropolis belongs to the Copper Age, Tiszapolgár and Bodrogkeresztúr cultures. All the grave were inhumated skeletons in orientation East-West, males on the right and women on the left side, both in the flexed positions with the face toward North, i.e. South. Two samples are included in this study.

- I17915/3561; PD14 (petrous bone), genetically male.
- I17914/3560; PD2 (petrous bone), genetically female.

Vojlovica – Humka (Early Bronze Age)

Contact: Vojislav Djordjević, Piotr Włodarczak, Mario Novak

The burial mound in Vojlovica was investigated in 1965 and 1969 as part of a rescue excavation. The site is located on the loess terrace between the valleys of the Danube and Tamiš rivers. The Vojlovica barrow is one of the few fully explored mounds in the southern part of the Pannonian Plain, associated with the Yamnaya communities. It had a diameter of ca. 35 meters and a height (preserved) 1.5 meters. A grave pit was located under the mound in the central part. It had the form of a chamber with dimensions of 1.75 x 0.9 m and a depth of 0.8 m. A characteristic element of the construction was a wooden roof, consisting of longitudinally oriented planks 4 m long. At the bottom of the grave, traces of six symmetrically arranged stakes were discovered - a structural element typical of barrow features connected with the Yamnaya communities. The deceased was placed on a mat, in the supine position, with the crouched lower limbs and the knees pointing upwards. The skeleton, especially the skull, was sprinkled with ocher. Two massive silver hair-rings were discovered by the head. The burial from Vojlovica therefore presents the features typical of the funeral ritual of steppe communities of Eastern European origin. Based on radiocarbon marking, the grave from Vojlovica is dated 2920-2884 calBCE (Poz-88701: 4290 ± 35 BP).

- I11446/341; central grave (bone), genetically female.

The skeleton of an adult individual (over 40 years; Fig. S 21) was fragmented and exhibited extensive post-mortem cortical damage. Degenerative osteoarthritis on the left shoulder, left elbow, and the right knee.

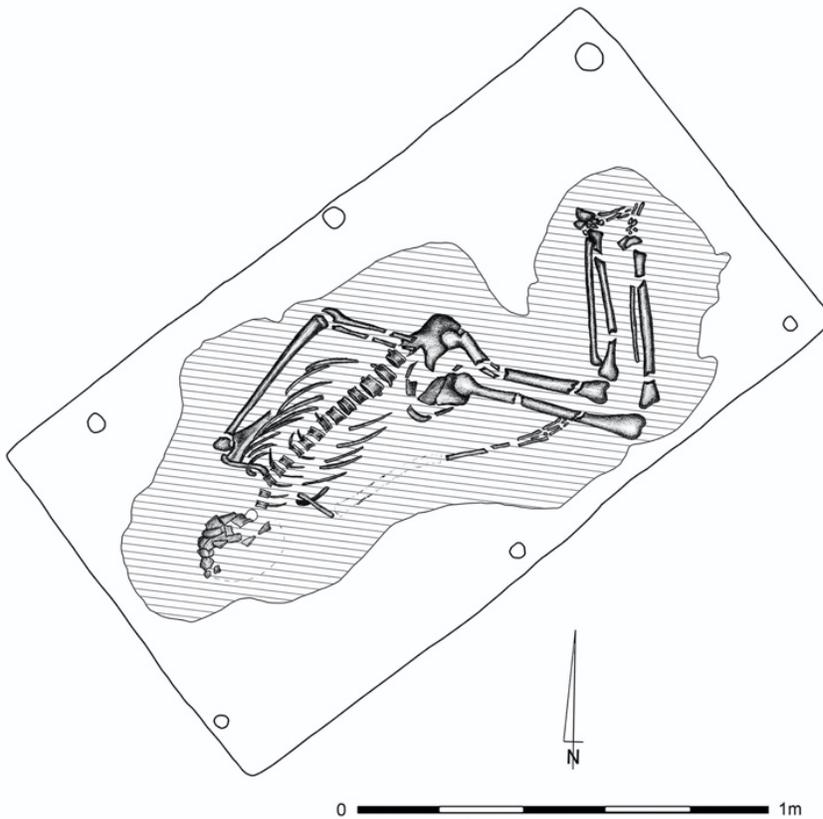


Fig. S 21 Drawing of a female burial from Vojlovica.

Mokrin Necropolis (Early Bronze Age)

The “Selište-Lalina humka” Early Bronze Age necropolis (so called Mokrin necropolis) is situated at the village Mokrin periphery. A total of 312 graves were found during the period from 1958 to 1969. All individuals are buried skeletally in a flexed position in a orientation in relation to the sides of the world and laid on the left or right side depending on the sex. Most individuals are buried with different grave goods.

- I16803/2792, Grave 55 (petrous bone), genetically female.

Nearly oblong grave pit with rounded corners, flat bottom and vertical sides. The orientation of the grave pit is south-north with slight deviation. The pit was filled by loess mixed with humus. Dimensions 100x80cm. It was found at a depth of 1,270m and dug very deep – up to 1600m (*).

The flexed skeleton, orientation south-north with deviation of 17° eastward, rested on the right side facing toward the south-east. The arms were flexed with bent hands reaching the chin. The legs were flexed and the femurs drawn high to the chin making an angle of 110°, the shins were drawn to the femurs and the feet extended. The skeleton, rather well preserved, belonged to a girl of age Infans II. Length of the skeleton 80cm.

Grave goods: In front of the face, on the finger-tips, a beaker with a handle, with ball-shaped bulge, unemphasized bottom and moulded transition shoulder-neck on which, opposite the

handle, there is a triangular ornament in relief turned by its base toward the mouth. Color grey. H-10.5, diameter of the bottom 2,0, of the mouth 5,7cm.

A necklace consisting of three pierced fangs of domestic dogs, two cylindrical bones cut short and 12 greenish kaolin beads (11 of them round and one biconical)

- I17916/3562, Grave 120 (petrous bone), genetically male.

Nearly oblong grave pit with rounded corners and flat bottom. Orientation north-south. It was filled by humus mixed with sand. Dimensions: length 124, width 75, depth 0.82cm. The eastern side of the pit was damaged when grave 119 was dug (**).

The flexed skeleton, orientation north-south, was laid on the left side facing eastward. The arms were flexed at the elbows with hands in the front of the skull. The knees were bent high, at an angle of 110° with regard to the body, the shins were drawn quite close to the femurs. The skeleton, rather well preserved, belonged to a man of age Maturus. Length of the skeleton 75cm. No grave goods.

References: (402):67, 98-99

Ostojicevo Necropolis (Early and Middle Bronze Age)

The “Stari Vinogradi” necropolis at the village of Ostojicevo belongs to Early and Middle Bronze Age. A total of 285 graves were discovered out of which 77 belong to the Early Bronze Age Maros culture (buried in a deeper level). The rest of 208 belong to Middle Bronze Age, i.e. late phase of Maros culture with different influences of Vatin and Hugelgraber cultures. Among 208 graves there are 103 graves of children (mostly newborn and Infans I) buried inside the urns following existing practice (Maros culture burial practice). The material is non-published. 4 samples are included in this study.

- I16814/3151; OS 160 (petrous bone), genetically male.
- I17912/3558; OS 013 (petrous bone), genetically female.
- I17913/3559; OS 002 (petrous bone), genetically female.
- I16813/3150; OS 119 (petrous bone), genetically male.

Grave (Urn) 2

A grave pit is not recognized.

Skeleton belongs to child – Infans I and was found at the bottom of the urn.

The urn is high with small flat bottom, biconical shape and with flaring rim. At the transition from the neck to the shoulder there are two parallel shallow flutes above which are plastic decorations. Below the flutes there are sheaf made from four shallow flutes with garlands between. Color is dark gray.

Grave (Urn) 13

A grave pit is not recognized.

Skeleton was found inside the urn (the urn was laid down with the opening toward north) buried in flexed position in orientation N-S (head-feet), on the left side. The arms are next to the body, the legs are strongly bent at the knees. The skull is at the opening, the feet at the bottom of the urn. The skeleton belongs to child - Infans I.

The urn (big pot) is with small and flat bottom. The transition from the neck to the shoulder is stressed and there are groups of two nipples. From the rim to the shoulder there are two massive ribbed handles. The color is gray.

Grave 119

A grave pit is not recognized.

Skeleton was buried in a flexed position, orientation N-S (with deviation of 25° towards East), on the left side looking towards East. The arms are bent at the elbows with outstretched hands in front of the face. The legs are strongly bent at the knees and pulled up to the body. The feet are outstretched. Skeleton belongs to a child – Infans II.

In front of the face there were a domestic animal ribbons and femur.

Behind the knees there was a small shallow biconical bowl with the flat bottom and moulded transition shoulder-neck. Two adjacent ribbed handles link a widely flaring rim with the shoulder. The color is gray-brown.

Grave 160

A grave pit is not recognized.

Skeleton was buried in a flexed position, orientation N-S (head-feet), on the left side, looking toward East. The arms are bent at the elbows with the upper arms close to the body. The shoulders are slightly curved towards the body. The legs are highly bent at the knees with parallel femurs and underlined lower legs.

The skeleton is poorly preserved, belongs to a child – Infans II.

No grave goods.

Padina–Gospođin Vir (Middle Bronze Age, Iron Gates)

Contact: Dušan Borić, Dragana Antonović

Padina–Gospođin Vir is situated on the right bank of the Danube in Serbia, in the area of the Danube Gorges. This site complex is composed of a series of interconnected and adjacent sites and was investigated in 1968–1970 by B. Jovanović from the Institute of Archaeology in Belgrade. Three connected coves marked as sectors I (675 m²), II (650 m²), and III (1100 m²) were investigated in the zone below 70 m asl, which was subsequently submerged beneath the reservoir created by the Iron Gates I dam. While the uncovered features at this site are largely dated to the Mesolithic and Early Neolithic, there were also Copper Age, Bronze Age, and Iron Age finds (403, 404). Burial 30, found at Sector II (block 1b, 2b), close to the surface in the layer of recent humus, was excavated on 11/07/1970. This is an articulated inhumation placed on its lateral left side in a flexed position. Physical anthropology analyses of the human remains suggested a possible female sex although genetic analyses confirmed a male sex of this individual. The individual is of old adult age. Lower right M2 (F2157, tooth 47) was used for genetic analyses reported here. Enamel from the same tooth was used for strontium isotope analysis, with the results suggesting local place of birth and early life for this individual (405). It has directly been AMS-dated to the Early Bronze Age (PSU-2379: 3885±20 BP, calibrated 2460–2296 calBCE at 95% confidence). Stable isotope analyses on the postcranial remains of this individual exhibit the values of $\delta^{13}\text{C} = -21.5\text{‰}$ and $\delta^{15}\text{N} = 12.1\text{‰}$ (Borić and Price 2012) while stable isotope analyses obtained on AMS burns from the dated tooth specimen are by and large consistent with these values: $\delta^{13}\text{C} = -21.0\text{‰}$ and $\delta^{15}\text{N} = 12.8\text{‰}$. Based on the $\delta^{15}\text{N}$ value of 12.8 ‰, there is a possibility that this individual consumed freshwater fish protein in moderate

quantities and that the obtained radiocarbon measurement needs to be corrected due to the intake of “old carbon.” We corrected this date using 545 ± 70 as the end point of a 100% freshwater diet and calculating then the percentage based on the $\delta^{15}\text{N}=12.8\text{‰}$ (54% freshwater diet). The corrected date is 3591 ± 58 BP, calibrated 2136–1767 calBCE at 95% confidence. Future ^{34}S isotope analyses on this specimen would be able to better characterize the fish protein contribution in the diet of this individual and would thus enable a better estimate of the individual’s chronological age. Metagenomic analyses of dental calculus from the same tooth specimen have also been recently reported (406). One sample is included in this study.

I5243/PADN, Grave 30 (petrous bone, molar), genetically male.

S2: Admixture modeling of Southern Arc individuals

We use the qpWave/qpAdm framework(8) to model the origins of 1,170 individuals of the Southern Arc (Methods).

A key tradeoff in this type of analysis is between (i) power to reject models (which increases with the number and data quality of individuals included in the Test population whose admixture history is under investigation), and (ii) granularity (treating individuals, sites, and periods separately to discover interesting inter-individual, geographic, and temporal patterns).

Ideally, in the service of goal (ii) we would like to test different sources for each individual separately; but, due to (i) many distinct models may not be rejected for each individual, and especially for those individuals with low data quality. Thus, goal (ii) itself may be jeopardized as individuals may be modeled in diverse ways, making it difficult to compare individuals using a common comparison basis (source populations) that will allow us to track differences of ancestry.

Typically, the (i)-(ii) tradeoff can be addressed by arbitrarily dividing samples into meta-groups (e.g., (9)) that combine individuals into populations; unfortunately, this has the downside of sacrificing granularity, counter to goal (ii), and of also rendering results subject to sampling bias, especially for clines of admixture: inferred mixture proportions are then a function of the sampling from different parts of the admixture cline or continuum (for more than 2 sources).

Here, we introduce a new way of performing qpWave/qpAdm analysis in a few stages which we outline below. Different decisions could be taken for each of these stages and should be investigated in the future, but our current implementation tests the basic idea of systematically generating a common admixture model to study comparatively a set of individuals, and of flexibly estimating ancestral proportions and differences without a priori fixing “hard” population assignments at a particular level of granularity:

1. We first perform analysis on the population considered as a whole, so as to find a model that works for the aggregate of all the individuals (“Total population”) we are trying to model.

2. We next cluster individuals based on their pairwise similarity without relying on their population labels; by doing so we can identify outliers and substructure within the Total population.

3. We infer admixture sources for each cluster inferred in step 2. In comparison to individual-based modeling we have increased power to reject models using qpWave, as each cluster contains many individuals and thus better-quality data. In comparison to modeling the Total population, each cluster is more homogeneous (consisting of a subset of the Total population grouped together by the clustering method). Thus, it may be modeled in a simpler way than the Total population for which the model must accommodate all clusters of individuals.

4. We apply the models of step 3 to all individuals, thus providing a common basis for the different individuals (within each cluster) against which their admixture proportions can be inferred.

5. Furthermore, we identify minimal sets of ancestral sources that can be used to model individuals across the different clusters, allowing us to compare clusters, populations, and individuals against each other using a common basis for the Southern Arc as a whole.

6. We finally estimate mixture proportions using the final set of sources.

The protocol outlined above allows us to derive a model that works reasonably well for the total population, clusters of individuals, and individuals themselves. Clearly, it might not be applicable for a very diverse set of individuals (say from the entire world) in which there are

multiple disjoint sets of models that are applicable for geographically distant populations (say Papuans, Greeks, and Yoruba) and the search for a single model that can accommodate all of them will either end in failure (as each model will only explain only a small subset of individuals and populations) or in a bloated model with many sources whose many parameters will be difficult to estimate effectively and with precision.

We describe the implementation of the stages of our protocol below. In all the analyses of this section we use the following set of 15 “Right” outgroup populations:

Base: Mbuti.DG(407), CHG(7), EHG(8, 9), IRN_Ganj_Dareh_N(10), ISR_Natufian_EpiP(10), Levant_PPN(10), MAR_Taforalt_EpiP(408), Mesopotamia, RUS_AfontovaGora3(75), RUS_MA1_HG(409), SRB_Iron_Gates_HG(3), TUR_C_Boncuklu_PPN(410), TUR_Marmara_Barçın_N((9) and this study), TUR_Pınarbaşı_EpiP(410), WHG(25, 75, 411)

This includes an African outgroup, hunter-gatherers from the Caucasus, mainland Europe, eastern Europe and Siberia, Epipaleolithic populations from Anatolia, the Levant, and North Africa, Pre-Pottery Neolithic farmers from Anatolia, Mesopotamia and the Levant, Neolithic farmers from Anatolia as well as early farmers from Iran.

We consider all the populations of **Base** except Mbuti also as sources (we do not include Mbuti as a source as we want all qpAdm models to use this remote Central African population as a common right basis population, and it is unlikely to have contributed to the populations of the region of interest). We also add the following sources:

Additional Sources: RUS_Yamnaya_Samara_EBA(8, 9, 34), IRN_HajjiFiruz_ChL((34) and this study), IRN_Seh_Gabi_ChL(10), IRN_TepeHissar_ChL(34)

The above additional sources are more recent in age than the sources of Base and hence less suitable to use as outgroups, so we confine their use only as Sources to account for ancestry in the Southern Arc from the north/east that may not be captured as well by the much earlier EHG/IRN_Ganj_Dareh_N included in the Base. Other more recent sources from the west (Europe) are not included as it is well established that later Europeans are descended from three sources(8, 10, 25, 36), with the addition of CHG/Iran-related ancestry in southeastern Europe and parts of the Mediterranean(3, 16, 20), all of which are included in our set of sources.

Part 1: Modeling the Total population

We begin by modeling the Total population. This gives us maximum power (as the Total population consists of hundreds of individuals) to distinguish between different models and is useful as a broad outline of the population of the Southern Arc from different times and localities considered as a whole, telling us what the main ancestries found there are.

Some of the sources...

IRN_Ganj_Dareh_N, ISR_Natufian_EpiP, Levant_PPN, Mesopotamia, SRB_Iron_Gates_HG, TUR_C_Boncuklu_PPN, TUR_Marmara_Barçın_N, TUR_Pınarbaşı_EpiP, IRN_HajjiFiruz_ChL, IRN_Seh_Gabi_ChL, IRN_TepeHissar_ChL

...include individuals of the Southern Arc and so we do not include them in the Total population, which consists of the remaining 1,066 of 1,170 individuals. We study how these sources can be modeled in terms of other populations in (11) on Neolithic origins (looking backward in time from them to trace their origins), but here we take them as given, and try to model the remainder of the Southern Arc (looking forward in time) in terms of them and other, non-Southern Arc sources.

The Total population cannot be modeled as a clade with any of the 16 sources ($p < 1e-61$) or any of their 120 combinations of pairs ($p < 0.002$). The top one of the 560 triples with feasible admixture proportions is barely not rejected at the $p=0.01$ level ($p=0.012$), but involves $61.9 \pm 1.7\%$ Mesopotamia, $11.9 \pm 0.7\%$ EHG, and $26.2 \pm 1.5\%$ TUR_C_Boncuklu_PPN ancestry, suggesting that in the coarse 3-way approximation the Total population must involve both Anatolian- and Mesopotamian-related Neolithic ancestry, but also input of eastern European ancestry.

We identify models that cannot be rejected with four sources (out of 1,820 combinations) for the Total population, listing them in Table S 1.

A	B	C	D	P-value	Mixture proportions				Standard Errors			
					A	B	C	D	A	B	C	D
EHG	Mesopotamia	TUR_C_Boncuklu_PPN	TUR_Pinarbaşı_EpiP	7.36E-02	0.115	0.605	0.151	0.129	0.009	0.019	0.179	0.179
EHG	Mesopotamia	TUR_C_Boncuklu_PPN	WHG	7.11E-02	0.092	0.632	0.253	0.023	0.012	0.018	0.016	0.009
EHG	Mesopotamia	SRB_Iron_Gates_HG	TUR_C_Boncuklu_PPN	6.23E-02	0.092	0.633	0.024	0.251	0.012	0.018	0.009	0.016
EHG	ISR_Natufian_EpiP	Mesopotamia	TUR_C_Boncuklu_PPN	1.48E-02	0.118	0.029	0.598	0.256	0.007	0.030	0.030	0.016
EHG	Mesopotamia	TUR_C_Boncuklu_PPN	TUR_Marmara_Barçin_N	6.53E-03	0.128	0.602	0.170	0.100	0.010	0.028	0.083	0.097
Mesopotamia	RUS_AfontovaGora3	SRB_Iron_Gates_HG	TUR_C_Boncuklu_PPN	4.13E-03	0.594	0.102	0.049	0.254	0.019	0.011	0.006	0.016
Mesopotamia	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barçin_N	WHG	2.87E-03	0.500	0.189	0.280	0.031	0.021	0.013	0.017	0.006
Mesopotamia	RUS_AfontovaGora3	TUR_C_Boncuklu_PPN	WHG	1.79E-03	0.589	0.104	0.257	0.051	0.019	0.011	0.016	0.005
EHG	MAR_Taforalı_EpiP	Mesopotamia	TUR_C_Boncuklu_PPN	1.56E-03	0.119	0.001	0.615	0.265	0.007	0.008	0.020	0.016
Mesopotamia	RUS_Yamnaya_Samara_EBA	SRB_Iron_Gates_HG	TUR_Marmara_Barçin_N	1.39E-03	0.506	0.185	0.032	0.277	0.022	0.014	0.007	0.017
EHG	Mesopotamia	TUR_Marmara_Barçin_N	WHG	1.37E-03	0.111	0.625	0.234	0.029	0.012	0.021	0.019	0.009
Mesopotamia	RUS_Yamnaya_Samara_EBA	TUR_C_Boncuklu_PPN	WHG	1.09E-03	0.554	0.148	0.271	0.027	0.020	0.014	0.015	0.006
Mesopotamia	RUS_Yamnaya_Samara_EBA	SRB_Iron_Gates_HG	TUR_C_Boncuklu_PPN	1.02E-03	0.558	0.145	0.027	0.269	0.020	0.015	0.008	0.016
EHG	Mesopotamia	SRB_Iron_Gates_HG	TUR_Marmara_Barçin_N	1.01E-03	0.111	0.626	0.031	0.232	0.012	0.021	0.009	0.019
Mesopotamia	RUS_MA1_HG	SRB_Iron_Gates_HG	TUR_C_Boncuklu_PPN	4.82E-04	0.605	0.083	0.045	0.268	0.020	0.010	0.007	0.017
Mesopotamia	RUS_AfontovaGora3	SRB_Iron_Gates_HG	TUR_Marmara_Barçin_N	2.31E-04	0.583	0.127	0.062	0.228	0.021	0.011	0.006	0.018
Mesopotamia	RUS_MA1_HG	TUR_C_Boncuklu_PPN	WHG	2.29E-04	0.600	0.083	0.269	0.049	0.019	0.009	0.017	0.005
Mesopotamia	RUS_AfontovaGora3	TUR_Marmara_Barçin_N	WHG	1.73E-04	0.576	0.129	0.230	0.065	0.021	0.010	0.018	0.005
Mesopotamia	SRB_Iron_Gates_HG	TUR_C_Boncuklu_PPN	WHG	1.08E-04	0.636	0.092	0.197	0.075	0.024	0.109	0.018	0.117

Table S 1 Models with 4 sources for the Total population. Models with feasible proportions in [0,1] range and $p > 1e-04$ are listed in the order of descending p-value for rank=3. Models that cannot be rejected at $p=0.01$ level are highlighted in red. The models which cannot be rejected and have low standard errors are highlighted in bold.

All plausible models (highlighted in bold) include Central Anatolian PPN farmers as a source(410), an eastern European source (EHG), and a Mesopotamian or Levantine source. Thus, in comparison to the best 3-way model, the 4-way models add a Levantine or Western/Balkan hunter-gatherer source. As the p-values of these models are low (< 0.08) we also examined 5-way models below (Table S 2), as we suspected that both Levantine and Western/Balkan hunter-gatherer sources would further improve the representation of the Southern Arc population.

A	B	C	D	E	P-value	Mixture proportions					Standard Errors					RMSE
						A	B	C	D	E	A	B	C	D	E	
ISR Natufian EpiP	Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	5.89E-01	0.034	0.481	0.177	0.017	0.292	0.042	0.043	0.012	0.148	0.154	0.100
CHG	EHG	Mesopotamia	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	5.29E-01	0.051	0.096	0.533	0.013	0.337	0.164	0.057	0.198	0.493	0.564	0.352
CHG	Mesopotamia	RUS AfontovaGora3	TUR Marmara Barcin N	TUR Pinarbasi EpiP	2.05E-01	0.003	0.566	0.172	0.081	0.188	1.825	3.845	0.195	5.825	7.35	3.637
EHG	Mesopotamia	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	WHG	1.88E-01	0.099	0.613	0.156	0.120	0.012	0.018	0.021	0.426	0.437	0.026	0.273
CHG	Levant PPN	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	1.68E-01	0.342	0.155	0.124	0.037	0.342	0.017	0.015	0.017	0.006	0.015	0.015
IRN HajjiFiruz ChL	ISR Natufian EpiP	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	1.45E-01	0.389	0.126	0.161	0.293	0.030	0.017	0.017	0.011	0.013	0.004	0.014
IRN Gani Dareh N	Mesopotamia	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	1.33E-01	0.145	0.478	0.068	0.262	0.047	0.042	0.071	0.110	2.443	2.863	1.728
EHG	ISR Natufian EpiP	Mesopotamia	TUR C Boncuklu PPN	WHG	1.30E-01	0.088	0.016	0.623	0.248	0.025	0.013	0.031	0.031	0.016	0.009	0.022
EHG	ISR Natufian EpiP	Mesopotamia	SRB Iron Gates HG	TUR C Boncuklu PPN	1.09E-01	0.101	0.613	0.014	0.181	0.091	0.014	0.020	0.014	0.031	0.016	0.022
EHG	Mesopotamia	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	1.09E-01	0.101	0.613	0.014	0.181	0.091	0.014	0.020	0.014	0.031	0.016	0.022
Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	9.20E-02	0.514	0.167	0.010	0.025	0.284	0.025	0.017	0.011	0.189	0.197	0.123
CHG	Levant PPN	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	9.15E-02	0.398	0.057	0.163	0.042	0.340	0.012	0.011	0.017	0.007	0.017	0.013
CHG	Levant PPN	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	9.10E-02	0.342	0.149	0.120	0.345	0.044	0.017	0.016	0.016	0.015	0.006	0.015
Mesopotamia	Levant PPN	TUR C Boncuklu PPN	TUR Marmara Barcin N	WHG	7.25E-02	0.099	0.628	0.172	0.074	0.026	0.015	0.032	0.076	0.093	0.009	0.056
IRN HajjiFiruz ChL	ISR Natufian EpiP	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	6.69E-02	0.397	0.130	0.152	0.035	0.286	0.019	0.018	0.012	0.005	0.013	0.014
Mesopotamia	RUS AfontovaGora3	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	5.89E-02	0.563	0.112	0.041	0.231	0.052	0.026	0.015	0.015	0.495	0.503	0.316
EHG	Mesopotamia	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Marmara Barcin N	5.86E-02	0.100	0.628	0.027	0.170	0.075	0.014	0.033	0.009	0.078	0.094	0.057
EHG	IRN Seh Gabi ChL	Levant PPN	Mesopotamia	TUR Pinarbasi EpiP	5.42E-02	0.118	0.244	0.109	0.281	0.247	0.077	3.293	1.057	4.872	5.522	2.682
Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	TUR Marmara Barcin N	WHG	4.56E-02	0.472	0.190	0.036	0.278	0.024	0.032	0.016	0.064	0.080	0.006	0.049
EHG	IRN Seh Gabi ChL	Levant PPN	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	3.72E-02	0.116	0.416	0.109	0.098	0.261	0.123	0.212	0.213	1.876	1.981	1.229
CHG	EHG	Levant PPN	TUR Marmara Barcin N	WHG	3.70E-02	0.397	0.054	0.156	0.343	0.050	0.012	0.011	0.017	0.016	0.007	0.013
IRN Gani Dareh N	Levant PPN	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	3.67E-02	0.278	0.096	0.140	0.070	0.418	0.245	0.209	0.208	1.380	1.549	0.946
ISR Natufian EpiP	Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	3.49E-02	0.073	0.445	0.193	0.261	0.027	0.025	0.027	0.012	0.017	0.005	0.019
Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Marmara Barcin N	2.79E-02	0.481	0.184	0.026	0.045	0.264	0.033	0.016	0.006	0.067	0.084	0.051
ISR Natufian EpiP	Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	2.38E-02	0.079	0.446	0.192	0.026	0.257	0.025	0.027	0.013	0.006	0.017	0.019
IRN HajjiFiruz ChL	Levant PPN	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	2.06E-02	0.409	0.092	0.182	0.288	0.030	0.017	0.014	0.012	0.014	0.005	0.013
IRN Gani Dareh N	MAR Tafarait EpiP	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	2.05E-02	0.257	0.019	0.145	0.449	0.129	0.840	0.327	0.331	4.041	4.052	2.602
Mesopotamia	RUS AfontovaGora3	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Marmara Barcin N	2.03E-02	0.592	0.115	0.055	0.170	0.067	0.031	0.013	0.007	0.072	0.085	0.522
CHG	Levant PPN	RUS AfontovaGora3	SRB Iron Gates HG	TUR Marmara Barcin N	1.94E-03	0.388	0.151	0.062	0.059	0.341	0.014	0.016	0.012	0.005	0.016	0.013
Mesopotamia	RUS AfontovaGora3	TUR C Boncuklu PPN	TUR Marmara Barcin N	WHG	1.78E-03	0.589	0.116	0.171	0.065	0.058	0.031	0.013	0.074	0.088	0.005	0.054
EHG	MAR Tafarait EpiP	Mesopotamia	SRB Iron Gates HG	TUR C Boncuklu PPN	1.740E-03	0.093	0.001	0.630	0.023	0.254	0.012	0.008	0.021	0.009	0.017	0.014
EHG	ISR Natufian EpiP	Mesopotamia	TUR C Boncuklu PPN	TUR Marmara Barcin N	1.709E-03	0.125	0.037	0.587	0.201	0.050	0.010	0.049	0.030	0.097	0.128	0.076
IRN Gani Dareh N	Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	6.11E-03	0.010	0.527	0.171	0.034	0.258	0.047	0.074	0.021	0.008	0.039	0.044
CHG	IRN Gani Dareh N	ISR Natufian EpiP	SRB Iron Gates HG	TUR Pinarbasi EpiP	6.08E-03	0.324	0.020	0.303	0.020	0.333	6.394	5.756	1.150	0.469	1.291	3.930
EHG	IRN Gani Dareh N	Mesopotamia	SRB Iron Gates HG	TUR Marmara Barcin N	5.72E-03	0.091	0.051	0.878	0.038	0.243	0.018	0.053	0.088	0.010	0.045	0.051
ISR Natufian EpiP	Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR C Boncuklu PPN	5.57E-03	0.056	0.514	0.143	0.021	0.250	0.027	0.032	0.014	0.008	0.015	0.021
ISR Natufian EpiP	Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	WHG	5.16E-03	0.051	0.514	0.149	0.262	0.025	0.027	0.031	0.013	0.015	0.006	0.021
IRN HajjiFiruz ChL	Levant PPN	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	4.99E-03	0.421	0.092	0.168	0.040	0.279	0.019	0.014	0.014	0.006	0.015	0.014
EHG	IRN Gani Dareh N	Mesopotamia	TUR Marmara Barcin N	WHG	4.62E-03	0.095	0.043	0.585	0.242	0.035	0.018	0.053	0.089	0.046	0.010	0.052
MAR Tafarait EpiP	Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	TUR Pinarbasi EpiP	3.83E-03	0.005	0.501	0.175	0.003	0.316	0.009	0.027	0.033	0.047	0.10	0.141
IRN Gani Dareh N	Levant PPN	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	3.76E-03	0.270	0.110	0.151	0.046	0.423	0.012	0.012	0.013	0.005	0.012	0.011
IRN TapeHisar ChL	TUR C Boncuklu PPN	SRB Iron Gates HG	TUR Marmara Barcin N	WHG	3.52E-03	0.343	0.107	0.021	0.108	0.422	0.167	0.179	0.132	3.531	3.568	2.248
EHG	IRN HajjiFiruz ChL	Levant PPN	TUR C Boncuklu PPN	WHG	3.15E-03	0.071	0.560	0.111	0.218	0.040	0.011	0.017	0.016	0.018	0.008	0.014
Levant PPN	Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	2.96E-03	0.025	0.474	0.203	0.269	0.029	0.022	0.026	0.014	0.019	0.006	0.019
EHG	IRN HajjiFiruz ChL	Mesopotamia	TUR Marmara Barcin N	WHG	2.80E-03	0.097	0.213	0.392	0.265	0.034	0.084	1.063	1.145	0.145	0.030	0.703
EHG	Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	TUR Marmara Barcin N	2.61E-03	0.121	0.592	0.014	0.153	0.119	0.112	0.201	0.221	0.245	0.333	0.234
Mesopotamia	RUS AfontovaGora3	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR C Boncuklu PPN	2.51E-03	0.578	0.068	0.052	0.040	0.261	0.023	0.033	0.047	0.010	0.016	0.029
CHG	Levant PPN	RUS MAT HG	SRB Iron Gates HG	TUR Marmara Barcin N	2.20E-03	0.397	0.143	0.050	0.055	0.354	0.013	0.017	0.009	0.005	0.017	0.013
EHG	IRN HajjiFiruz ChL	Mesopotamia	SRB Iron Gates HG	TUR Marmara Barcin N	2.14E-03	0.085	0.291	0.371	0.038	0.265	0.099	1.200	1.297	0.047	0.158	0.735
Mesopotamia	RUS AfontovaGora3	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	2.02E-03	0.518	0.045	0.128	0.287	0.041	0.025	0.030	0.043	0.018	0.009	0.028
EHG	IRN HajjiFiruz ChL	Levant PPN	SRB Iron Gates HG	TUR C Boncuklu PPN	1.79E-03	0.069	0.559	0.113	0.047	0.213	0.011	0.017	0.016	0.008	0.016	0.014
Mesopotamia	RUS AfontovaGora3	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	WHG	1.75E-03	0.569	0.053	0.067	0.265	0.039	0.022	0.031	0.044	0.016	0.009	0.027
Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR C Boncuklu PPN	WHG	1.68E-03	0.575	0.096	0.021	0.245	0.062	0.029	0.031	0.090	0.023	0.093	0.062
Mesopotamia	RUS AfontovaGora3	SRB Iron Gates HG	TUR Marmara Barcin N	TUR Pinarbasi EpiP	1.58E-03	0.608	0.124	0.065	0.189	0.014	0.104	0.024	0.009	0.334	0.260	0.195
Mesopotamia	RUS MAT HG	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	1.53E-03	0.515	0.026	0.147	0.275	0.037	0.024	0.018	0.031	0.017	0.007	0.021
EHG	Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	1.47E-03	0.043	0.543	0.120	0.265	0.029	0.041	0.049	0.069	0.024	0.008	0.043
Mesopotamia	RUS MAT HG	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR C Boncuklu PPN	1.42E-03	0.572	0.042	0.082	0.032	0.272	0.023	0.020	0.034	0.008	0.016	0.022
EHG	IRN HajjiFiruz ChL	ISR Natufian EpiP	TUR Marmara Barcin N	WHG	1.35E-03	0.078	0.508	0.100	0.277	0.037	0.010	0.017	0.021	0.015	0.006	0.015
IRN HajjiFiruz ChL	Levant PPN	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR C Boncuklu PPN	1.28E-03	0.469	0.125	0.138	0.040	0.228	0.021	0.015	0.015	0.007	0.015	0.015
Levant PPN	Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	1.27E-03	0.027	0.479	0.200	0.029	0.284	0.022	0.026	0.015			

Nonetheless, they establish that the number of these sources must be at least 4-5 and that when considering 5-way models these sources must include:

1. An “eastern” source representing northern Mesopotamia, the southern Caucasus, and Iran
2. A “Levantine” source representing Natufians and PPN farmers from the Levant
3. A “western” Anatolian source represented by the farmers of Northwestern/Central Anatolia
4. An “eastern European/steppe” source representing the Eastern hunter-gatherers or later steppe pastoralists
5. A “mainland European/Balkan” source representing the widely distributed Western European hunter-gatherers or the more specific hunter-gatherers from the Balkans (Iron Gates)

Part 2: Clustering of individuals

There are many ways of clustering the individuals, e.g. by applying a clustering method on PCA co-ordinates, or multidimensional scaling applied to pairwise similarities (e.g., of outgroup f_3 -statistics of the form $f_3(A, B)$ for a pair of individuals A, B). Given that our end goal is to test individuals relative to the Base set, a natural way to cluster them is to use qpWave to compute the probability of rejecting the clade of a pair of individuals Left=(A, B) against Right=Base. For individuals that belong in one of the Base populations (e.g., two individuals from TUR_Marmara_Barçın_N), we exclude their populations from the Right set.

The end result of this procedure are = 683,865 p-values $P(A, B)$ which can be viewed as a graph with weighted edges in which high $P(A, B)$ indicates that A, B cannot be well-distinguished by the Base outgroups, while a very low $P(A, B)$ indicates that they can.

We considered different ways of using these data to cluster individuals. One idea is to detect *cliques* in this graph, such that within each clique all pairs of individuals are adjacent. A drawback of this method is that it requires us to choose an arbitrary threshold (e.g. $p=0.01$) to declare two individuals adjacent, resulting in some false positives/negatives, and also discarding the useful information potentially captured by the p-values (e.g., two individuals are not adjacent if $p=1e-30$ or $p=0.009$ and adjacent if $p=0.011$ and $p=0.5$). A further drawback is that it may not work well for clines of ancestry: suppose that a set of individuals is made up of two ancestral sources in differing proportions; a chain of neighboring individuals with similar ancestry proportions along this clade may have high $P(A, B)$, but individuals at opposing ends of the cline will tend to have very low $P(A, B)$ and thus the totality of individuals of the cline will not form a clique.

We decided instead to detect *communities* in our graph data using the R package *igraph*(412) (<http://igraph.org>); these are more loosely defined as sets of individuals with many connections between them and few between different communities. Moreover, the strength of connections is captured by the weight of an edge between individuals A, B taken as the $P(A, B)$. This is a more flexible concept for which numerous algorithms are available and implemented in the *igraph* package. Note that we do not take the inferred communities at face value or suggest that they represent “real” historical communities: they are simply a way of dividing a set of individuals into large groups in furtherance of goal (i). We emphasize that a great variety of techniques could potentially be used to carry this clustering step of our framework, and we do not claim that the chosen method is best, but it serves as a reasonable implementation of this step. As we will see, our choice of methodology is validated by the observation that the the inferred communities do show a partial correspondence to non-genetic groupings.

We used the following clustering methods on our graph, listing the number of inferred communities for each of them.

- `cluster_fast_greedy(413)` [13 clusters]
- `cluster_infomap(414, 415)` [10 clusters]
- `cluster_louvain(416)` [9 clusters]
- `cluster_spinglass(417)` [10 clusters]
- `cluster_walktrap(418)` [44 clusters]

An additional method (`cluster_leading_eigen(419)`) did not converge in our application, so we did not consider it. We decided against using any of these methods on its own, as our goal is not to find the “true” communities (which may not exist in our continuous Southern Arc data), and the different methods split our individuals into 9-44 different clusters, thus being more or less prone to lumping/splitting individuals and grouping the individuals at different levels of granularity. Rather, we concatenated the community labels from the five methods, so that, e.g., Cluster3.1.5.2.5 includes individuals assigned to community #3 from “fast_greedy”, community #1 for “infomap”, and so on. There were a total of 71 such “Combined” communities, each of which contains individuals grouped together by each of five methods, thus increasing our certainty that they can be usefully co-analyzed. We note that one of the methods (`cluster_walktrap`) produces many more clusters than the others methods, but we found in practice that it was useful in separating groups of individuals that were meaningfully different from an archaeologically and geographic point of view.

Note that by creating these Combined communities we are potentially breaking down the clusters defined by each method substantially: if there was no structure in our data at all, we would expect community labels proposed by each method to be random choices independent of each other, and the number of communities to grow to such an extent that each individual would be assigned its own “Combined” community label. On the contrary, many individuals are assigned the same label by all five different methods (Table S 3; Fig. S 22; Fig. S 23) and the 17 major clusters account for the great majority (1030/1170) of the individuals.

	Mnemonic	ALB	ARM	AZE	BGR	BIH	CYP	GRC	HRV	IRN	IRQ	ISR	JOR	LBN	MDA	MKD	MNE	ROU	SRB	SYR	TUR	Total		
Cluster3.3.6.10.1	Balkan	18			28	1			64					4	8	15	13	9	5		7	172		
Cluster7.1.4.3.18	Levant		1									43	23	29							8	32	136	
Cluster7.1.4.3.5	AnatoliaMain							4				3		1								114	122	
Cluster3.1.5.2.5	EastMed				13			37	3			32	11					1				17	114	
Cluster5.2.7.6.20	SCaucasusMain		109																			1	110	
Cluster5.2.7.6.6	SCaucasusNIran	4	56							31		1										17	109	
Cluster3.4.5.2.19	AnatoliaNeol	2			6			3	8						1			3	4			27	54	
Cluster5.1.4.3.18	AnatoliaMesopotamia		1	2						4	1	1				1					3	37	50	
Cluster3.6.5.2.16	NBalkanChL				5													33	3			4	41	
Cluster3.4.5.2.5	BalkanNChL	1			7		1	2	2						1	1	4	1			4	24		
Cluster5.1.7.6.6	WestAsianMisc		9	1						4	1	2										4	21	
Cluster6.5.8.7.11	SerbiaHG																		18				18	
Cluster3.3.6.10.5	BalkanMisc1				3			1	4						2	1		1			1	13		
Cluster3.1.6.10.5	BalkanMisc2				6										2	2						3	13	
Cluster3.7.2.9.4	Elran										12												12	
Cluster3.7.2.9.2	IranMisc										11												11	
Cluster5.1.4.3.6	AnatoliaSEMisc		1							2												7	10	
Cluster6.5.8.7.3	I4582 I4607 I4655_published I4657_published I4660 I4917 I5235 I5773_published M95.SG																	4	5				9	
Cluster3.8.6.10.6	cim357.SG cim358.SG I10439 I10449 I18801_d I19488 I20086 I6185 I6186				2									5				2					9	
Cluster3.8.6.10.13	I10421 I10438 I11446 I18793 I18794 I20071 I20077 I20083 I6184				2									5				1	1				9	
Cluster3.6.5.2.5	ANI159-ANI181 ANI160 I18117_d I20807_d I2425 I2426 I2428 I2430 I2431				7													2					9	
Cluster3.2.7.6.6	I13949 I14605 I16553 I19340 I20329 I2328_all MA2196_final.SG RISE413.SG RISE416.SG		6						1													2	9	
Cluster6.5.8.7.10	I4870 I4875 I4876 I4877 I4881_published I4882 I5407																		7				7	
Cluster6.5.8.7.12	I4081_published I5238 I5411 I5436 M96.SG OC.SG																	5	1				6	
Cluster7.1.5.3.5	I20225 I20226 I20233 I20257 I8366																						5	5
Cluster3.9.5.2.5	Bon001.SG ZHAG_BON004.A0101_Luk10 ZHJ_BON024.A0101_Luk84 ZKO_BON001.A0101_Luk7 ZMOJ_BON014.A0101_Luk21																						5	5
Cluster3.8.6.10.7	I10412 I10420 I10436 I12510 I2163				1									4									5	
Cluster3.8.6.10.5	Cioclovina1_published_d I17642 Muierii2_scy193.SG scy332.SG														2			3					5	
Cluster6.5.8.7.17	I4874 I4878 I4880 I4914_published																		4				4	
Cluster5.10.7.6.6	I1661 I1662 I1665 I1674								4														4	
Cluster3.1.4.3.5	ASH2-3 I10543 I13580 I6924						1				2											1	4	
Cluster3.7.2.9.9	AH4.SG I1947 I1954								3														3	
Cluster3.3.6.2.5	I18115 I19487 I4666_published				1												1	1				3		
Cluster7.1.5.2.5	I10542 I10547																					2	2	
Cluster3.8.6.10.15	I4529 I4531																					2	2	
Cluster3.7.2.9.14	I1290 I1945								2														2	
Cluster3.6.6.2.5	I0706 I20808				1													1					2	
Cluster3.4.5.2.16	I2427 I7128				1																		2	
Cluster1.1.4.3.8	I8369 SFI-44.SG													1								1	2	
Cluster9.3.9.8.35	I5232																		1				1	
Cluster8.8.1.4.26	GB.SG																		1				1	
Cluster6.5.8.7.34	I4873																			1			1	
Cluster6.5.8.7.32	I2534																			1			1	
Cluster5.1.7.3.6	I4483																					1	1	
Cluster4.7.2.9.39	I8728								1														1	
Cluster4.7.2.9.30	I11459								1														1	
Cluster4.7.2.9.29	I11456								1														1	
Cluster3.9.5.2.24	Bon002.SG																					1	1	
Cluster3.8.6.10.42	scy303.SG													1									1	
Cluster3.8.6.10.28	I10495																					1	1	
Cluster3.8.6.10.25	cim359.SG													1									1	
Cluster3.7.7.6.6	I6661																					1	1	
Cluster3.7.7.6.2	I11476								1														1	
Cluster3.7.2.9.38	I8726								1														1	
Cluster3.7.2.9.31	I1946								1														1	
Cluster3.7.2.9.22	AH2.SG								1														1	
Cluster3.7.2.9.21	AH1.SG								1														1	
Cluster3.3.6.1.1	I14158																					1	1	
Cluster3.3.6.10.27	I10494																					1	1	
Cluster3.1.7.6.6	I6457																						1	
Cluster3.1.6.10.1	SI-41.SG										1			1									1	
Cluster3.1.5.2.44	ZBC IPB001.B-C0101_Luk2-Pinarbasi																					1	1	
Cluster3.1.5.10.5	I20183				1																		1	
Cluster2.7.2.9.33	I4097_all								1														1	
Cluster2.7.2.6.23	ALA019																					1	1	
Cluster13.7.2.9.43	WC1.SG								1														1	
Cluster12.8.6.10.41	Oase1_d																			1			1	
Cluster11.8.3.6.40	MA2195_final.SG																					1	1	
Cluster1.1.5.5.37	I8372																					1	1	
Cluster1.1.5.2.5	SFI-43.SG													1									1	
Cluster10.3.3.10.36	I5243																					1	1	
TOTAL																							1170	

Table S 3 Number of individuals within each Combined community and observations. For communities with <10 individuals we list the individual IDs of its members. We label the seventeen communities with at least 10 individuals from their area of greater representation. The labels of all 1,170 individuals can be found in Data S5.

The detailed cluster labels are indicative of the relationship between the different clusters. For example three clusters of samples from the Balkans (Balkan, BalkanMisc1, BalkanMisc2) share the pattern 3.*.6.10.* (where * is a placeholder) and a singleton cluster (Cluster3.1.5.2.44)

of the Epipaleolithic sample from Anatolia(410) shares a pattern with the Neolithic Anatolian cluster (Cluster3.4.5.2.19)

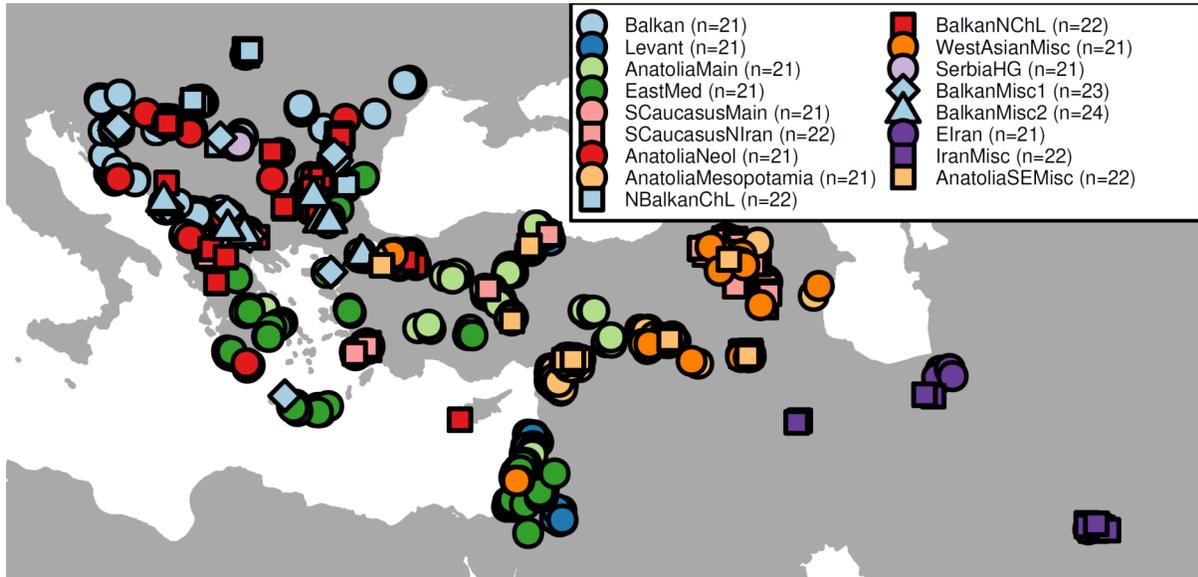


Fig. S 22 Geographical distribution of Big Seventeen clusters. Jitter is applied to data points to avoid overlap of points with the same geographical co-ordinates. Clusters are plotted in order of decreasing number of members to avoid obscuring small clusters under bigger ones.

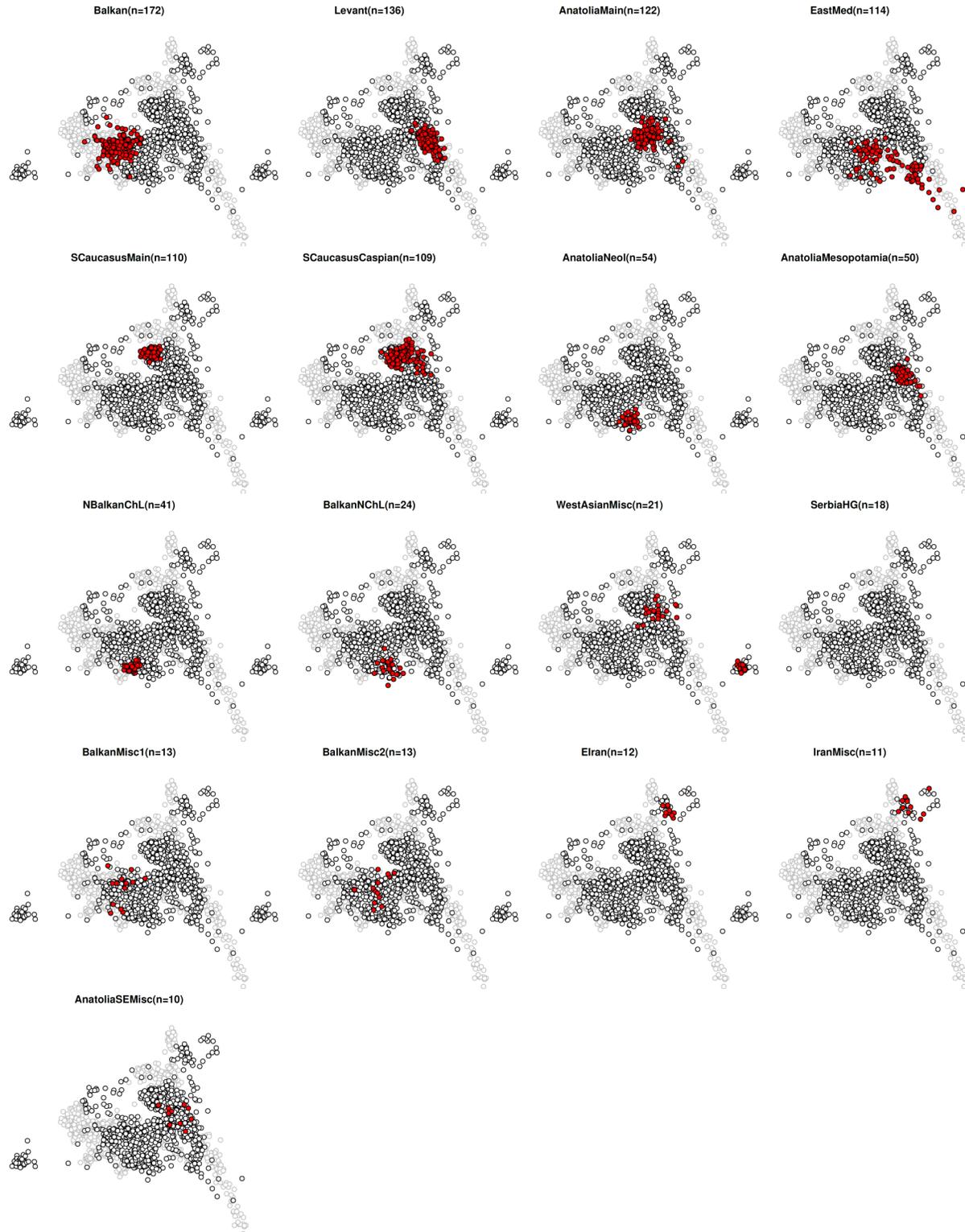


Fig. S 23 Big Seventeen clusters in West Eurasian PCA. We show the position of Southern Arc individuals assigned to each of the clusters projected on a PCA computed on present-day West Eurasians (grey).

Part 3: Admixture modeling of clusters

Having identified clusters within the population of the Southern Arc, we now proceed to model them in terms of the same sources we used for the Total population. We first show (Table S 4) the estimated mixture proportions of 14 Big Seventeen clusters in terms of the best 5-way model of the Total population (we limit analysis to clusters with at least 10 individuals, so 3 of the 17 clusters are not shown as they include individuals from the Sources and hence not from the Total population):

- The “Caucasus” (CHG) component is maximized in the Caucasus, Southeastern Anatolia and Iran and is present in all clusters except the Anatolian and European Neolithic-related clusters
- The “Eastern European” (EHG) component is maximized in the Balkans and the South Caucasus/N Iran and is minimized in Anatolia, the Eastern Mediterranean, the rest of Iran, and the Levant
- The “Levant” (Levant_PPN) component is maximized in the Levant and is appreciably present in all clusters except the Anatolia/Europe Neolithic and Iran ones.
- The “Balkan hunter-gatherer” (SRB_Iron_Gates_HG) component is maximized in the Balkans and is absent elsewhere
- The “western Neolithic” (TUR_Marmara_Barcin_N) is minimized in the Caucasus/N Iran/Levant/Iran and maximized in Anatolian/European Neolithic.

Note the interesting paradox that while the 5-way Total population model fits the Total population (Table S 2), when it is applied to subsets (clusters) of the Total population (Table S 4) p-values are quite small for some of the clusters. Conversely, further down, we model ancestry of individuals and discover that they mostly fit a 5-way model. Thus, it is important to remember that if a model “fits” (in terms of P-value) a particular set of individuals it may still include subsets that are less well-explained by the model; and, conversely, that sets that don’t “fit” (in terms of P-value) may fail because of the presence in them of a small number of non-fitting individuals. Thus, it is important to examine data at different levels of granularity (from the individual to Total population levels) as we attempt to do here.

	P-value	Mixture Proportions					Standard Errors				
		CHG	EHG	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	CHG	EHG	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N
Balkan	2.19E-03	0.229	0.140	0.077	0.105	0.450	0.010	0.009	0.014	0.006	0.014
Levant	2.24E-02	0.450	-0.016	0.393	-0.005	0.178	0.017	0.014	0.024	0.009	0.023
AnatoliaMain	1.42E-01	0.380	0.024	0.146	0.000	0.450	0.013	0.011	0.017	0.007	0.018
EastMed	2.08E-04	0.200	0.020	0.234	0.015	0.531	0.011	0.010	0.017	0.006	0.017
SCaucasusMain	1.05E-03	0.610	0.104	0.104	0.003	0.179	0.018	0.015	0.023	0.010	0.023
SCaucasusNIran	4.65E-01	0.630	0.067	0.171	-0.010	0.142	0.019	0.016	0.024	0.010	0.024
AnatoliaNeol	4.41E-02	0.032	-0.004	0.026	0.023	0.923	0.011	0.009	0.016	0.006	0.017
AnatoliaSE	2.65E-03	0.566	-0.020	0.258	-0.015	0.211	0.018	0.016	0.025	0.010	0.024
NEBalkans	8.13E-03	0.049	-0.015	0.036	0.136	0.795	0.010	0.009	0.015	0.006	0.016
BalkanChL	1.92E-05	0.005	0.034	0.085	0.017	0.859	0.014	0.013	0.022	0.008	0.023
WestAsianMisc	2.67E-03	0.613	0.009	0.181	0.000	0.198	0.022	0.019	0.030	0.012	0.028
BalkanMisc1	6.80E-07	0.177	0.184	0.161	0.100	0.377	0.029	0.028	0.042	0.017	0.038
BalkanMisc2	2.11E-01	0.292	0.067	0.123	0.054	0.464	0.021	0.020	0.030	0.012	0.030
IranMisc	1.37E-04	1.204	0.026	0.041	-0.059	-0.212	0.040	0.035	0.059	0.022	0.054
Balkan	2.19E-03	0.229	0.140	0.077	0.105	0.450	0.010	0.009	0.014	0.006	0.014

Table S 4 Clusters in terms of the 5-way Total population model.

We next model the different clusters using combinations of 1-5 sources, as we did for the Total population. For each cluster we tabulate feasible models (proportions in [0,1] and p-value>0.01) and discuss the best-fitting models which we highlight in bold

A	B	C	D	E	P	Proportions					Std. Errors					
						A	B	C	D	E	A	B	C	D	E	
IRN_Ganj_Dareh_N	RUS_Yamnaya_Samara_EBA	TUR_C_Boncuklu_PPN	TUR_Pinarbasi_EpiP	WHG		0.024	0.108	0.261	0.041	0.550	0.039	0.154	0.118	1.957	1.967	0.091
CHG	Levant_PPN	RUS_Yamnaya_Samara_EBA	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.043	0.094	0.059	0.297	0.094	0.456	0.012	0.011	0.013	0.005	0.012	
CHG	RUS_Yamnaya_Samara_EBA	TUR_C_Boncuklu_PPN	TUR_Pinarbasi_EpiP	WHG	0.060	0.153	0.231	0.118	0.453	0.045	0.177	0.148	2.018	2.039	0.086	
IRN_TepeHissar_ChL	Levant_PPN	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	WHG	0.065	0.054	0.047	0.339	0.479	0.081	0.009	0.011	0.010	0.012	0.004	
CHG	Levant_PPN	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	WHG	0.072	0.077	0.051	0.320	0.468	0.085	0.012	0.012	0.013	0.012	0.005	
IRN_HajjiFiruz_ChL	Levant_PPN	RUS_Yamnaya_Samara_EBA	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.076	0.113	0.042	0.311	0.094	0.440	0.015	0.011	0.011	0.005	0.012	
IRN_Seh_Gabi_ChL	Levant_PPN	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	WHG	0.082	0.067	0.046	0.340	0.466	0.082	0.011	0.011	0.010	0.012	0.004	
IRN_Ganj_Dareh_N	Levant_PPN	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	WHG	0.083	0.058	0.044	0.329	0.486	0.083	0.011	0.012	0.012	0.012	0.004	
CHG	Levant_PPN	RUS_Yamnaya_Samara_EBA	TUR_C_Boncuklu_PPN	TUR_Pinarbasi_EpiP	0.095	0.043	0.046	0.368	0.211	0.331	0.544	0.323	0.497	2.886	3.116	
Levant_PPN	Mesopotamia	RUS_Yamnaya_Samara_EBA	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.108	0.024	0.126	0.322	0.091	0.437	0.013	0.018	0.011	0.005	0.013	
EHG	Mesopotamia	TUR_C_Boncuklu_PPN	TUR_Pinarbasi_EpiP	WHG	0.138	0.153	0.346	0.347	0.090	0.064	0.036	0.048	1.034	1.060	0.063	
IRN_Ganj_Dareh_N	Levant_PPN	RUS_Yamnaya_Samara_EBA	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.163	0.084	0.045	0.296	0.098	0.477	0.012	0.011	0.013	0.005	0.012	
EHG	Levant_PPN	Mesopotamia	TUR_Marmara_Barcin_N	TUR_Pinarbasi_EpiP	0.182	0.263	0.014	0.371	0.091	0.261	0.283	0.467	1.700	6.307	4.514	
CHG	IRN_HajjiFiruz_ChL	SRB_Iron_Gates_HG	TUR_C_Boncuklu_PPN	TUR_Marmara_Barcin_N	0.268	0.016	0.475	0.185	0.287	0.038	4.412	6.939	0.273	3.933	6.694	
IRN_HajjiFiruz_ChL	Levant_PPN	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	WHG	0.331	0.093	0.039	0.331	0.455	0.082	0.014	0.011	0.010	0.012	0.004	
Levant_PPN	Mesopotamia	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	WHG	0.613	0.025	0.101	0.341	0.452	0.081	0.013	0.017	0.010	0.012	0.004	

Table S 5 Balkan cluster

The Balkan cluster can be well-modeled (Table S 5) as a 5-way mixture in which the Anatolian Neolithic makes about half and steppe pastoralist (Yamnaya) ancestry about 1/3 of the ancestry. The remainder of the ancestry includes ~1/10 of contribution from both hunter-gatherers of Europe (WHG) and the Mesopotamian Neolithic. The contribution of the 5th source (Levant_PPN) is negligible, suggesting that the Mesopotamian Neolithic (which resides on a CHG/Levant_PPN cline) is largely sufficient to account for this type of ancestry and thus the CHG/Levant_PPN-related ancestry of this cluster in the Total model can be largely explained via the Mesopotamian Neolithic which includes both.

A	B	C	P	Proportions			Std. Errors		
				A	B	C	A	B	C
IRN_HajjiFiruz_ChL	ISR_Natufian_EpiP	TUR_C_Boncuklu_PPN	0.018	0.503	0.366	0.131	0.017	0.017	0.012
CHG	Levant_PPN	TUR_Marmara_Barcin_N	0.024	0.430	0.401	0.169	0.012	0.023	0.022
ISR_Natufian_EpiP	Mesopotamia	TUR_C_Boncuklu_PPN	0.204	0.237	0.620	0.143	0.026	0.027	0.015
IRN_HajjiFiruz_ChL	ISR_Natufian_EpiP	TUR_Marmara_Barcin_N	0.337	0.500	0.348	0.152	0.016	0.019	0.015

Table S 6 Levant cluster

The Levant cluster is well-modeled (Table S 6) as a 3-way mixture in which the local Natufian Epipaleolithic hunter-gatherers make up half of the ancestry with the rest related to both Anatolia and Iran. (10, 420) This model makes geographical sense as Anatolia/Iran border the Levant from the north and east, with the intermediate region of Mesopotamia which indeed soaks up the Iran-related influence in one of the feasible models.

A	B	C	D	P	Proportions				Std. Errors			
					A	B	C	D	A	B	C	D
CHG	Levant_PPN	RUS_MA1_HG	TUR_Marmara_Barcin_N	0.010	0.374	0.135	0.026	0.465	0.013	0.017	0.008	0.017
IRN_Ganj_Dareh_N	Mesopotamia	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	0.020	0.047	0.528	0.085	0.340	0.049	0.084	0.014	0.046
IRN_Seh_Gabi_ChL	TUR_C_Boncuklu_PPN	TUR_Pinarbasi_EpiP	WHG	0.039	0.479	0.440	0.074	0.007	0.166	3.591	3.586	0.136
CHG	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.048	0.401	0.136	0.011	0.452	0.010	0.017	0.005	0.018
CHG	Levant_PPN	TUR_Marmara_Barcin_N	WHG	0.077	0.399	0.134	0.451	0.016	0.009	0.017	0.018	0.004
CHG	EHG	Levant_PPN	TUR_Marmara_Barcin_N	0.238	0.374	0.028	0.146	0.451	0.011	0.006	0.017	0.017
CHG	Levant_PPN	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	0.314	0.352	0.143	0.053	0.452	0.013	0.016	0.011	0.017

Table S 7 AnatoliaMain

The main Anatolian cluster can be well-modeled (Table S 7) as a 4-way mixture in which the Anatolian Neolithic ancestry is about half, CHG ancestry about a third, Levantine ancestry ~14% and non-Near Eastern ancestry of ~5% is related to steppe pastoralists. How this latter

ancestry came to Anatolia is an important question that will be further discussed, but we note (a) the absence of Balkan hunter-gatherer ancestry, which might be expected from Balkan source populations, such as e.g., those of the Balkan cluster, and (b) the low amount of the steppe ancestry overall, which is about ~6-fold lower than in the Balkan cluster. Thus, steppe populations which had a substantial influence in the Balkans as elsewhere in mainland Europe(8, 36), Central/South Asia(10, 34) seem to have had only a minor influence in Anatolia.

A	B	C	D	P	Proportions				Std. Errors			
					A	B	C	D	A	B	C	D
Levant_PPN	Mesopotamia	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	0.028	0.180	0.214	0.112	0.494	0.016	0.017	0.008	0.016

Table S 8 EastMed

The EastMed cluster is genetically and geographically diffuse (Fig. S 22 and Fig. S 23) so the inferred mixture proportions (Table S 8) are simply the averages of a cline and also point to the fact that the diverse individuals from the Balkans to the Levant making up this cluster can be modeled as derived from a number of sources (in different proportions), rather than that they are genetically very similar. The fact that this cluster was not subdivided by any of the employed methods suggests what is also visible by simple PCA (Fig. S 23) that there is no clear break between the Aegean and the Levant in genetic space, although as we will see in further analyses the two ends of this cline differ in their overall genetic makeup.

A single 4-way model fits this cluster, encompassing ancestry from the geographical Mediterranean arc from Anatolia/Europe->Mesopotamia->Levant complemented by ~1/10 steppe ancestry. We note that (a) Mesopotamia suffices to model the ancestry of this cluster, so the CHG/Levantine blend in this cluster does not require extra CHG-related ancestry, (b) as in AnatoliaMain the “European” influence in the EastMed cluster does not involve hunter-gatherer populations but only steppe ones whose modest contribution of ~1/10 was effected without extra CHG or Balkan hunter-gatherer ancestry even though presumably both were present in either the eastern (via the Caucasus) or western (via the Balkans) route into the Mediterranean region, suggesting that this was not a protracted event as any steppe migrations southward that remained in territory occupied by either CHG or Balkan hunter-gatherers would have acquired (and then transmitted) some of this ancestry southward.

A	B	C	D	P	Proportions				Std. Errors			
					A	B	C	D	A	B	C	D
CHG	EHG	Mesopotamia	TUR_Marmara_Barcin_N	0.015	0.164	0.169	0.617	0.051	0.050	0.012	0.068	0.031
IRN_HajjiFiruz_ChL	ISR_Natufian_EpiP	Mesopotamia	RUS_Yamnaya_Samara_EBA	0.033	0.603	0.034	0.075	0.288	1.497	0.426	1.808	0.110
CHG	EHG	IRN_HajjiFiruz_ChL	TUR_Pinarbaşı_EpiP	0.149	0.067	0.150	0.706	0.078	0.037	0.009	0.043	0.017
CHG	EHG	IRN_HajjiFiruz_ChL	TUR_Marmara_Barcin_N	0.217	0.060	0.155	0.690	0.096	0.052	0.009	0.066	0.023
CHG	IRN_HajjiFiruz_ChL	RUS_Yamnaya_Samara_EBA	TUR_Marmara_Barcin_N	0.263	0.026	0.577	0.290	0.107	0.044	0.053	0.013	0.020
CHG	IRN_HajjiFiruz_ChL	RUS_Yamnaya_Samara_EBA	TUR_Pinarbaşı_EpiP	0.266	0.019	0.615	0.281	0.085	0.034	0.035	0.015	0.015

Table S 9 SCaucasusMain

The SCaucasusMain cluster (Table S 9) is composed virtually entirely of individuals from Armenia within the South Caucasus region. In terms of the Total model previously discussed, this cluster was composed largely of CHG-related ancestry, but it fits well a model in which the CHG ancestry is replaced from ancestry related to Chalcolithic Iran (Hajji Firuz). These observations are not inconsistent with each other as Iran and the Caucasus share deep common ancestry,(10, 34) and it makes sense that the populations of Armenia of Chalcolithic and later

date share common history with contemporary populations of Iran rather than having evolved in complete isolation from them since the Paleolithic date of the CHG samples. (7)

Anatolian-related ancestry in this cluster reaches only $\sim 1/10$, consistent with this cluster being maximally differentiated from the Anatolian Neolithic cluster on a geographical east-west axis and a genetic top-bottom axis in PCA space (Fig. S 22; Fig. S 23).

About $\sim 3/10$ of the ancestry of this cluster is derived from steppe pastoralists, similar levels to those observed for the Balkan cluster. Thus, steppe ancestry emanating from eastern Europe dispersed southward both in a western direction into southeastern Europe and also in an eastern direction across the Caucasus. Steppe pastoralists have mixed ancestry with about half of their ancestry derived from eastern European hunter-gatherers and the rest from the south(7-10) (Supplementary Text S5) and this is indeed reflected in the results of models in which the Yamnaya are replaced by EHG as a source in which the amount of EHG ancestry is roughly half. We caution, however, that in the Caucasus it is not clear that the steppe ancestry is derived only from steppe pastoralist migrations as we will see that it is also present in Chalcolithic samples from Armenia that predate the formation of the Yamnaya.

A	B	C	D	P	Proportions				Std. Errors			
					A	B	C	D	A	B	C	D
IRN HajjiFiruz ChL	MAR Taforalt EpiP	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	0.010	0.722	0.029	0.182	0.067	0.022	0.007	0.012	0.015
IRN Ganj Dareh N	Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	0.012	0.186	0.526	0.176	0.113	0.035	0.050	0.014	0.026
CHG	EHG	IRN HajjiFiruz ChL	ISR Natufian EpiP	0.014	0.067	0.092	0.690	0.152	0.030	0.008	0.038	0.024
IRN Ganj Dareh N	Levant PPN	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	0.017	0.437	0.096	0.193	0.275	0.012	0.015	0.010	0.015
IRN Ganj Dareh N	Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	0.019	0.211	0.472	0.193	0.124	0.045	0.075	0.013	0.040
EHG	IRN Ganj Dareh N	Mesopotamia	TUR C Boncuklu PPN	0.025	0.089	0.245	0.540	0.126	0.009	0.033	0.051	0.026
CHG	EHG	IRN HajjiFiruz ChL	Levant PPN	0.030	0.168	0.095	0.603	0.134	0.035	0.007	0.045	0.018
IRN HajjiFiruz ChL	MAR Taforalt EpiP	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	0.031	0.738	0.033	0.187	0.043	0.019	0.007	0.011	0.014
CHG	EHG	Mesopotamia	TUR C Boncuklu PPN	0.032	0.226	0.083	0.602	0.089	0.044	0.011	0.055	0.023
IRN HajjiFiruz ChL	ISR Natufian EpiP	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	0.032	0.675	0.126	0.184	0.015	0.025	0.024	0.010	0.014
IRN Seh Gabi ChL	IRN TepeHissar ChL	ISR Natufian EpiP	Mesopotamia	0.092	0.035	0.306	0.320	0.339	10.858	4.858	1.884	7.839
CHG	EHG	Levant PPN	TUR Marmara Barcin N	0.166	0.624	0.069	0.167	0.140	0.016	0.009	0.024	0.023
CHG	Levant PPN	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	0.224	0.571	0.160	0.130	0.139	0.020	0.022	0.016	0.021

Table S 10 SCaucasusNIran

The SCaucasusNIran cluster (Table S 10) overlaps with the SCaucasusMain cluster but is genetically and geographically more diffuse, also encompassing samples from N Iran and some samples from Turkey. The relationship with the SCaucasusMain cluster is also evident in the assignment of individuals to the two clusters (Cluster5.2.7.6.6 and Cluster5.2.7.6.20) where only one of the clustering methods divides the two groups.

The main difference of this cluster to the SCaucasusMain one is the presence of some southern (Mesopotamian or Levantine) ancestry which makes up around $\sim 16\%$, a proportion largely subtracted from the amount of steppe ancestry which diminishes to around $\sim 13\%$

A	B	C	P	Proportions			Std. Errors		
				A	B	C	A	B	C
RUS MA1 HG	TUR C Boncuklu PPN	TUR Marmara Barcin N	0.015	0.012	0.011	0.976	0.005	0.041	0.040
TUR C Boncuklu PPN	TUR Marmara Barcin N	TUR Pınarbaşı EpiP	0.233	0.046	0.862	0.093	0.121	0.052	0.091

Table S 11 AnatoliaNeol

The AnatoliaNeol cluster (Table S 11) encompasses Neolithic samples from Anatolia and Southeastern Europe. Consistent with previous analyses(3, 9, 421) these samples can be modeled derived largely from Neolithic Northwestern Anatolia.

			Proportions		Std. Errors	
A	B	P	A	B	A	B
Mesopotamia	TUR_C_Boncuklu_PPN	0.088	0.866	0.134	0.020	0.020

Table S 12 AnatoliaMesopotamia

The AnatoliaMesopotamia cluster (Table S 12) includes samples from SE and Hatay Provinces of Turkey, Iraq, Azerbaijan, and Syria, as well as samples from Dinkha Tepe in the Azerbaijan region of Iran. It can be modeled as a simple model of predominantly Mesopotamian Neolithic ancestry with a little Central Anatolian ancestry, suggesting continuity of the diverse samples it encompasses with the earliest Neolithic inhabitants of Northern Mesopotamia sampled from SE Turkey and northern Iraq in our study.

				Proportions				Std. Errors				
A	B	C	D	P	A	B	C	D	A	B	C	D
CHG	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.012	0.037	0.040	0.128	0.795	0.008	0.014	0.004	0.016
IRN_Ganj_Dareh_N	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.014	0.031	0.035	0.130	0.804	0.007	0.015	0.004	0.016
IRN_TepeHissar_ChL	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.022	0.034	0.037	0.130	0.799	0.006	0.014	0.004	0.016
IRN_Seh_Gabi_ChL	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.028	0.044	0.035	0.131	0.790	0.008	0.014	0.004	0.016
IRN_HajjiFiruz_ChL	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.060	0.055	0.031	0.129	0.785	0.010	0.014	0.004	0.016
Levant_PPN	Mesopotamia	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.089	0.018	0.066	0.131	0.786	0.015	0.013	0.004	0.016

Table S 13 NorthBalkanChL

The NorthBalkanChL cluster (Table S 13) is tight in PCA space (Fig. S 23) and is dominated by the Chalcolithic Bodrogkeresztur individuals but encompasses other Neolithic/Chalcolithic individuals from the Balkans. It is characterized by a predominance of Anatolian Neolithic ancestry as the AnatoliaNeol cluster encompasses early Neolithic samples from the Balkans, but with ~13% hunter-gatherer ancestry and also ~7% Mesopotamian Neolithic ancestry. The different models agree that either Mesopotamian or a combination of Iran/Levant ancestry is required to model this cluster suggesting that during the Neolithic and Chalcolithic period ancestry other than that from NW Anatolia (from further east) also made its way into southeastern Europe. In (11) we show that the pottery Neolithic of Anatolia such as that of Barcin can be modeled as a mixture of Anatolian Epipaleolithic hunter-gatherers and ancestry from the east (both Mesopotamian and Levantine). This raises the possibility that other such mixtures existed in the Anatolian sources of the European Neolithic and that a population with a mix quite similar to- but not identical to the Barcin Neolithic may have been involved in the Neolithic settlement of Europe.

				Proportions				Std. Errors				
A	B	C	D	P	A	B	C	D	A	B	C	D
IRN_Ganj_Dareh_N	Levant_PPN	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.027	0.069	0.020	0.025	0.886	0.010	0.021	0.005	0.022
IRN_Ganj_Dareh_N	Levant_PPN	TUR_Marmara_Barcin_N	WHG	0.050	0.079	0.013	0.898	0.009	0.009	0.021	0.022	0.005
IRN_Ganj_Dareh_N	Mesopotamia	SRB_Iron_Gates_HG	TUR_Marmara_Barcin_N	0.020	0.003	0.147	0.021	0.830	0.039	0.086	0.005	0.050
IRN_Ganj_Dareh_N	Mesopotamia	TUR_Marmara_Barcin_N	WHG	0.046	0.043	0.078	0.875	0.004	0.039	0.085	0.049	0.005
IRN_Ganj_Dareh_N	SRB_Iron_Gates_HG	TUR_C_Boncuklu_PPN	TUR_Marmara_Barcin_N	0.033	0.049	0.018	0.006	0.927	0.010	0.006	0.058	0.056
IRN_Ganj_Dareh_N	TUR_C_Boncuklu_PPN	TUR_Marmara_Barcin_N	WHG	0.061	0.059	0.020	0.920	0.001	0.010	0.057	0.056	0.005
IRN_HajjiFiruz_ChL	TUR_C_Boncuklu_PPN	TUR_Marmara_Barcin_N	TUR_Pinarbaşı_EpiP	0.123	0.037	0.160	0.680	0.123	0.316	2.266	0.375	1.864

Table S 14 BalkanNChL

The BalkanNChL cluster (Table S 14) is more diffuse than the NBalkanChL cluster just discussed, encompassing samples of both Neolithic and Chalcolithic age, as well as samples from more southern parts of southeastern Europe (Albania, Greece, and North Macedonia) in

addition to those from the North Balkans. In terms of ancestry this cluster too exhibits primarily Anatolian Neolithic related ancestry complemented by more eastern ancestry (Mesopotamia or Iran-related). It contrasts with the NBalkanChL cluster in having no Balkan or Western hunter-gatherer ancestry.

Thus, the three clusters made up primarily of Anatolian Neolithic-related ancestry are contrasted: AnatoliaNeol includes neither hunter-gatherer nor “eastern” ancestry; NBalkanChL includes both; BalkanNChL includes only “eastern” ancestry. The EastMed cluster which includes the majority of samples from the Aegean also lacks the hunter-gatherer ancestry.

We can think of two scenarios for the low hunter-gatherer ancestry in parts of Southeastern Europe: (i) the hunter-gatherers did not contribute substantially to later populations of the southern Balkans and Aegean after the arrival of the Neolithic economy from Anatolia, or (ii) they were similar to the early farmers of western Anatolia. Pre-Neolithic samples from the Aegean and areas to the north of it may help distinguish between these two possibilities: is the lack of hunter-gatherer in the Aegean relative to the north Balkans due to negligible absorption/absence of hunter-gatherers in the area, or is it due to the hunter-gatherers of the area being unlike those of the rest of Europe and more similar to the neighboring farmers of Anatolia?

A	B	C	P	Proportions			Std. Errors		
				A	B	C	A	B	C
IRN HajjiFiruz ChL	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	0.010	0.766	0.089	0.145	0.025	0.014	0.019
EHG	Mesopotamia	TUR Pınarbaşı EpiP	0.017	0.069	0.917	0.015	0.010	0.022	0.021
Mesopotamia	RUS Yamnaya Samara EBA	TUR Pınarbaşı EpiP	0.021	0.848	0.117	0.036	0.025	0.015	0.020
IRN HajjiFiruz ChL	Levant PPN	RUS Yamnaya Samara EBA	0.022	0.745	0.144	0.111	0.027	0.019	0.014
Mesopotamia	RUS_MA1_HG	TUR C Boncuklu PPN	0.081	0.820	0.082	0.098	0.026	0.011	0.021
EHG	Mesopotamia	TUR Marmara Barcin N	0.084	0.083	0.910	0.007	0.011	0.029	0.028
EHG	Mesopotamia	TUR C Boncuklu PPN	0.162	0.069	0.867	0.065	0.010	0.023	0.021
Mesopotamia	RUS AfontovaGora3	TUR C Boncuklu PPN	0.168	0.798	0.107	0.095	0.025	0.013	0.020
Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	0.287	0.814	0.146	0.041	0.030	0.015	0.025
Mesopotamia	RUS_Yamnaya_Samara_EBA	TUR_C_Boncuklu_PPN	0.457	0.796	0.120	0.084	0.025	0.014	0.020

Table S 15 WestAsianMisc

The WestAsianMisc cluster (Table S 15) includes an eclectic collection of samples from different countries that overlaps geographically with the AnatoliaMesopotamia cluster previously discussed. In terms of ancestry it is also quite similar composed of primarily Mesopotamian Neolithic with some Central Anatolian ancestry, but it contrasts with the AnatoliaMesopotamia cluster in having also ~12% steppe ancestry.

Our discussion of clusters so far thus exhibits a pattern of diminishing steppe ancestry in the West Asia from SCaucasusMain (around 30%) to half of that in SCaucasusNIran and WestAsianMisc to very low amounts in AnatoliaMain to ~0% in AnatoliaMesopotamia and the Levant clusters.

A	B	C	D	P	Proportions				Std. Errors			
					A	B	C	D	A	B	C	D
IRN Ganj Dareh N	RUS_MA1_HG	TUR Marmara Barcin N	WHG	0.015	0.185	0.168	0.517	0.129	0.023	0.021	0.016	0.009
Mesopotamia	RUS_MA1_HG	SRB Iron Gates HG	TUR C Boncuklu PPN	0.020	0.325	0.149	0.120	0.406	0.031	0.019	0.012	0.025
Mesopotamia	RUS_MA1_HG	TUR C Boncuklu PPN	WHG	0.052	0.310	0.160	0.418	0.112	0.031	0.018	0.025	0.009
IRN HajjiFiruz ChL	IRN Seh Gabi ChL	MAR Taforalt EpiP	TUR C Boncuklu PPN	0.117	0.081	0.220	0.142	0.557	22.448	18.159	0.468	3.930
MAR Taforalt EpiP	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N	0.121	0.104	0.298	0.101	0.497	0.011	0.018	0.011	0.015
MAR Taforalt EpiP	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG	0.200	0.098	0.321	0.504	0.077	0.011	0.017	0.015	0.009

Table S 16 BalkanMisc1

We were intrigued by the fact that the few individuals of the BalkanMisc1 cluster (Table S 16) show ancestry from Epipaleolithic North Africans represented by Taforalt,(408) while otherwise possessing the same types of ancestry as the bigger Balkan cluster. Thus, we fit this model in individuals of the cluster; most of these have proportions that are less than 10% and less than 2 standard errors greater than zero, so the presence of this ancestry in them is questionable. kum4.SG, a low-coverage Neolithic sample from Kumtepe(422) has 18.1±7.3% (Z=2.5). The most convincing case is Vim2b.SG, a medieval individual from Serbia(423) with an estimate of 20.4±1.9%.

A	B	C	D	P	Proportions				Std. Errors				
					A	B	C	D	A	B	C	D	
Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N		0.010	0.361	0.166	0.051	0.422	0.036	0.023	0.010	0.026
Mesopotamia	RUS AfontovaGora3	TUR Marmara Barcin N	WHG		0.011	0.431	0.112	0.375	0.082	0.027	0.014	0.023	0.007
CHG	Levant PPN	TUR Marmara Barcin N	WHG		0.013	0.341	0.096	0.470	0.093	0.016	0.031	0.031	0.007
Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG		0.031	0.354	0.170	0.424	0.052	0.034	0.021	0.025	0.009
IRN HajjiFiruz ChL	TUR C Boncuklu PPN	TUR Pinarbaşı EpiP	WHG		0.237	0.511	0.040	0.387	0.062	0.097	1.400	1.367	0.053
CHG	TUR C Boncuklu PPN	TUR Marmara Barcin N	TUR Pinarbaşı EpiP		0.979	0.287	0.209	0.009	0.494	0.033	0.355	0.122	0.256

Table S 17 BalkanMisc2

The distinguishing feature of a second minor cluster in the Balkans (BalkanMisc2; Table S 17) is its high proportion of Mesopotamian Neolithic-related ancestry (~35%) higher than in all Balkan-related clusters we have discussed above. We show the individual ancestry proportions for the model in

Table S 18.

	P	A	B	C	D	A	B	C	D	Z-score of A	Population
I14499	0.398	-0.176	0.456	0.733	-0.013	0.347	0.264	0.194	0.074	-0.508	MNE Cetina BA 1d.rel I13168
I19497	0.370	-0.075	0.261	0.802	0.013	0.305	0.142	0.219	0.046	-0.246	BGR KapitanAndreevo IA
I15844	0.617	0.029	0.298	0.648	0.024	0.163	0.097	0.118	0.038	0.177	BGR Stambolovo IA
I19494	0.985	0.085	0.193	0.690	0.032	0.200	0.117	0.145	0.047	0.426	BGR KapitanAndreevo IA
I7233	0.003	0.185	0.167	0.596	0.052	0.058	0.036	0.045	0.015	3.188	MKD Anc
I19500	0.493	0.301	0.166	0.481	0.052	0.066	0.043	0.049	0.017	4.563	BGR Anc
I19490	0.968	0.323	0.095	0.488	0.094	0.146	0.097	0.104	0.041	2.211	BGR KapitanAndreevo IA
I16584	0.212	0.384	0.290	0.290	0.036	0.171	0.128	0.109	0.045	2.244	TUR Marmara Apollonia Rom
I10167	0.311	0.387	0.306	0.287	0.019	0.094	0.059	0.070	0.025	4.119	MKD Anc
I14821	0.897	0.417	0.185	0.341	0.056	0.055	0.037	0.040	0.016	7.590	TUR Marmara Balıkesir Byz
I14820	0.012	0.484	0.166	0.308	0.042	0.061	0.037	0.045	0.016	7.931	TUR Marmara Balıkesir Byz
I19495	0.572	0.682	-0.134	0.313	0.140	0.294	0.192	0.199	0.067	2.319	BGR KapitanAndreevo IA
RISE595.SG	0.027	4.969	-1.891	-2.814	0.735	5.212	2.241	3.714	0.739	0.953	MNE LBA

Table S 18 “Mesopotamian” ancestry in BalkanMisc2 cluster in terms of the highlighted model of Table S 17

We observe that this ancestry is observed in Byzantine era individuals from Anatolia (where it is not surprising) as well as ancient ones from Bulgaria, Montenegro, and North Macedonia.

A	B	C	P	Proportions			Std. Errors		
				A	B	C	A	B	C
IRN Ganj Dareh N	RUS MA1 HG	TUR C Boncuklu_PPN	0.012	0.811	0.108	0.082	0.022	0.015	0.014
IRN Ganj Dareh N	Levant PPN	RUS MA1 HG	0.014	0.795	0.086	0.119	0.025	0.016	0.015
IRN Ganj Dareh N	RUS AfontovaGora3	TUR C Boncuklu_PPN	0.018	0.772	0.148	0.080	0.023	0.018	0.013
IRN Ganj Dareh N	IRN TepeHissar ChL	RUS AfontovaGora3	0.030	0.479	0.377	0.144	0.060	0.057	0.016
IRN Ganj Dareh N	Levant PPN	RUS AfontovaGora3	0.035	0.744	0.089	0.168	0.026	0.015	0.018
IRN Ganj Dareh N	RUS MA1 HG	TUR Marmara Barcin N	0.079	0.800	0.119	0.081	0.022	0.016	0.015
IRN Ganj Dareh N	RUS MA1 HG	TUR Pınarbaşı EpiP	0.101	0.812	0.101	0.087	0.020	0.015	0.014
IRN Ganj Dareh N	RUS AfontovaGora3	TUR Marmara Barcin N	0.103	0.757	0.160	0.083	0.024	0.018	0.014
IRN Ganj Dareh N	IRN HajjiFiruz ChL	RUS AfontovaGora3	0.161	0.649	0.189	0.162	0.034	0.027	0.017
IRN Ganj Dareh N	IRN TepeHissar ChL	RUS MA1 HG	0.170	0.481	0.408	0.110	0.060	0.056	0.013
IRN Ganj Dareh N	RUS AfontovaGora3	TUR Pınarbaşı EpiP	0.175	0.770	0.144	0.086	0.022	0.018	0.013
IRN Ganj Dareh N	IRN HajjiFiruz ChL	RUS MA1 HG	0.190	0.685	0.196	0.120	0.034	0.028	0.015
IRN Ganj Dareh N	IRN Seh Gabi ChL	RUS AfontovaGora3	0.203	0.577	0.253	0.170	0.043	0.036	0.017
IRN Ganj Dareh N	IRN Seh Gabi ChL	RUS MA1 HG	0.290	0.604	0.265	0.131	0.045	0.038	0.015
IRN Ganj Dareh N	Mesopotamia	RUS MA1 HG	0.624	0.702	0.180	0.118	0.036	0.029	0.015
IRN Ganj Dareh N	Mesopotamia	RUS AfontovaGora3	0.805	0.657	0.179	0.164	0.037	0.027	0.018

Table S 19 IranMisc

Finally, the IranMisc cluster (Table S 19) derives most of its ancestry from the Neolithic of Iran (Ganj Dareh used as a source), but with ancestry from both the west (Mesopotamia) and east (Ancient North Eurasians of Siberia)(75, 409).

Summary of part 3

The history of the Southern Arc which we will discuss in greater detail below encompasses a set of processes that formed “genomic bridges” between West Asia and Europe.

- The Mesopotamian/Levantine-West Anatolian-Southeastern European cline formed by differential admixture of Mesopotamian/Levantine and West Anatolian Neolithic populations.
- The expansion of populations from this cline into Europe and the South Caucasus brought them into contact with the pre-existing hunter-gatherer populations, resulting in additional European and Caucasus hunter-gatherer/Iran Neolithic-related ancestry in the northwest and eastern wing of the Southern Arc.
- Finally, the expansion of steppe-related ancestry from North of the Black Sea into both Southeastern Europe and the South Caucasus brought substantial ancestry of this type in both directions, reaching minima in the southern portions of the region, in the Levant, Eastern Mediterranean, and Anatolia.

Part 4: Applying models to individuals

The analysis of Part 3 disclosed the broad patterns of ancestry within the Southern Arc. We next apply the inferred models from Part 3 on 946 individuals belonging to the clusters of Table S 4 so that we can obtain patterns of ancestry at finer detail. The models considered are listed in Table S 20.

911 of the 946 individuals (~96%) fit at least one of these models ($p > 0.01$ and proportions in $[0,1]$). All of them do so if we allow the mixture proportions to be outside the $[0,1]$ interval but within 3 standard errors of 0 or 1.

Mesopotamia	TUR C Boncuklu PPN		
EHG	Mesopotamia	TUR C Boncuklu PPN	
EHG	Mesopotamia	TUR Marmara Barcin N	
EHG	Mesopotamia	TUR Pinarbaşı EpiP	
IRN Ganj Dareh N	IRN HajjiFiruz ChL	RUS AfontovaGora3	
IRN Ganj Dareh N	IRN HajjiFiruz ChL	RUS MA1 HG	
IRN Ganj Dareh N	IRN Seh Gabi ChL	RUS AfontovaGora3	
IRN Ganj Dareh N	IRN Seh Gabi ChL	RUS MA1 HG	
IRN Ganj Dareh N	IRN TepeHissar ChL	RUS AfontovaGora3	
IRN Ganj Dareh N	IRN TepeHissar ChL	RUS MA1 HG	
IRN Ganj Dareh N	Levant PPN	RUS AfontovaGora3	
IRN Ganj Dareh N	Levant PPN	RUS MA1 HG	
IRN Ganj Dareh N	Mesopotamia	RUS AfontovaGora3	
IRN Ganj Dareh N	Mesopotamia	RUS MA1 HG	
IRN Ganj Dareh N	RUS AfontovaGora3	TUR C Boncuklu PPN	
IRN Ganj Dareh N	RUS AfontovaGora3	TUR Marmara Barcin N	
IRN Ganj Dareh N	RUS AfontovaGora3	TUR Pinarbaşı EpiP	
IRN Ganj Dareh N	RUS MA1 HG	TUR C Boncuklu PPN	
IRN Ganj Dareh N	RUS MA1 HG	TUR Marmara Barcin N	
IRN Ganj Dareh N	RUS MA1 HG	TUR Pinarbaşı EpiP	
IRN HajjiFiruz ChL	ISR Natufian EpiP	TUR C Boncuklu PPN	
IRN HajjiFiruz ChL	ISR Natufian EpiP	TUR Marmara Barcin N	
IRN HajjiFiruz ChL	Levant PPN	RUS Yamnaya Samara EBA	
IRN HajjiFiruz ChL	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	
ISR Natufian EpiP	Mesopotamia	TUR C Boncuklu PPN	
Mesopotamia	RUS AfontovaGora3	TUR C Boncuklu PPN	
Mesopotamia	RUS MA1 HG	TUR C Boncuklu PPN	
Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN	
Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	
Mesopotamia	RUS Yamnaya Samara EBA	TUR Pinarbaşı EpiP	
Mesopotamia	TUR C Boncuklu PPN	TUR Pinarbaşı EpiP	
RUS AfontovaGora3	RUS MA1 HG	TUR C Boncuklu PPN	
RUS MA1 HG	TUR C Boncuklu PPN	TUR Marmara Barcin N	
TUR C Boncuklu PPN	TUR Marmara Barcin N	TUR Pinarbaşı EpiP	
CHG	Levant PPN	TUR Marmara Barcin N	
EHG	SRB Iron Gates HG	TUR C Boncuklu PPN	TUR Pinarbaşı EpiP
IRN Ganj Dareh N	Levant PPN	RUS Yamnaya Samara EBA	TUR Marmara Barcin N
IRN Ganj Dareh N	Levant PPN	SRB Iron Gates HG	TUR Marmara Barcin N
IRN Ganj Dareh N	Mesopotamia	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN
IRN Ganj Dareh N	Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N
CHG	EHG	IRN HajjiFiruz ChL	ISR Natufian EpiP
IRN HajjiFiruz ChL	ISR Natufian EpiP	Mesopotamia	RUS Yamnaya Samara EBA
IRN HajjiFiruz ChL	ISR Natufian EpiP	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN
CHG	EHG	IRN HajjiFiruz ChL	Levant PPN
IRN HajjiFiruz ChL	Levant PPN	SRB Iron Gates HG	TUR Marmara Barcin N
IRN HajjiFiruz ChL	MAR Taforalt EpiP	RUS Yamnaya Samara EBA	TUR C Boncuklu PPN
IRN HajjiFiruz ChL	MAR Taforalt EpiP	RUS Yamnaya Samara EBA	TUR Marmara Barcin N
IRN HajjiFiruz ChL	TUR C Boncuklu PPN	TUR Pinarbaşı EpiP	WHG
IRN Seh Gabi ChL	IRN TepeHissar ChL	ISR Natufian EpiP	Mesopotamia
IRN Seh Gabi ChL	Levant PPN	SRB Iron Gates HG	TUR Marmara Barcin N
IRN Seh Gabi ChL	TUR C Boncuklu PPN	TUR Pinarbaşı EpiP	WHG
IRN TepeHissar ChL	Levant PPN	SRB Iron Gates HG	TUR Marmara Barcin N
CHG	EHG	IRN HajjiFiruz ChL	TUR Marmara Barcin N
Levant PPN	Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N
Levant PPN	Mesopotamia	SRB Iron Gates HG	TUR Marmara Barcin N
CHG	EHG	IRN HajjiFiruz ChL	TUR Pinarbaşı EpiP
Mesopotamia	RUS AfontovaGora3	TUR Marmara Barcin N	WHG
Mesopotamia	RUS Yamnaya Samara EBA	SRB Iron Gates HG	TUR Marmara Barcin N
Mesopotamia	RUS Yamnaya Samara EBA	TUR Marmara Barcin N	WHG
CHG	IRN HajjiFiruz ChL	RUS Yamnaya Samara EBA	TUR Marmara Barcin N
CHG	IRN HajjiFiruz ChL	RUS Yamnaya Samara EBA	TUR Pinarbaşı EpiP
CHG	Levant PPN	RUS MA1 HG	TUR Marmara Barcin N
CHG	Levant PPN	RUS Yamnaya Samara EBA	TUR Marmara Barcin N
CHG	Levant PPN	SRB Iron Gates HG	TUR Marmara Barcin N
CHG	Levant PPN	TUR Marmara Barcin N	WHG
CHG	TUR C Boncuklu PPN	TUR Marmara Barcin N	TUR Pinarbaşı EpiP
CHG	EHG	Levant PPN	TUR Marmara Barcin N
EHG	IRN Ganj Dareh N	Mesopotamia	TUR C Boncuklu PPN
CHG	EHG	Mesopotamia	TUR C Boncuklu PPN
CHG	EHG	Mesopotamia	TUR Marmara Barcin N

Table S 20 A total of 113 Models considered for individuals. These models with $K=1, 2, \dots, 4$ fit at least one of the clusters of Table S 4 ($p\text{-value} \geq 0.01$ and mixture proportions within $[0,1]$). They are a small subset of 4,047 different models with as many sources drawn from the 18 different sources

Part 5: Identifying a minimal set of sources

The models of Table S 20 involve all 18 sources. We want to identify a subset of them that involve a smaller number of sources, as this would allow us to compare individuals using the same (smaller) set of ancestral populations. In Fig. S 24 we plot the number of individuals with feasible models (with proportions strictly within $[0,1]$ vs. within $\pm 3s.e.$ of the ends of $[0,1]$) for $K=1, 2, \dots, 10$.

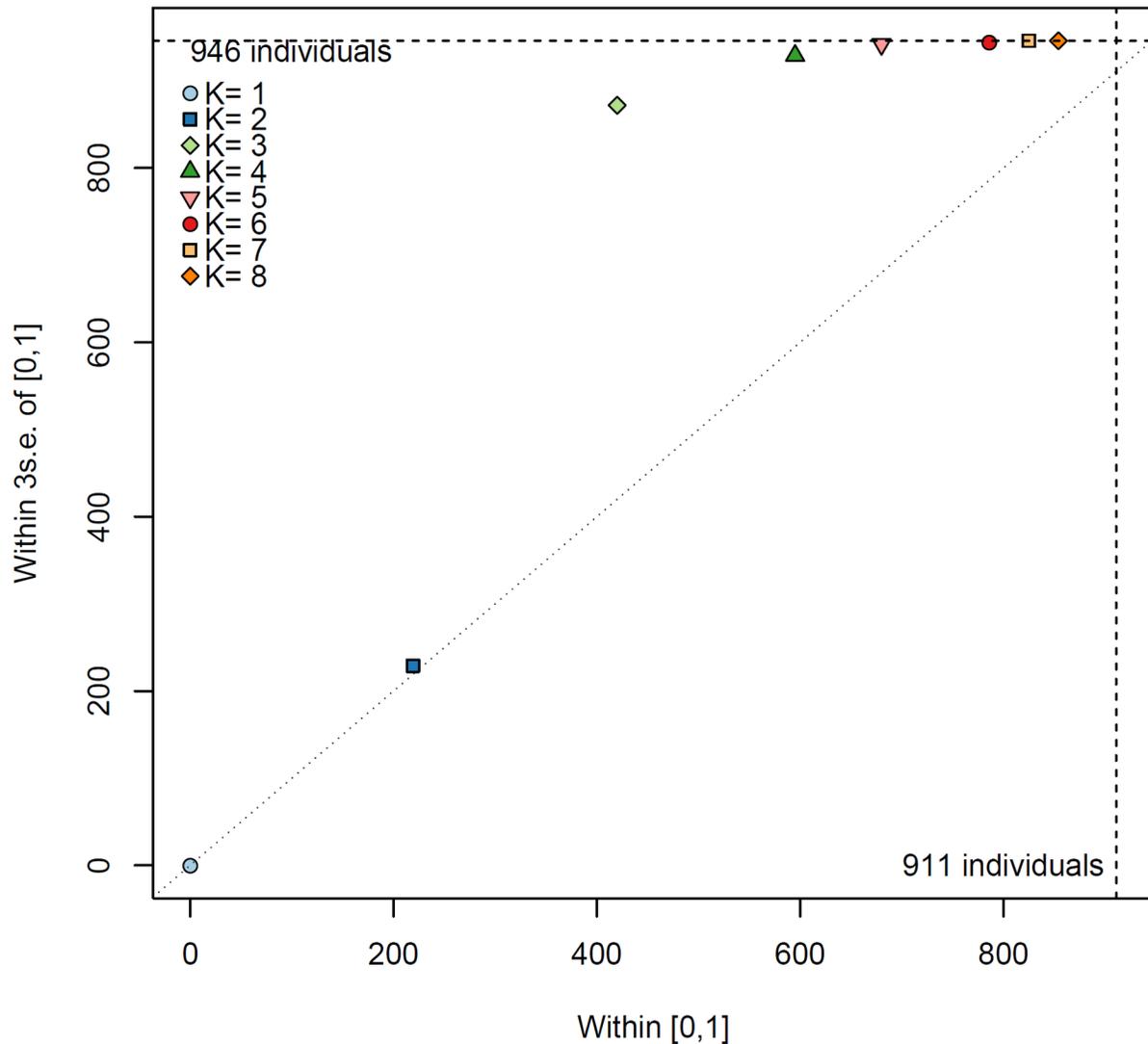


Fig. S 24 Identifying minimum set of sources explaining most individuals of the Southern Arc.

There is marginal utility beyond $K=5$ in explaining additional individuals: nearly all of them can fit models with sources from a set of 5 total sources. We list below the top-5 models that explain most individuals

1. CHG EHG Levant_PPN Mesopotamia TUR_Marmara_Barcin_N
2. CHG EHG Levant_PPN SRB_Iron_Gates_HG TUR_Marmara_Barcin_N
3. CHG EHG Levant_PPN TUR_Marmara_Barcin_N WHG
4. CHG EHG IRN_HajjiFiruz_ChL Levant_PPN TUR_Marmara_Barcin_N
5. CHG Levant_PPN RUS_Yamnaya_Samara_EBA SRB_Iron_Gates_HG TUR_Marmara_Barcin_N

Thus, by examining individuals we arrive at a qualitatively similar finding as we did when we examined the Total population: individuals of the Southern Arc can be mostly explained by five sources of ancestry: Caucasus hunter-gatherers, Mesopotamia or Levantine Neolithic, Steppe or Eastern hunter-gatherers, Western Anatolian Neolithic, and European/Balkan hunter-gatherer ancestry. Note, however, that the sets of models thus identified are not identical in their source populations as the ones identified for the Total population (Table S 4), although the highlighted model is also the best model for the Total population.

In order not to potentially miss out on some good models, we also fit 4- and 5-way models of Table S 1 and Table S 2 for all the individuals. We summarize the performance of the models of Table S 1, Table S 2, and Table S 20 in Fig. S 25. Based on this, we identify the mini-cluster of 2 models on the right of Fig. S 25b as having simultaneously low standard errors, high P-values for individuals, and many individuals with $P > 0.01$ and thus appropriate as a common set of ancestral populations against which we can compare the different individuals. These two models are again the best model for the Total population, also highlighted above and its variant in which SRB_Iron_Gates_HG is replaced by WHG. Thus, we decided to proceed using the best model for the Total population as the Final model also for the individuals.

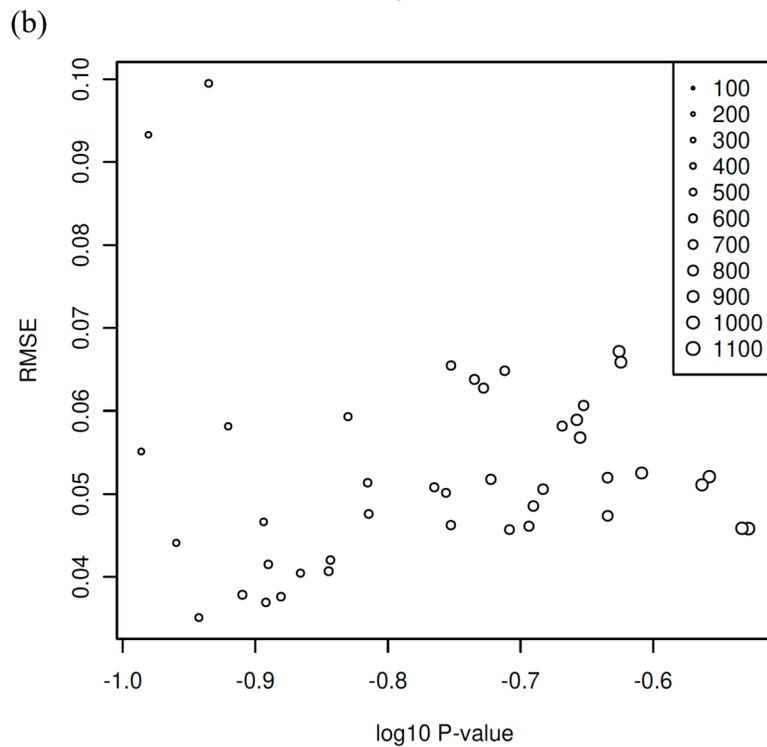
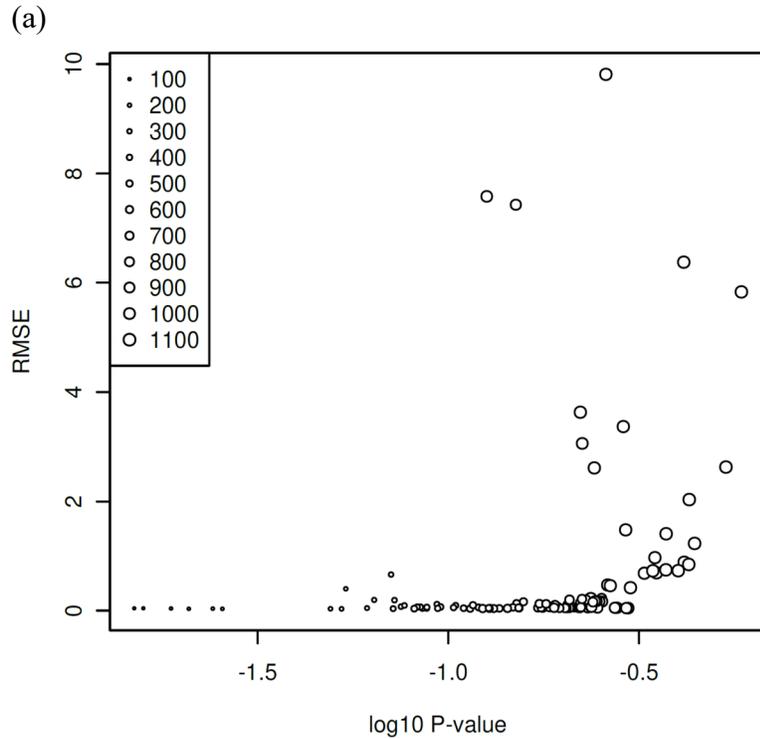


Fig. S 25 Comparing model performance on individuals. In the top panel (a) we show all models; in the bottom (b), a subset of models with $RMSE < 0.1$ and mean $P\text{-value} > 0.1$. The size of the circles indicates the number of individuals with $P > 0.01$. The 5-way model used in our paper and its variant with WHG instead of SRB_Iron_Gates_HG as a source form a mini cluster at the bottom right of panel (b) combining high p-values and small standard errors.

Part 6: Final mixture proportions

The Final model has 4.6% median RMSE across the individuals, so it performs well overall, but the standard errors are higher for some of the individuals and also some mixture coefficients are outside the $[0,1]$ interval making visualization difficult. Practically, a mixture coefficient of e.g., $10\pm 10\%$ could be consistent with negligible to substantial ancestry from a particular source, while a coefficient of $-1\pm 2\%$ is consistent with zero ancestry but difficult to visualize in a conventional bar plot which requires a positive set of admixture weights that sum to unity.

It is unavoidable that mixture estimation performance may vary substantially across individuals of different data quality. A possible solution to this problem is to examine models of different subsets of the 5 sources. This would allow us to use the same sources for all individuals (thus allowing comparison between them) but making zero some subset of the 5 sources. A drawback of this approach is that it would artificially display ancestry differences between individuals due to data quality. For example, if individual X is of much better quality than Y, then a 5-way model may be well-estimated for X but poorly for Y. We could identify a 3-way model that fits Y, but this would suggest that Y had no ancestry from the remaining 2 sources, when in fact X and Y were drawn from the same population.

qpAdm performs optimization of the mixture coefficients under the constraint that they sum up to unity, thus allowing for coefficients outside the $[0,1]$ interval. In order to solve the visualization difficulty described above, we re-estimated admixture coefficients using the method we previously developed in Supplementary Information section 9 of (8). (qpAdm is described in section 10 of the same reference.) While our initial goal was to solve the visualization problem, we realized that it also helped improve our estimation of mixture proportions as we describe below.

Briefly, there are two main differences between that method (which we name F4adm here) and qpAdm.

First, it uses the following model of admixture:

$$f_4(\text{Test}, O_1; O_2, O_3) = \sum_{i=1}^K \alpha_i f_4(\text{Ref}_i, O_1; O_2, O_3)$$

In which statistics involving the *Test* population and a triple $O_1; O_2, O_3$ of Right populations is expressed as a weighted sum of those involving K reference populations (representatives of the sources of admixture). By writing the left-side of that equation as:

$$\sum_{i=1}^K \alpha_i f_4(\text{Test}, O_1; O_2, O_3) = \sum_{i=1}^K \alpha_i f_4(\text{Ref}_i, O_1; O_2, O_3)$$

And moving the right side to the left, we obtain:

$$\sum_{i=1}^K \alpha_i [f_4(\text{Test}, O_1; O_2, O_3) - f_4(\text{Ref}_i, O_1; O_2, O_3)] = 0$$

Or, using the equality of the difference of f_4 -statistics with another f_4 -statistic(77):

$$\sum_{i=1}^K \alpha_i f_4(\text{Test}, \text{Ref}_i; O_2, O_3) = 0$$

which is the qpAdm formulation of the admixture problem (with pairs, rather than triples of outgroups).

Note that while the two formulations similarly assume perfect knowledge of the f -statistics involved, in practice there is an advantage to using the first one. The key insight is that each statistic $f_4(\text{Test}, \text{Ref}_i; O_2, O_3)$ of the qpAdm formulation corresponds to several $f_4(\text{Test}, O_1; O_2, O_3) - f_4(\text{Ref}_i, O_1; O_2, O_3)$ differences (for different choices of O_1). But, the former is estimated on only the set of SNPs common to the four populations, while the latter on a

larger set of SNPs, and particularly so for low coverage *Test* or *Ref* populations. At the limit, when both *Test* and *Ref* populations are low coverage the intersection of SNPs common to both approaches zero and the statistic $f_4(\text{Test}, \text{Ref}_i; O_2, O_3)$ is very poorly estimated, while $f_4(\text{Test}, O_1; O_2, O_3)$ and $f_4(\text{Ref}_i, O_1; O_2, O_3)$ are much better estimated. For an O_1 that is more or less complete (e.g., Mbuti.DG in our setup), these statistics are estimated in the intersection of SNPs common to (Test, O_2, O_3) and (Ref_i, O_2, O_3) , rather than the much smaller intersection of $(\text{Test}, \text{Ref}_i, O_2, O_3)$.

The problem of low intersection of SNPs in the computation of qpAdm-style statistics was noticed in (424) where the problem was to test whether damaged and undamaged reads of a Harappan individual with highly degraded DNA formed a clade; the solution there was to express the qpAdm-style statistic (with two outgroups) as the difference of two F4admixture-style statistics (with three outgroups; introducing one high quality outgroup). This idea was generalized recently in the software qpfstats (<https://github.com/DReichLab/AdmixTools/blob/master/qpfs.pdf>) which computes qpAdm-style statistics via regression in a large set of populations and is used as a preprocessing step for qpAdm which then uses the regressed set of statistics instead of the (poorly estimated) raw ones. This step is not needed in the F4admixture formulation which operates in the space of outgroup triples natively.

In the discussion that follows, when we refer to qpAdm, we use the original qpAdm formulation (without preprocessed f-statistics), as qpfstats is limited to a set of ~30 populations due to computational issues and is not configured for hundreds of individuals as in our application.

The second difference between F4admixture and qpAdm is that the former has the additional constraint of mixture proportions within the [0,1] interval. Proportions outside this interval are sometimes useful, e.g., because they might point towards ghost populations that have more of a particular type of ancestry than any of the sampled populations. (8, 25) It is trivial to modify F4admixture to remove that constraint if required. In the present application, as we wanted to also visualize the mixture proportions, we choose the original formulation.

A weakness of F4admixture as originally proposed in (8) is that it did not report standard errors of the mixture proportions. We now estimate these using a chromosome jackknife (78), recomputing the f-statistics deleting each of the chromosomes in turn and estimating the admixture proportions. We use the number of SNPs in each chromosome as its block size. Another issue is that it required a common set of populations for which the f_4 -statistics are computed. There are a total of $15 \binom{14}{2} = 1365$ statistics for the 17 Base populations, but only $14 \binom{13}{2} = 1092$ for populations that are both sources and part of the Base (e.g., WHG). For a model with five sources, the common statistics for all five sources are $10 \binom{9}{2} = 360$. We used probabilistic PCA (ppca in pcaMethods package of R / <https://www.rdocumentation.org/packages/pcaMethods/versions/1.64.0/topics/ppca>) to perform PCA on the matrix whose rows are Test individuals and Sources (Base except Mbuti.DG) and whose columns are the 1,365 f_4 -statistics. This allows us to visualize the individuals in the principal components of the space defined by the f_4 -statistics and also fills in missing values.

In Table S 21 we compare the qpAdm standard errors with those from F4admixture which we ran in a variety of ways:

- The full set of 1,365 f_4 -statistics vs. 360 common statistics

- Full constraints ($[0,1]$ proportions summing to unity) vs. partial constraints (summing to unity)
- Optimization was performed either on the f_4 -statistics matrix or on the first 5 principal components

For all methods, we show both the median and mean of the RMSE of the standard errors across the individuals.

qpAdm		F4admix							
		1,365 f_4 -statistics							
		Proportions within $[0,1]$				Proportions unconstrained			
		f4		pca		f4		pca	
mean	median	mean	median	mean	median	mean	median	mean	median
0.060	0.045	0.049	0.044	0.064	0.056	0.059	0.049	0.097	0.082
		360 common f_4 -statistics							
		mean	median	mean	median	mean	median	mean	median
		0.056	0.048	0.058	0.051	0.067	0.053	0.074	0.058

Table S 21 Comparison of qpAdm and F4admix standard errors. We plot for each considered method the mean and median of the RMSE across 946 individuals.

Notice that the mean is higher than the median for qpAdm, whereas the two statistics are similar for F4admix, suggesting that the distribution of qpAdm errors is skewed to the right. We confirm this in Fig. S 26 where we show a histogram of the distribution of the ratio of standard errors of qpAdm over those of F4admix.

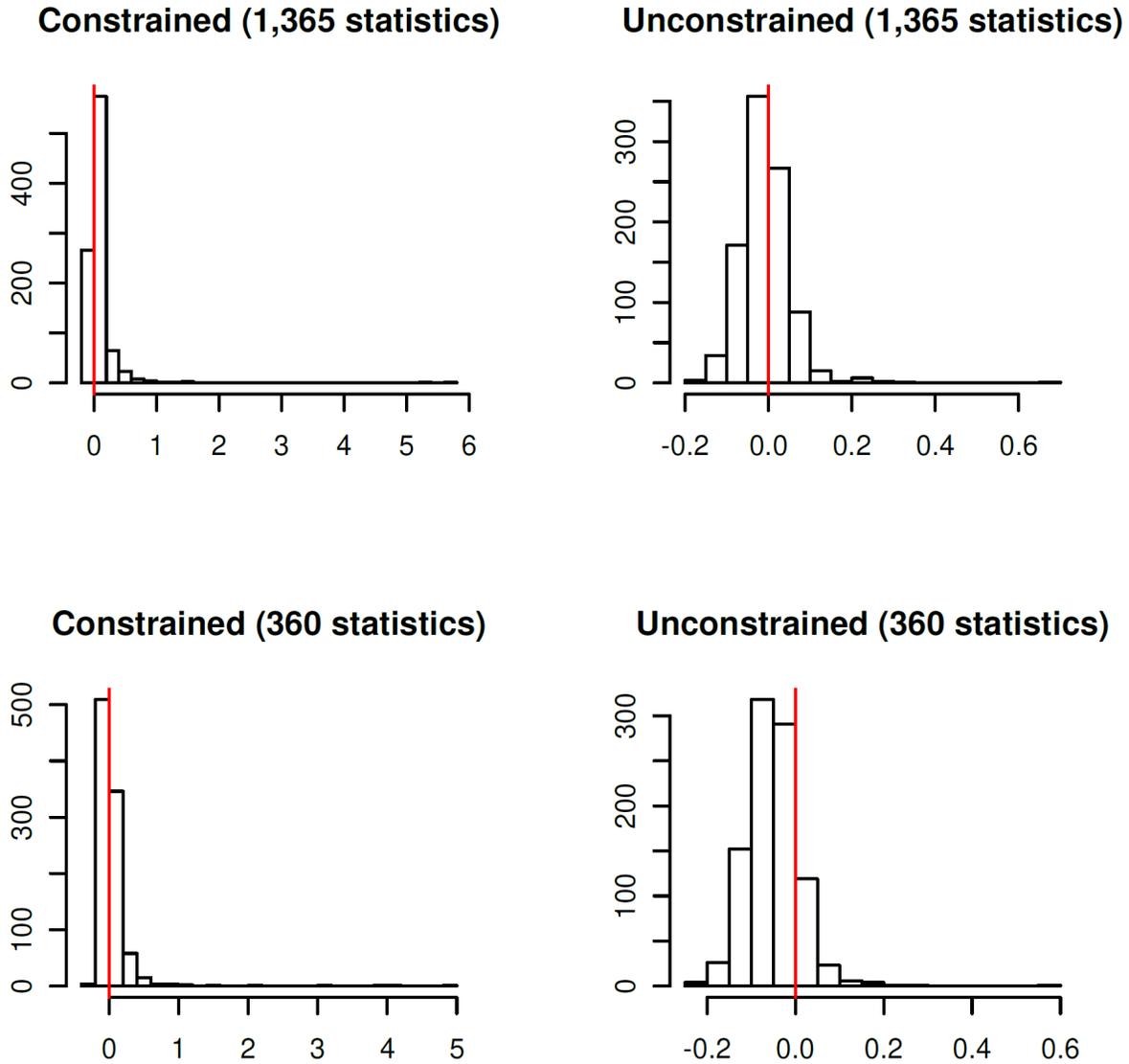


Fig. S 26 Comparison of qpAdm and F4adm standard error distribution. We plot a histogram of $\log_{10} \frac{RMSE_{qpAdm}}{RMSE_{F4adm}}$

Based on our discussion of the statistics involved we expect that qpAdm errors increase for low coverage individuals. In Fig. Fig. S 27 we plot the same ratio as in Fig. S 26 against the number of autosomal SNPs covered in each individual. We observe several outliers in which qpAdm estimates standard errors by orders of magnitude higher than F4adm and an increase of its standard errors relative to F4adm in the lowest quantiles of coverage as per our expectation.

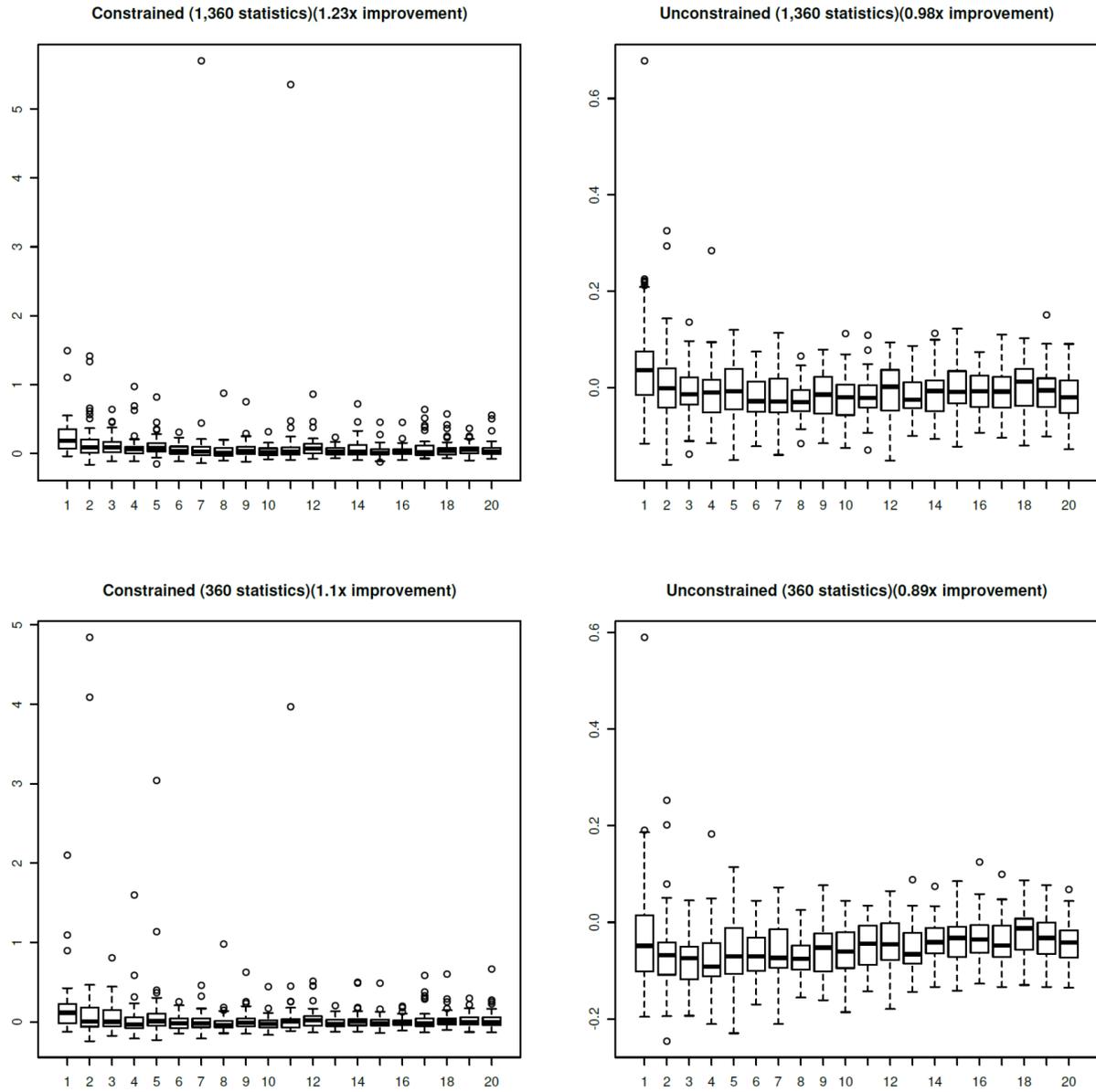


Fig. S 27 Comparison of qpAdm and F4adm standard errors for quantiles of SNP coverage. We show $\log_{10} \frac{RMSE_{qpAdm}}{RMSE_{F4adm}}$ for vigintiles of the SNP coverage distribution. The bottom 5% of coverage has up to ~34k SNPs.

Mixture proportions of Source individuals

Individuals from Source populations could be trivially assigned a value of 100% ancestry from their source population as e.g., supervised ADMIXTURE analysis(425). We experimented with a slightly different approach. Consider that the representation of a population (e.g., SRB_Iron_Gates_HG) and its constituent individuals is the same in the space of f_4 -statistics used: each is defined as a 1,365-long vector in this space. We can thus estimate the ancestry of individuals from source populations as we would any non-source individuals. These will form a “cloud” in the space of f_4 -statistics around the population vector and we expect them to be mostly derived from their source population plus noise. The mixture proportions of source individuals derived from their own population are not particularly interesting in terms of ancestry, but are useful for two reasons: first, they show that their dispersion from the population mean is not substantial, as they all derive the overwhelming majority of their ancestry from its expected source; second, they show that the source populations do not include any substantial outliers, i.e., individuals with ancestry proportions from other sources; this is an important check as these source populations are used to infer the ancestry of all other individuals.

The mixture proportions of all individuals (constrained in $[0,1]$) are shown in graphical form in Fig. S 2 and numerically with their jackknife estimates in Data S5 In Supplementary Text S3 we use the block jackknife estimates and visualize them using “ancestral variation diagrams” allowing us to survey the entirety of the Southern Arc using the 5-way model developed in this section.

S3: The landscape of ancestry in the Southern Arc

In Supplementary Text S2 we described how we obtained admixture estimates on a 5-source population model for individuals of the Southern Arc. In this section we will examine these estimates in different levels of spatial and temporal granularity and record our observations on patterns of ancestry within the Southern Arc.

To aid us in writing this “genetic history” of the Southern Arc, we introduce a new type of visualization that will allow us to quickly compare the ancestry of individuals and populations. We present an example of this visualization in Fig. S 28.

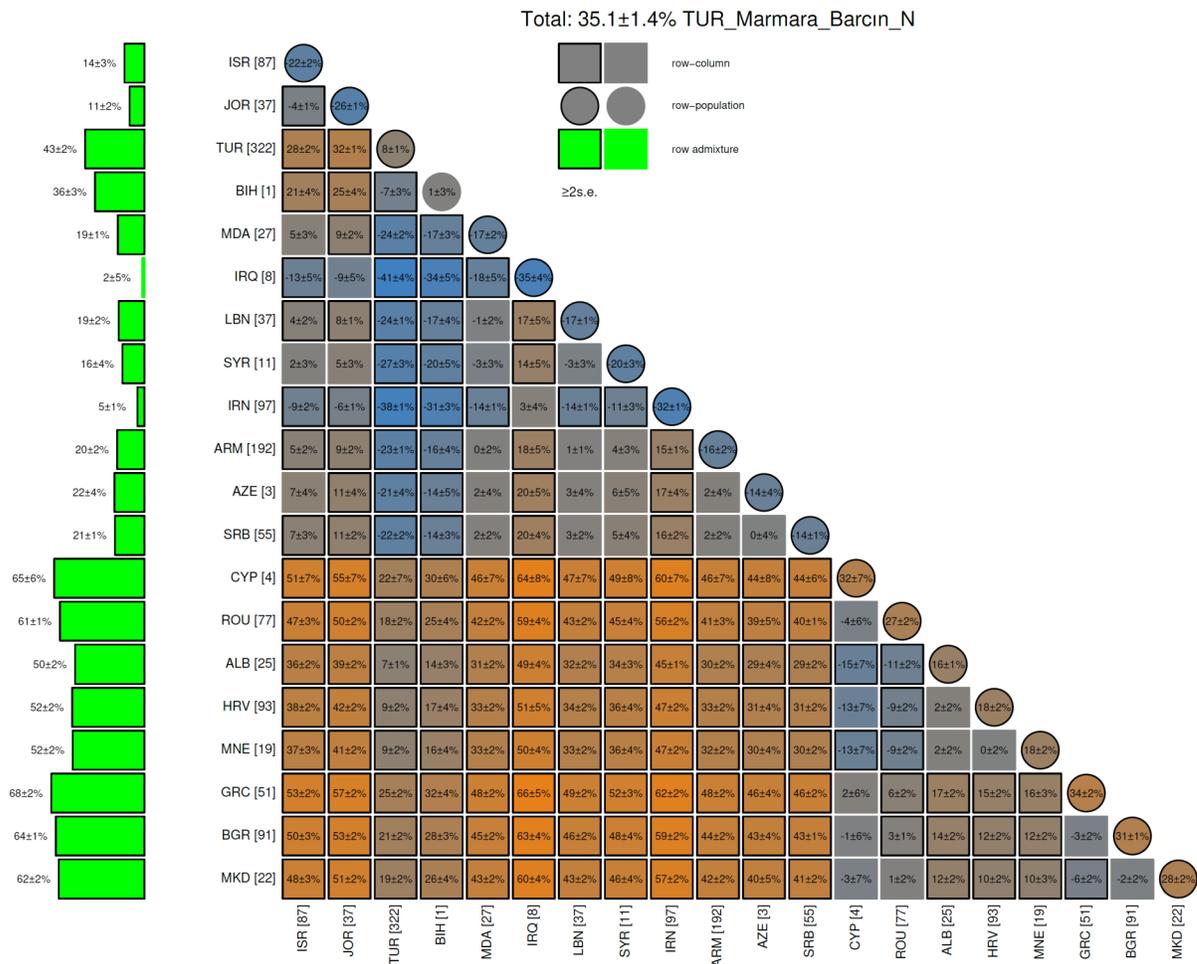


Fig. S 28 Ancestral variation diagram (example by-country)

The diagram above presents levels of TUR_Marmara_Barcin_N-related ancestry for populations corresponding to countries (thus TUR includes all individuals sampled from Turkey). In different applications of our diagram, we may decide to compare ancestry of individuals or populations, and to group them by time, space, or whatever else criteria is useful for analysis. Such diagrams can be generated on-the-fly using the raw admixture proportions for individuals as input (Data S5).

The breakdown by countries is useful to allow us to explain the workings of the diagram:

- The title shows the average (across all countries) of the TUR_Marmara_Barcin_N-related ancestry which is $35.1 \pm 1.4\%$.
- On the left there are green bars with absolute estimates of ancestry (with jackknife-computed standard errors) for each row (in this case country) as computed in Supplementary Text S2. As expected, the Western Neolithic ancestry associated with NW Anatolian farmers is higher in Southeastern Europe, Anatolia, and Cyprus, and less so in Mesopotamia, the South Caucasus, Iran, and the Levant. Each of these countries has of course intra-population variation that is not shown here, e.g., the overall proportion for Turkey is 43%, but of course it is $\sim 100\%$ for the Neolithic NW Anatolians that make up the source of this component. Thus, it is important to examine patterns of ancestry at different levels of granularity as we will do in this section.
- The round shapes along the diagonal quantify precisely how the populations differ from the overall average of populations. Thus, Turkey, being centrally located within the Southern Arc differs by $8 \pm 1\%$ from the overall average, while Armenia, being the eastern flank of the Southern Arc has less ($-16 \pm 2\%$) NW Anatolian-related ancestry, and Bulgaria has more ($31 \pm 1\%$). Note that these differences are computed by excluding each population from the computation of the overall average; thus Bulgaria has $\sim 31\%$ more ancestry than the average of all other countries except Bulgaria (it is possible to generate diagrams in which the difference is computed against the average of all countries).
- Finally, the square shapes of the lower triangular matrix show the differences between the ancestry of each row minus the ancestry of each column. Thus, North Macedonia has no significant difference from Romania ($1 \pm 2\%$) but much more than Armenia ($42 \pm 2\%$)

Before we proceed, we also highlight three visual cues present in the diagram. First, percentages that differ by at least 2 standard errors are highlighted with black borders. Second, positive/negative percentages are shaded with colors towards the red/blue end of the spectrum. Third, rows are clustered (using the `hclust` hierarchical cluster function in R) by their overall percentages of ancestry (across all five sources) in order to bring genetically similar ones closer together. Finally, the numbers within brackets next to the population labels are the sample sizes for each population.

Technical detail of standard error computation

Let α_i be an admixture proportion for an individual i computed by F4admix and let α_i^k be an admixture proportion for the same individual in which chromosome k has been deleted. By applying the block jackknife (with block length being the number of SNPs of the deleted chromosome) we obtain a mean \pm standard error of the admixture proportion for the individual: $\hat{\alpha}_i \pm s_i$. The proportions plotted in the ancestral variation diagram are computed as follows, using the individual-level α_i and α_i^k as inputs:

- For a population consisting of a set of individuals S , the population admixture proportion is $\alpha_S = \frac{1}{|S|} \sum_{i \in S} \alpha_i$ and for each deleted chromosome it is $\alpha_S^k = \frac{1}{|S|} \sum_{i \in S} \alpha_i^k$. The green bar shows the block jackknife-estimated $\hat{\alpha}_S \pm s_S$.
- The proportion plotted in the title is the average of all plotted populations; thus, if the set of populations is P then we compute $\alpha_P = \frac{1}{|P|} \sum_{S \in P} \alpha_S$ and $\alpha_P^k = \frac{1}{|P|} \sum_{S \in P} \alpha_S^k$. The title shows the block jackknife-estimated $\hat{\alpha}_P \pm s_P$.

- The population difference between two populations S and Q is $\alpha_{S,Q} = \alpha_S - \alpha_Q$ and for each deleted chromosome it is $\alpha_{S,Q}^k = \alpha_S^k - \alpha_Q^k$. The lower triangular matrix shows the block jackknife estimated $\hat{\alpha}_{S,Q} \pm s_{S,Q}$.

- The individual-population difference between individual i and its population S is computed as $\alpha_{i,S} = \alpha_i - \alpha_{S \setminus \{i\}}$ and for each deleted chromosome it is $\alpha_{i,S}^k = \alpha_i^k - \alpha_{S \setminus \{i\}}^k$. The diagonal of the ancestral variation diagram shows the block jackknife estimated $\hat{\alpha}_{i,S} \pm s_{i,S}$

We first present ancestral variation diagrams for five countries with ≤ 11 individuals, in which all the samples can be easily discerned within a single diagram.

Bosnia-Herzegovina

Only a single individual of unknown date but probably prehistoric (3000-1BCE) was sampled from Bosnia Herzegovina (I19561) so we only list its admixture proportions which are estimated to be: 0.343 ± 0.043 CHG 0.179 ± 0.041 EHG -0.008 ± 0.006 Levant_PPN 0.127 ± 0.022 SRB_Iron_Gates_HG 0.358 ± 0.031 TUR_Marmara_Barcin_N. Its ancestry and placement in the Balkan cluster in the previous section suggests that it may be of Bronze Age or later date as other members of that cluster.

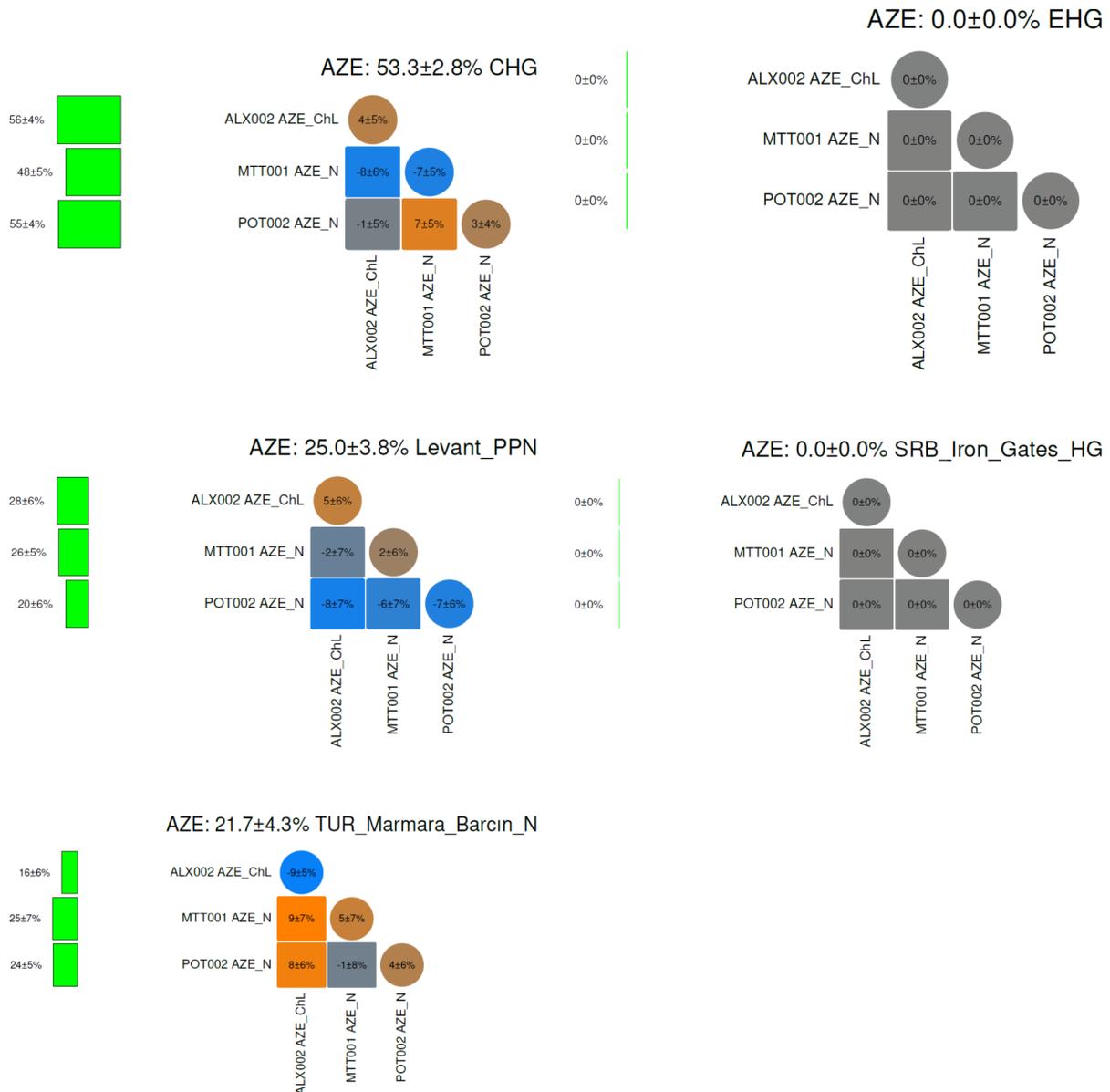


Fig. S 29 Azerbaijan

Azerbaijan

We analyzed 3 individuals from Azerbaijan recently published(14) (Fig. S 29). We detect no temporal structure in the data and the individuals are composed primarily of half CHG ancestry and the remainder of Levantine/Anatolian ancestry as their geographical position would predict. There is no trace of the European ancestry components in these individuals.

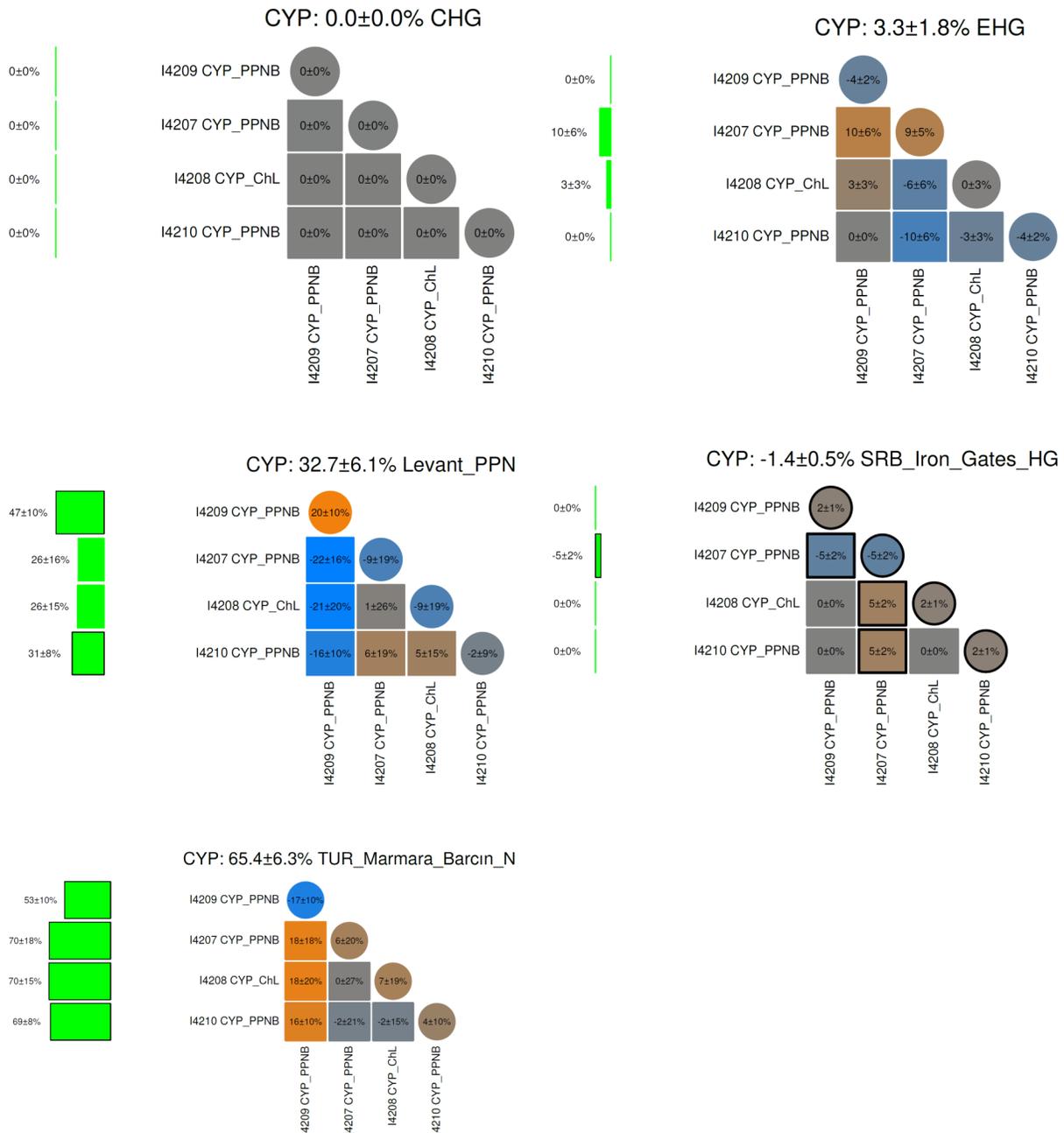


Fig. S 30 Cyprus

Cyprus

In Cyprus (Fig. S 30) two of the five elements are represented: West Anatolian Neolithic is the majority element and Levant the minority one. Ancestry differences between either individuals or individuals and the population as a whole do not exceed 2 standard errors. Our data thus suggest that the Pre-Pottery Neolithic population of Cyprus had ancestry related both to the Anatolian mainland to its north and the Levant to its east, a geographically plausible conclusion. In (6) we show that it can be modeled with only Central Anatolian ancestry and may

be clinal between NW Anatolia and the Levant, while being overall more similar to the former (as the admixture proportions here also indicate). Cyprus may represent one genomic bridge between the Levant and Anatolia/Europe and future sampling may better flesh out the population of these eras and fill in the rest of the population history of Cyprus until the present day.

Iraq

Individuals from Iraq (Fig. S 31) are also primarily modeled as a mixture of two sources, in which Caucasus-related ancestry forms the majority element and Levantine ancestry the minority one. The samples labeled IRQ_Nemrik9_PPN are included together with a nearby (<200km) sample from Mardin, Turkey into Mesopotamia_PPN in our analyses of (11) where the origin of Neolithic populations is discussed, due to their geographic proximity and that fact that they possess the same basic ancestral composition according to our estimates. Another sample (I6441) from the Middle Assyrian period (LBA) of Mesopotamia has largely the same ancestral composition as these PPN samples, a finding which we also confirm in (11) in which the ancestry of all Mesopotamian individuals is modeled; it would be tempting to see local continuity here, although this should be tentative given the fact that only a single individual from the Bronze Age has been sampled and the geographical extent of populations with similar ancestry is unknown.

We include some additional low-coverage samples from Iraq in our figure. The easternmost samples from Shanidar and Bestansur have more Caucasus-related ancestry (similar to samples from Iran that we will discuss further down) than the samples from the pre-pottery Neolithic North Mesopotamia site of Nemrik9 which have correspondingly more Levant-related ancestry.

An advantage of our procedure of estimating individual-level proportions is that we can include low coverage and potentially contaminated individuals in the ancestral variation diagram to check whether or not they are statistically different from other individuals and thus assess by how much low coverage affects the standard errors of their admixture estimates, and by how much contamination (which may stem from a population of unknown ancestry) affects admixture proportion estimates. Thus, the analyst need not always have to make a hard decision on what constitutes low coverage or whether some fraction of contamination in a sample would materially influence conclusions drawn from it, but can assess each individual of interest.

For example, EHG ancestry is detected only in a contaminated sample from Nemrik9 (sexratio=0.055, mtcontam=[0.597,0.83]) and in an outlier individual from Shanidar (mtcontam=[0.753,0.95], damage.ss.half=0.061) so overall, we do not detect this type of ancestry in our earliest samples from Iraq. We note that in our aggregation of Nemrik9 samples into the Mesopotamian PPN population (11) we do not include the low coverage and potentially contaminated and ancestrally divergent individual which we could assess by means of the diagram above.

Notably, Anatolia Neolithic-related ancestry is absent or very low in our Iraq samples; this suggests that the presence of this type of ancestry that is later observed (e.g., in Chalcolithic Levant(420) or Iran(34)) cannot be derived from Mesopotamia but must have been transmitted from other areas of the Near East where it was present (such as Anatolia itself).

Our Neolithic samples of Iraq fill the gap between the centers of the Neolithic in Anatolia, Iran, and the Levant(10) and suggest that genetically intermediate populations existed in the Near Eastern heartland between Anatolia, the South Caucasus, the Zagros, and the Levant, a point which we discuss in detail in (11). An important consequence of this finding is that the presence of either Caucasus- or Levant-related ancestry elsewhere in West Eurasia and beyond need not have been derived from the hitherto sampled populations of the Caucasus and the Levant. It may have also been drawn from geographically intermediate regions such as Mesopotamia where the ratio of the two elements is overall 2:1 but with individual variation. Further sampling of Iraq and neighboring Syria from the earliest periods may further shape our understanding of the

landscape of ancestry from the core of the Fertile Crescent and disclose how this area both affected and was influenced by surrounding areas of the Near East.

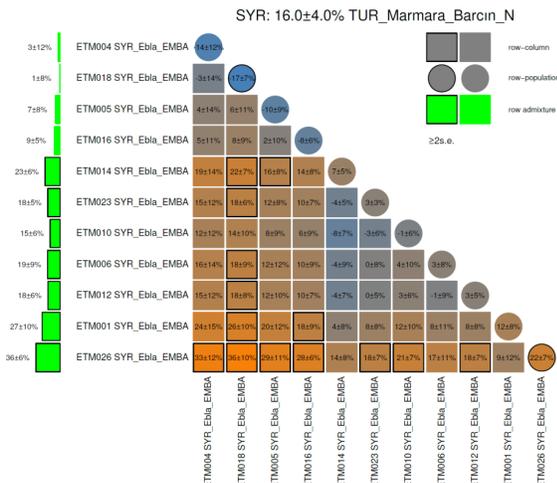
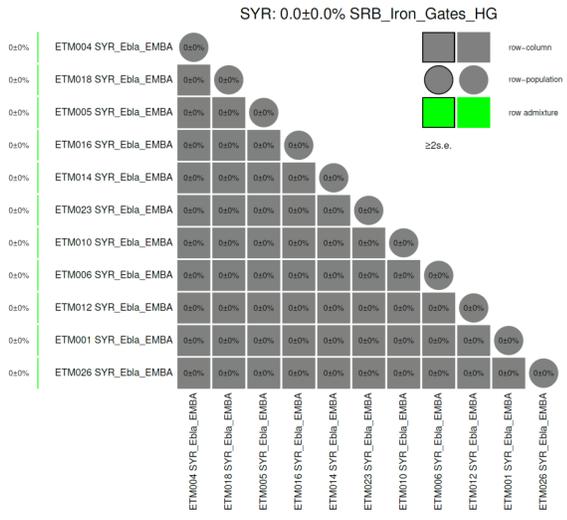
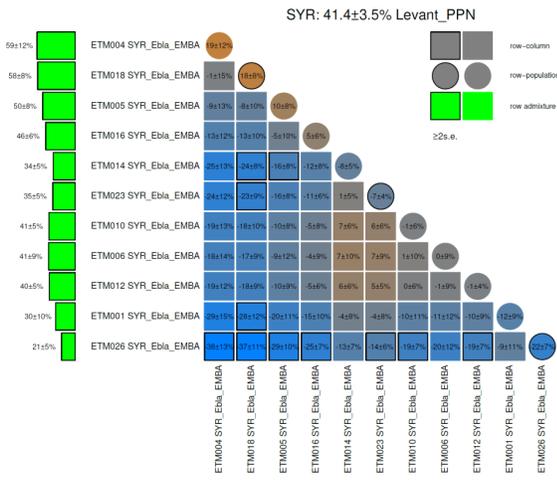
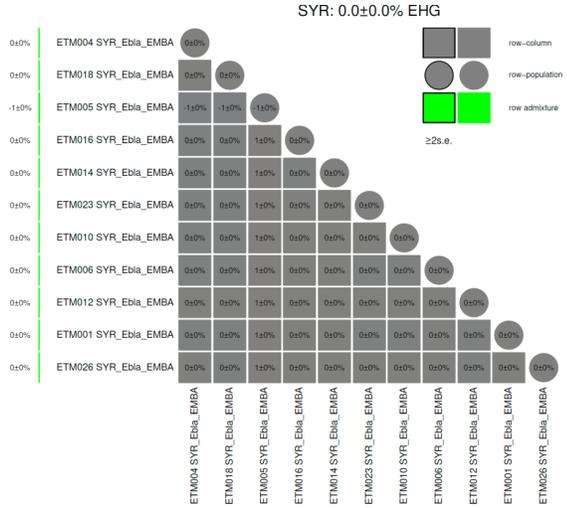
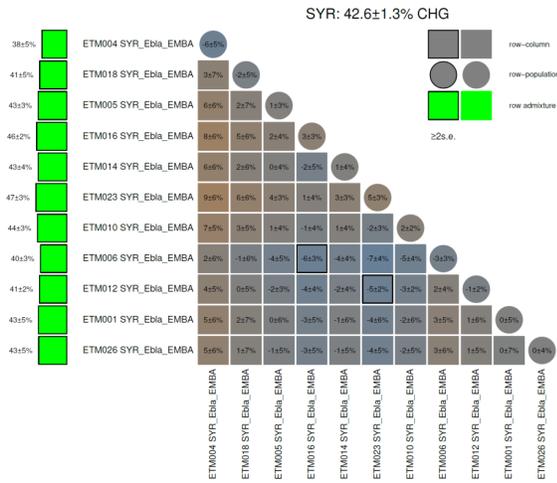


Fig. S 32 Syria

Syria

We reanalyzed Early-to-Middle Bronze Age samples from Ebla in Syria (Fig. S 32).⁽¹⁴⁾ The ancestry of people living at the site of Ebla is potentially relevant to understanding the question of the origins of Indo-European languages because of the presence of Anatolian language personal names in trade records (Anatolian languages are the earliest-known branch of the Indo-European language family).⁽⁴²⁶⁾ If some of the sampled individuals had ancestry from Anatolian language speakers, it is interesting that none of them have any EHG ancestry, similar to people from Turkey that we will examine below. The Levantine ancestry is of equal importance here in the northern Levant as that of the CHG component in contrast to areas of the north where the latter predominates. Note also the presence of Anatolian-related ancestry in many individuals from this Bronze Age sample from the Levant, a phenomenon which we will also observe in samples from Israel. Note also that the presence of some samples with higher/lower-than-average Anatolian Neolithic ancestry and of non-significant and low levels of such ancestry, unlike the case for both the CHG/Levantine ancestry which is convincingly present in all individuals. This may suggest that in Syria the population was at least partially similar to that of Iraq and the southern Levant (Israel/Jordan) in being a simpler CHG/Levantine mix prior to the arrival of Anatolian-related ancestry.

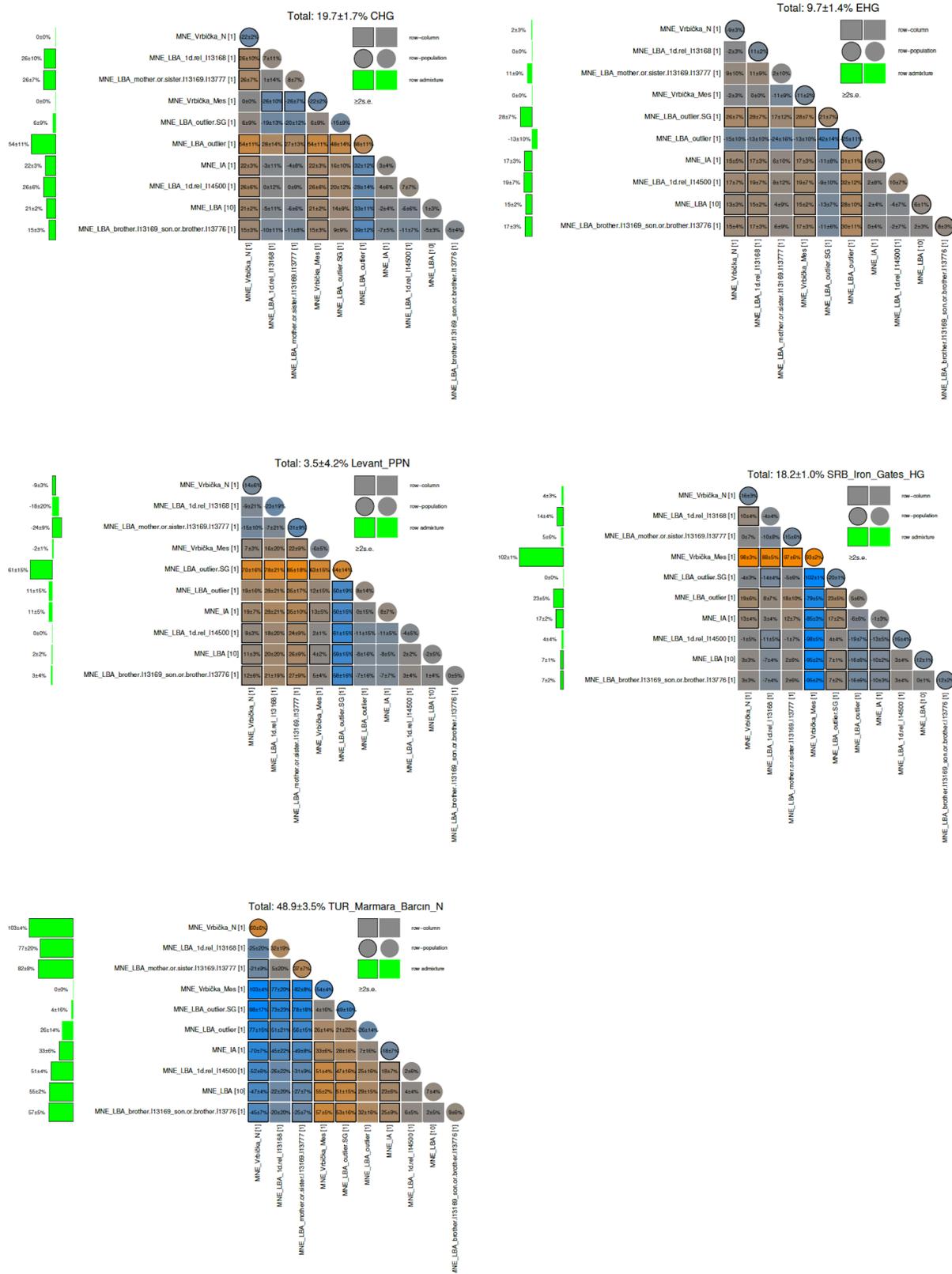


Fig. S 33 Montenegro

Montenegro

Our samples from Montenegro (Fig. S 33) are mainly from the Late Bronze Age (Velika Gruda) and such individuals possess the three main components of European ancestry of Anatolian Neolithic (~50%), Eastern European hunter-gatherer (~12%), and Balkan hunter-gatherer ancestry (~18%). One later individual of the Iron Age (MNE_IA; I13170) differs by having reduced Neolithic ancestry ($-21\pm 7\%$ relative to the rest). Whether this individual represents an outlier of the later population or signifies a real change in population ancestry in the intervening period between the end of the 2nd millennium and the 1st millennium BCE remains to be determined.

A previously published Late Bronze Age individual from Velika Gruda(4) (RISE595.SG1 MNE_LBA_outlier.SG) has a highly unusual combination of high Levantine ($61\pm 15\%$) with some EHG ($28\pm 7\%$) ancestry, and a newly sampled outlier individual has a high proportion of CHG ancestry (I13166; MNE_LBA_outlier; $54\pm 11\%$). Two individuals from Vrbička cave appear to be entirely Anatolian Neolithic (I16994; MNE_Vrbička_N) and Balkan hunter-gatherer (I16995; MNE_Vrbička_Mes) in ancestry.

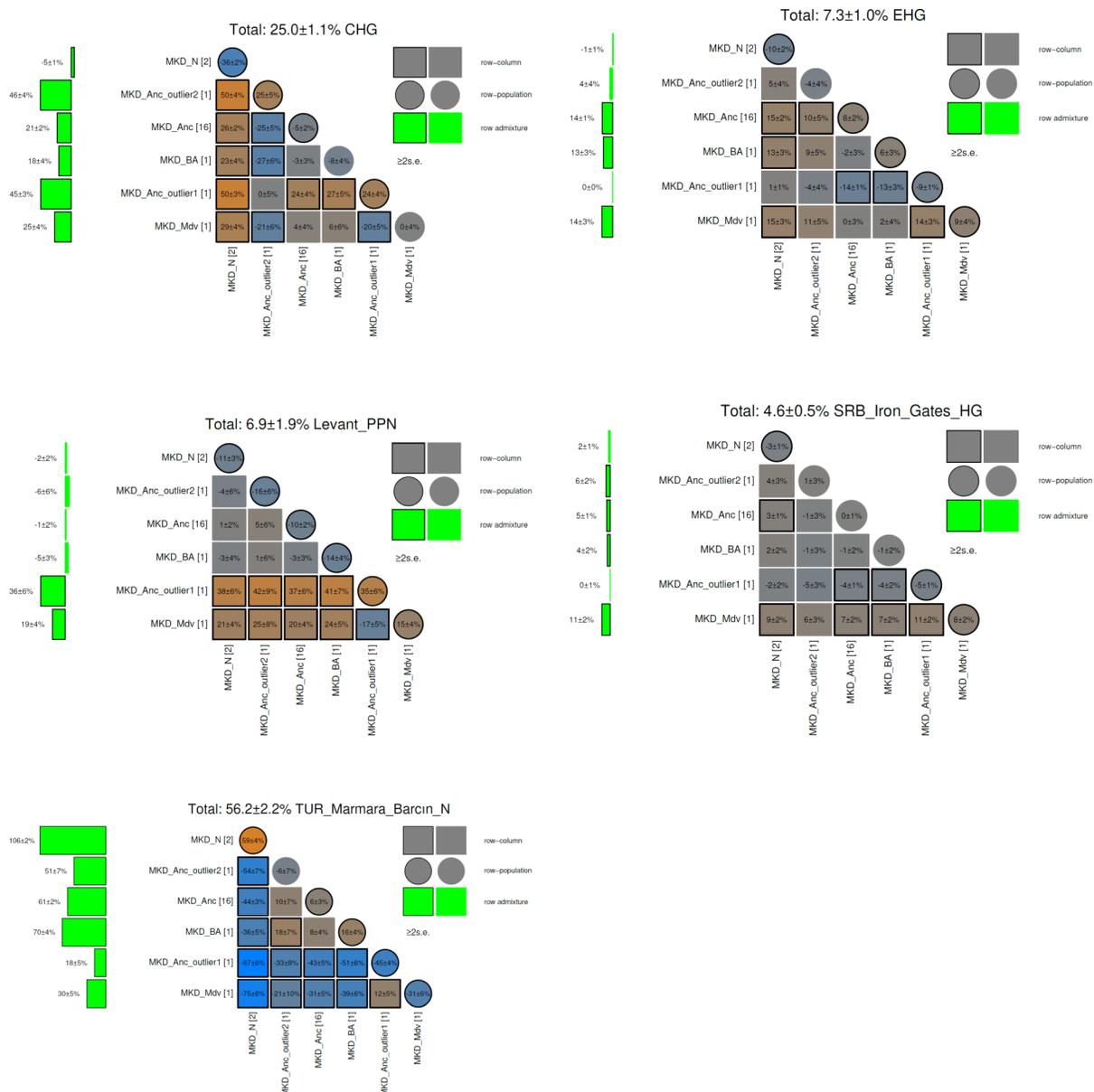


Fig. S 34 North Macedonia

North Macedonia

Our samples from North Macedonia (Fig. S 34) are of particular interest as this country is at the heart of the southeastern wing of the Southern Arc, surrounded by Albania, Serbia, Bulgaria, and Greece. North Macedonia is thus transitional between the Aegean and the rest of Europe and between east and west within the Balkans. Most individuals sampled are from the 1st millennium BCE and are labeled MKD_Anc. The population had primarily Anatolian Neolithic and CHG/EHG ancestry. The 1st millennium individuals are genetically similar to a single MKD_BA individual from the Bronze Age (17231; 1367-1124 calBCE from Ulanci-Veles) suggesting that the 1st millennium BCE population had continuity with at least the Late Bronze Age.

There are two outliers within this population. I10392/MKD_Anc_outlier1 has high CHG and Levant_PPN and no EHG ancestry and clusters with Near Eastern populations. I10167/MKD_Anc_outlier2 has high CHG and no EHG/Levant_PPN ancestry. These outliers are from a time when North Macedonia was part of the political continuum formed by the eastward expansion of Alexander the Great and his successors and it is plausible that these outliers represent people with ancestry from West Asia, particularly in the case of I10392 who also possessed substantial Levantine ancestry.

A medieval individual (MKD_Mdv/I2530; 992-1040 calCE, Tumba S. Opticari, Bitola) also has some of the Levantine ancestry which, together with more than average Balkan hunter-gatherer ancestry replace a portion of the Anatolian Neolithic ancestry in the region: the Medieval individual has $-31 \pm 5\%$ less Anatolian Neolithic ancestry than the MKD_Anc population. A possible migration from the north prior to the time of this individual (which has previously been proposed for medieval Southeastern Europe on the basis of modern data(427, 428)) would explain the diminution of Anatolian Neolithic and increase of hunter-gatherer ancestry.

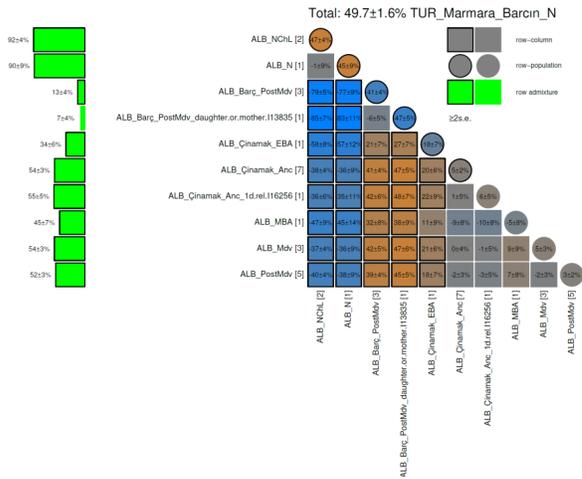
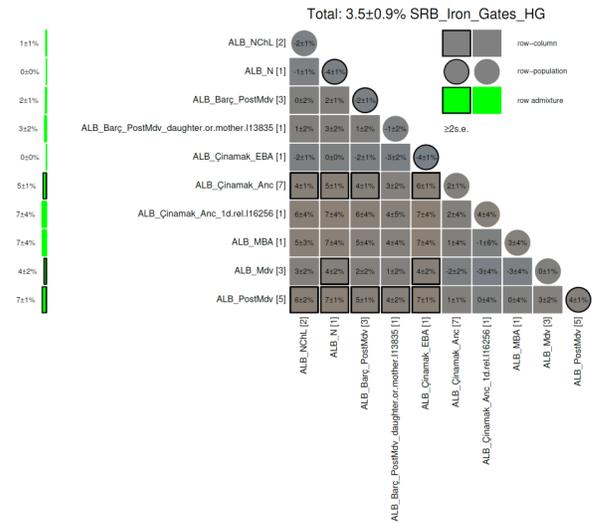
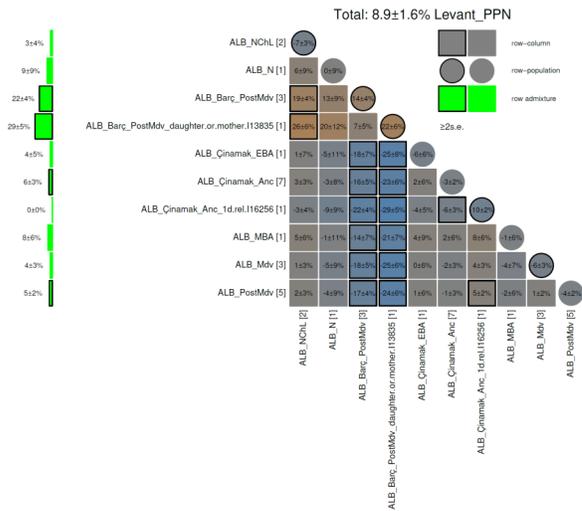
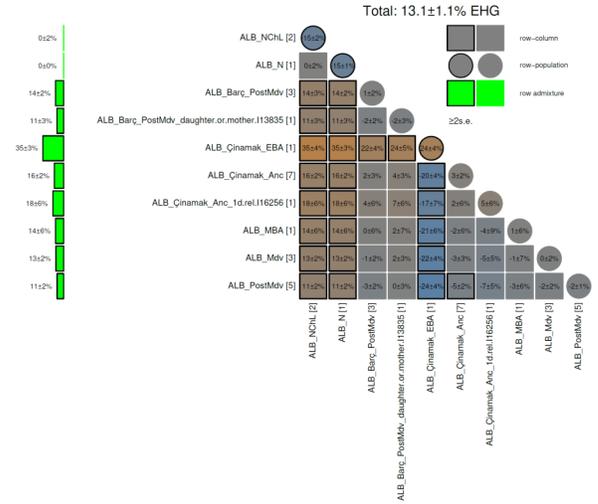
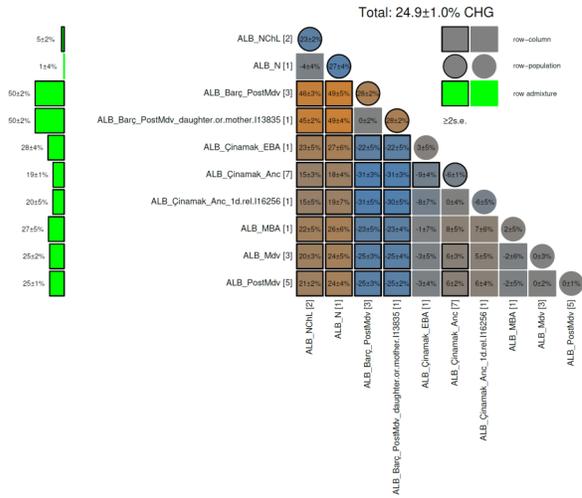


Fig. S 35 Albania

Albania

The samples from Albania (Fig. S 35) range from the Neolithic to medieval period and present a very interesting picture of the evolution of the population there, with some surprises. Early Neolithic to Copper Age Albania is dominated by Anatolian Neolithic-related ancestry without any evidence for the absorption of any European hunter-gatherer population. Two Neolithic-to-Chalcolithic samples from Tren Cave at the southern border of lake Prespa (one of which, I13840 is dated to 4245-4051 calBCE) show a trace amount of CHG ancestry ($5\pm 2\%$ in total and $7\pm 3\%$ in I13840) on top of the Anatolian Neolithic background, similar to samples from the Aegean that we will discuss in our section on Greece.

EHG ancestry becomes ubiquitous after this time and reaches up to $35\pm 3\%$ in an outlier individual (I14689) from Çinamak; such high levels of EHG ancestry are of course not unheard of in mainland Europe as they were found in individuals of the Corded Ware culture(8). This individual, the earliest known one with EHG ancestry from the western Balkans dates to the same period (2831-2480 calBCE). This suggests a parallel appearance of steppe ancestry in Central Europe and in the western Balkans, well beyond the geographical limits of the steppe itself. The bulk of the individuals from Çinamak are from the 1st millennium BCE and have a lower $16\pm 2\%$ EHG ancestry on average.

We identify four post-medieval individuals from Barç who stand out in having substantial levels of both Caucasus- and Levant-related ancestry in contrast to all other samples from the country. In Principal Component Analysis (PCA) these individuals superficially resemble samples from the South Caucasus (Armenia) also included in our study. However, the analysis of outliers in (6) suggests the presence of East Asian ancestry in these outlier individuals, suggesting that they had ancestry from the east which could have been mediated e.g., by Turkic ancestors either via Anatolia or the Balkans which had been recipients of such ancestry of Turkic nomads during medieval times.

Other than these outliers, the population of Albania from the Middle Bronze Age to the post-medieval period appears to be largely made up of the same components in similar proportions: Anatolian Neolithic ($\sim 1/2$), CHG ($\sim 1/5-1/4$), and EHG ($\sim 10-15\%$) ancestry.

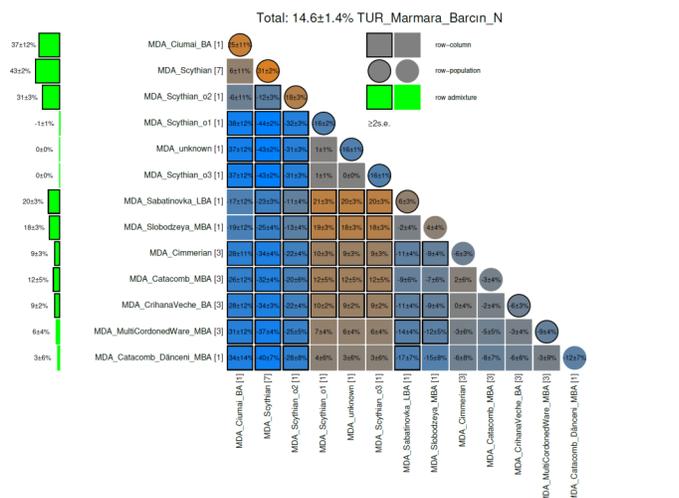
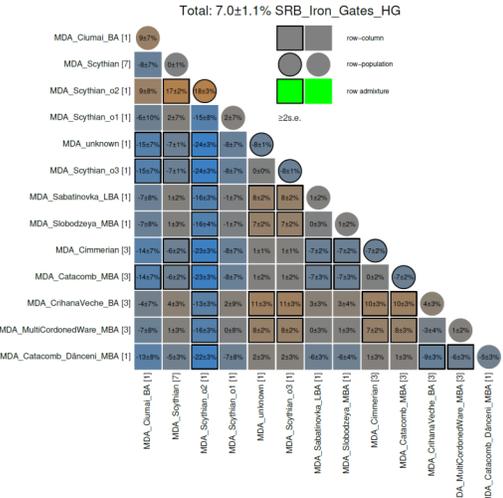
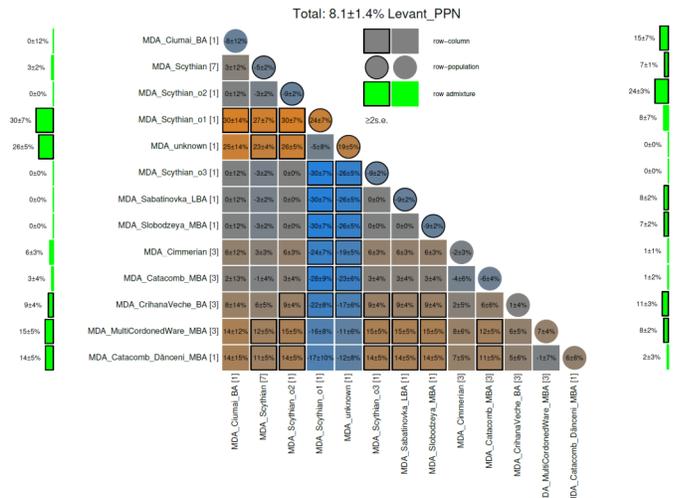
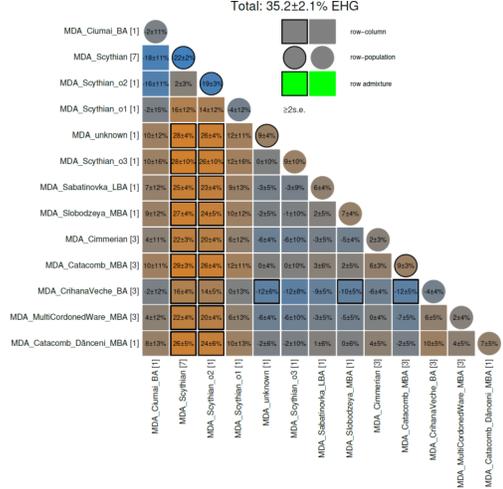
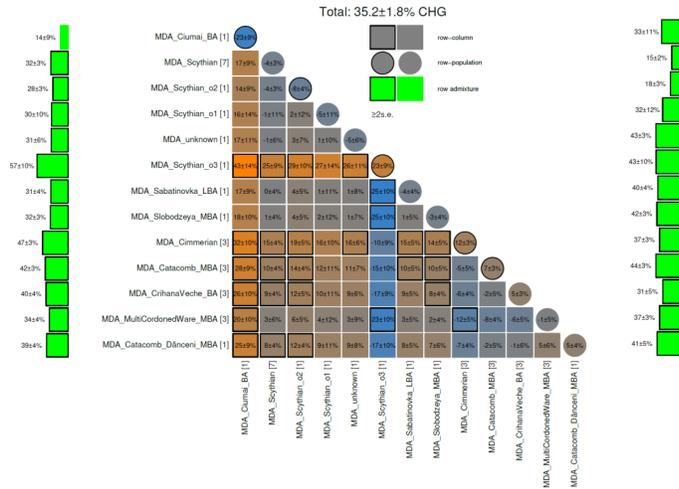


Fig. S 36 Moldova

Moldova

Our samples from Moldova (Fig. S 36) are geographically closest to the steppe lands within our definition of the Southern Arc. Not surprisingly, the two primary ancestral components are EHG and CHG in about equal proportions reflecting the main genetic composition of steppe populations.(7-10)

One Scythian outlier (MDA_Scythian_o1; scy193.SG) previously published(429) has substantial Levantine ($30\pm 7\%$) ancestry but no ($-1\pm 1\%$) Anatolian ancestry and would thus appear to have southern Near Eastern ancestry in addition to his steppe ancestry. This type of ancestry is also present in a sample of unknown provenance (I20086; MDA_unknown; initially assigned to Eneolithic to Bronze Age period but possessing an R-M417 Y-chromosome and East Eurasian ancestry which may indicate a much later date). Another Scythian outlier (MDA_Scythian_o2; scy303.SG) has substantial Balkan hunter-gatherer ancestry ($24\pm 3\%$). A third Scythian outlier (MDA_Scythian_o3; scy332.SG) has almost double the CHG ancestry of the others ($57\pm 10\%$) and would thus appear to have ancestry related to the Caucasus/Iran.

The main Scythian cluster had $43\pm 2\%$ Anatolian Neolithic ancestry, suggesting that it includes ancestry from the local farming population of southeastern Europe and was not derived only from the steppe where Anatolian Neolithic ancestry in putative Scythians from further east was low.(430, 431) The amount of Anatolian Neolithic ancestry was lower in other steppe-derived groups from the country such as samples of the Catacomb culture and Cimmerians.

The overall picture of our samples from Moldova reflect a population on the western border of the steppe where the CHG/EHG mix predominates but in which ancestry from both Anatolian Neolithic and Balkan hunter-gatherers, local to southeastern Europe since the Neolithic/Mesolithic is also found to various degrees in individuals and populations. The high amounts of steppe-derived EHG ancestry in Moldova contrast with other parts of southeastern Europe studied in our paper where high EHG ancestry is unusual except in isolated individuals.

We also examined (Fig. S 37) the newly reported individuals from Moldova associated with the Catacomb culture with those from the North Caucasus Catacomb culture(17) allowing us to compare the two locales on opposite sides of the Black Sea. In both, the CHG/EHG mix predominates and one individual (I20088; Purcari) has a significant amount ($17\pm 4\%$) of Anatolian Neolithic ancestry, in contrast to analogous individuals from Catacomb cultures of the Caucasus, while not having an excess of either CHG or Levantine-related ancestry, suggesting plausibly that it acquired this ancestry by admixture with Anatolian Neolithic-derived farmers.

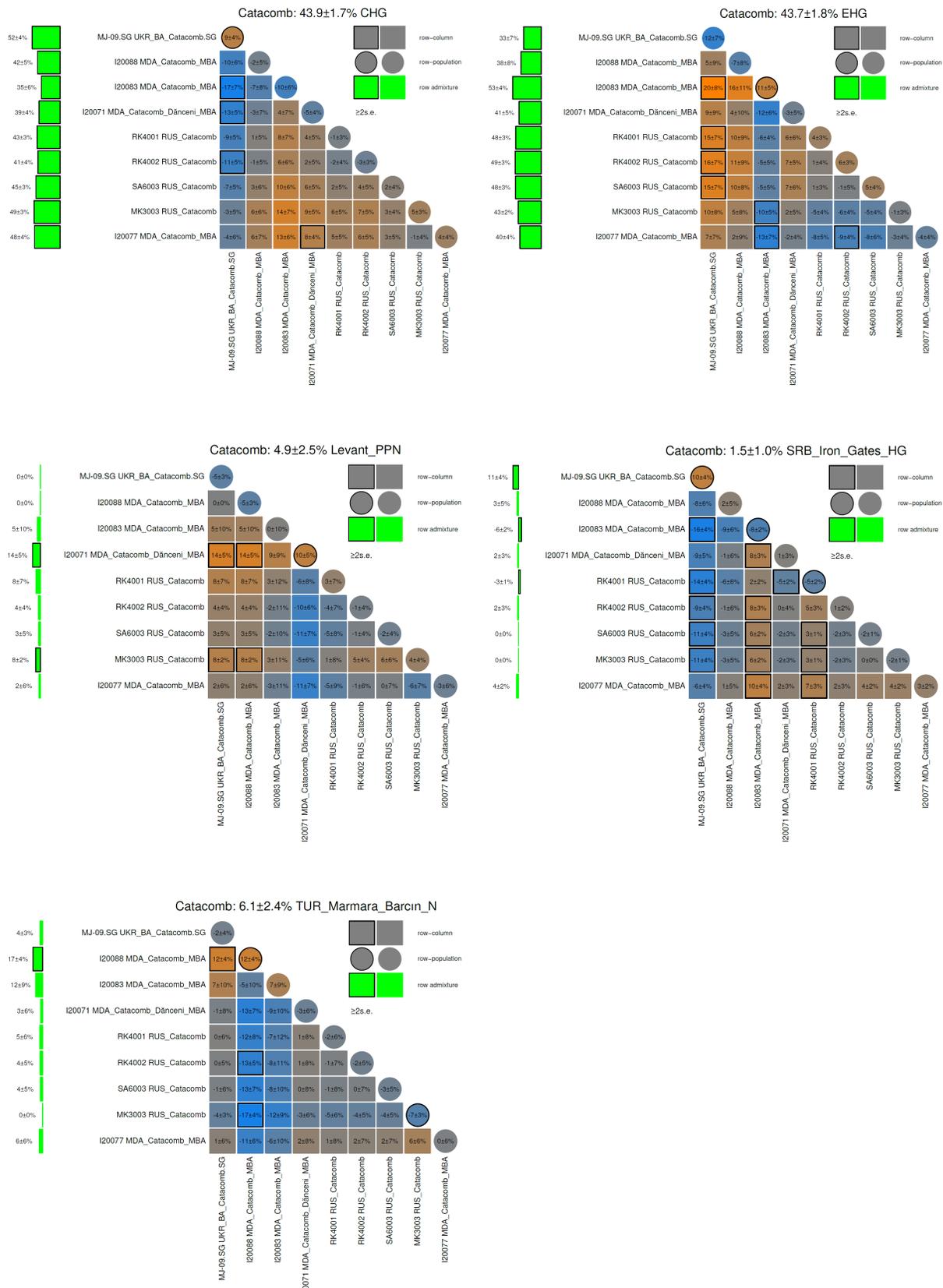


Fig. S 37 Catacomb culture individuals

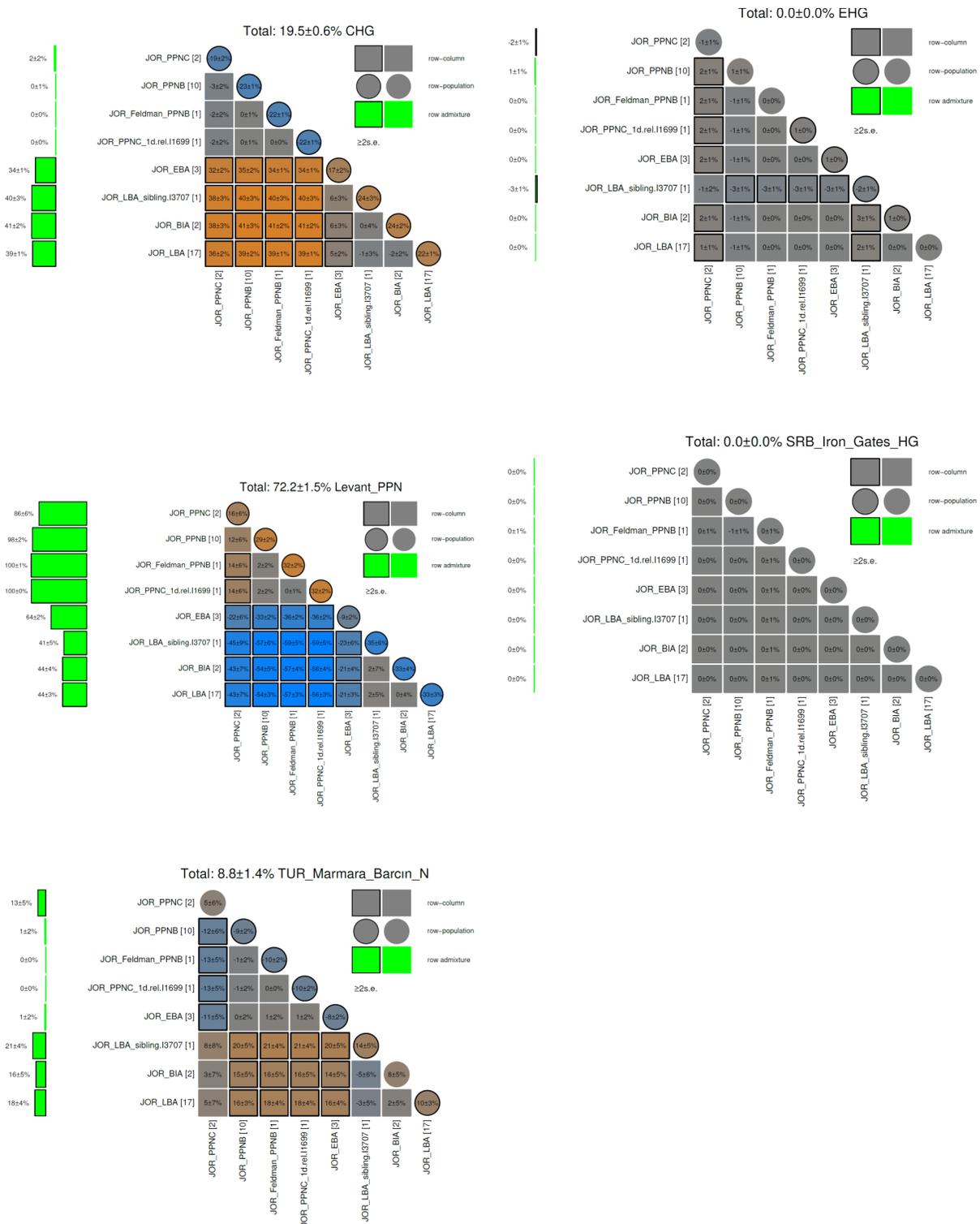


Fig. S 38 Jordan

Jordan

We detected an interesting pattern (Fig. S 38) in previously sampled individuals from Jordan(10, 410, 432) The PPN samples from Jordan are made up of ancestry labeled Levant_PPN which is not surprising as they largely define this population.

The sample of Early Bronze Age individuals from 'Ain Ghazal(10) (JOR_EBA) show a 2/3-1/3 mixture of Levant_PPN and CHG ancestry; these were previously modeled(10) as a mixture of 56% Levant Neolithic and 44% Iran Chalcolithic (Seh Gabi) ancestry. In the section on Iran in this paper we model Seh Gabi as 75% CHG and 25% Levant Neolithic ancestry, and thus the model of (10) implies a total of $56\% + .44 * 25\% = 67\%$ Levantine ancestry, in close agreement with our modeling here.

Strikingly, the later Bronze (JOR_LBA) and Iron Age (JOR_BIA) samples from Jordan recently published(432) from Baq'ah, a thousand years later possess ~15-20% Anatolian Neolithic ancestry; the pattern is general in individuals from this site. A simple mix without Anatolian ancestry was not feasible for Israel Chalcolithic samples(420) earlier than both 'Ain Ghazal and Baq'ah. It now appears that the Anatolian Neolithic ancestry which was not evident in 3rd millennium BCE at the southern edge of the Levant had become ubiquitous there by the Late Bronze Age.

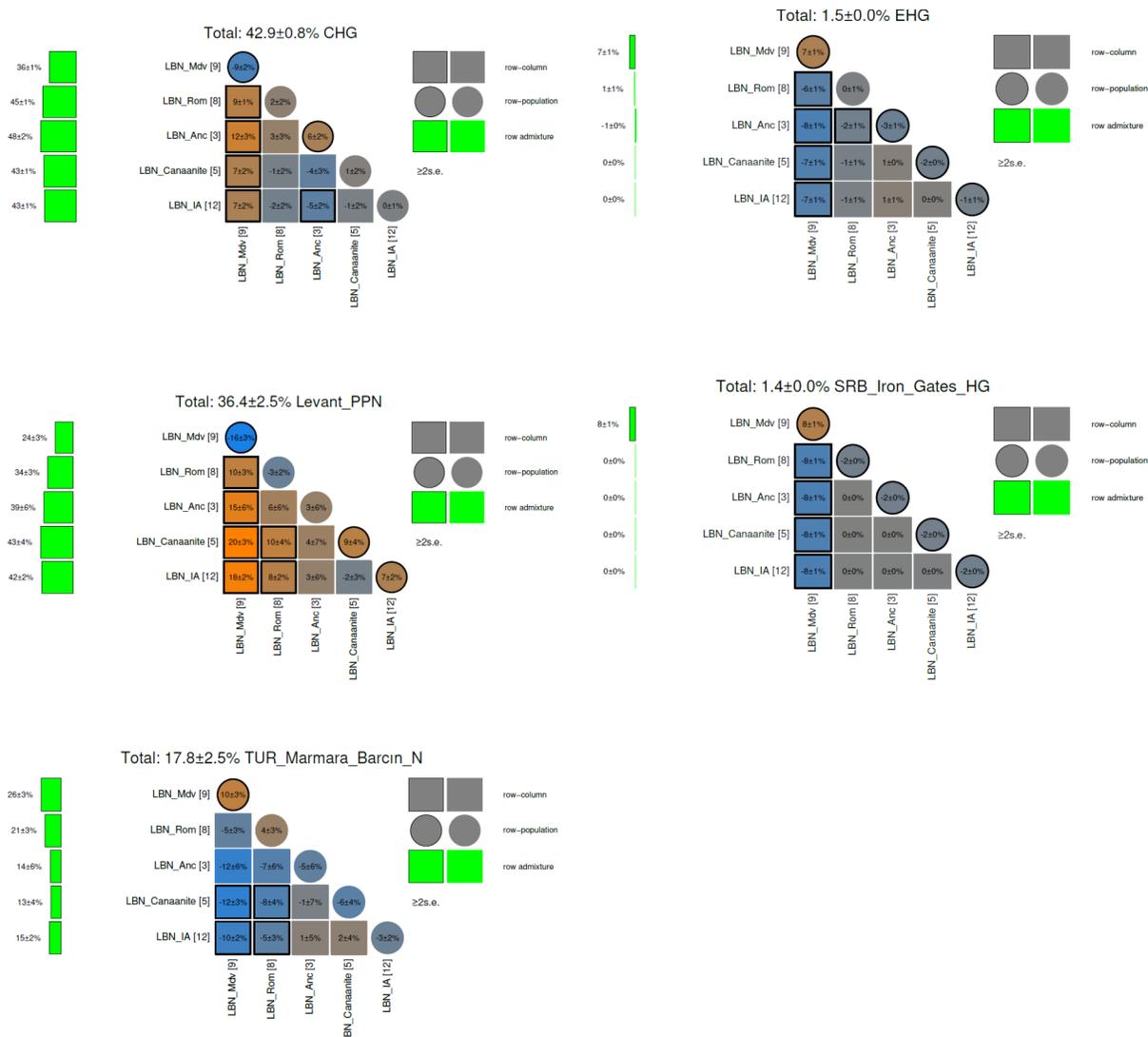


Fig. S 39 Lebanon

Lebanon

We also re-analyzed previously sampled individuals from Lebanon(433-435) from the northern Levant (Fig. S 39). Iron Age, Canaanite, and 1st millennium BC samples are all similar in their genetic proportions and also similar to the LBA samples from Jordan just discussed, with a balance of Levant/CHG ancestry predominating and some Anatolian Neolithic input. In the Roman period there is a slight increase of Anatolian ancestry at the expense of Levantine ancestry. The medieval sample is most distinctive with the presence of both European hunter-gatherer types of ancestry.

To better understand intra-population variability in the Roman and Medieval periods we also show per-individual mixture proportions (Fig. S 40).

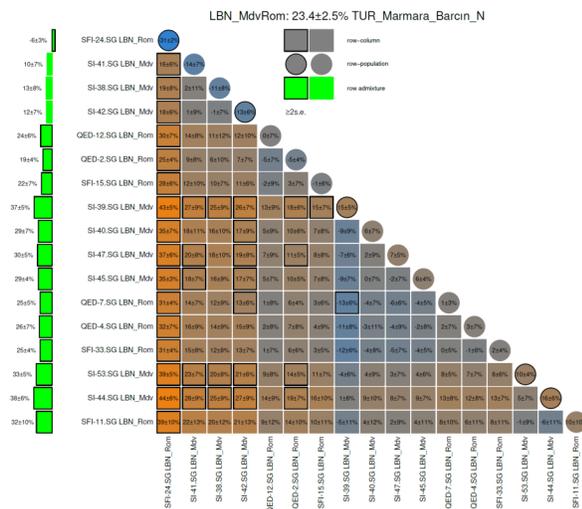
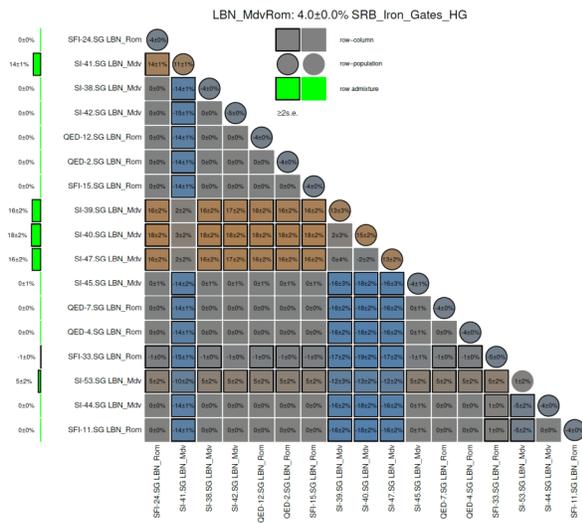
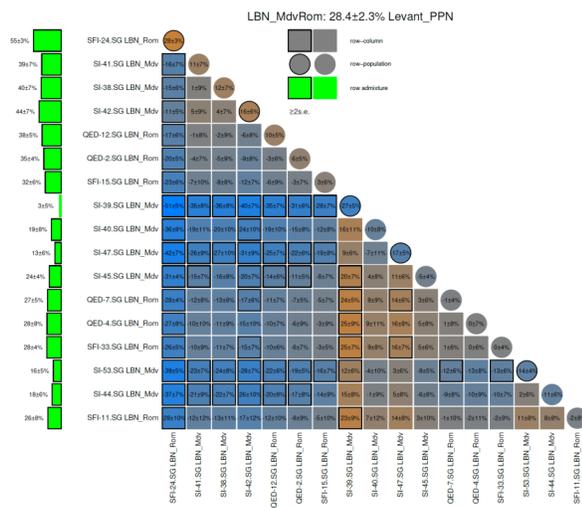
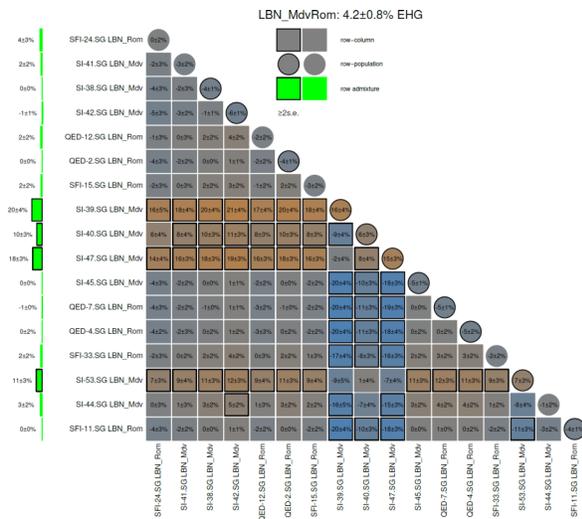
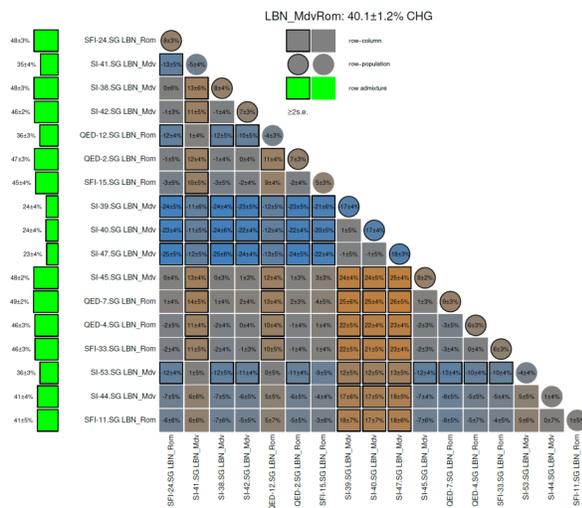


Fig. S 40 Roman and Medieval Lebanon

A Roman era individual (SFI-24) lacks Anatolian Neolithic ancestry and has more Levantine ancestry than average. The medieval variation is more striking with many individuals lacking the European hunter-gatherer components which are only present in a few of them which are probably descendants of Europeans who were present in the area during the time of the Crusades.(434)

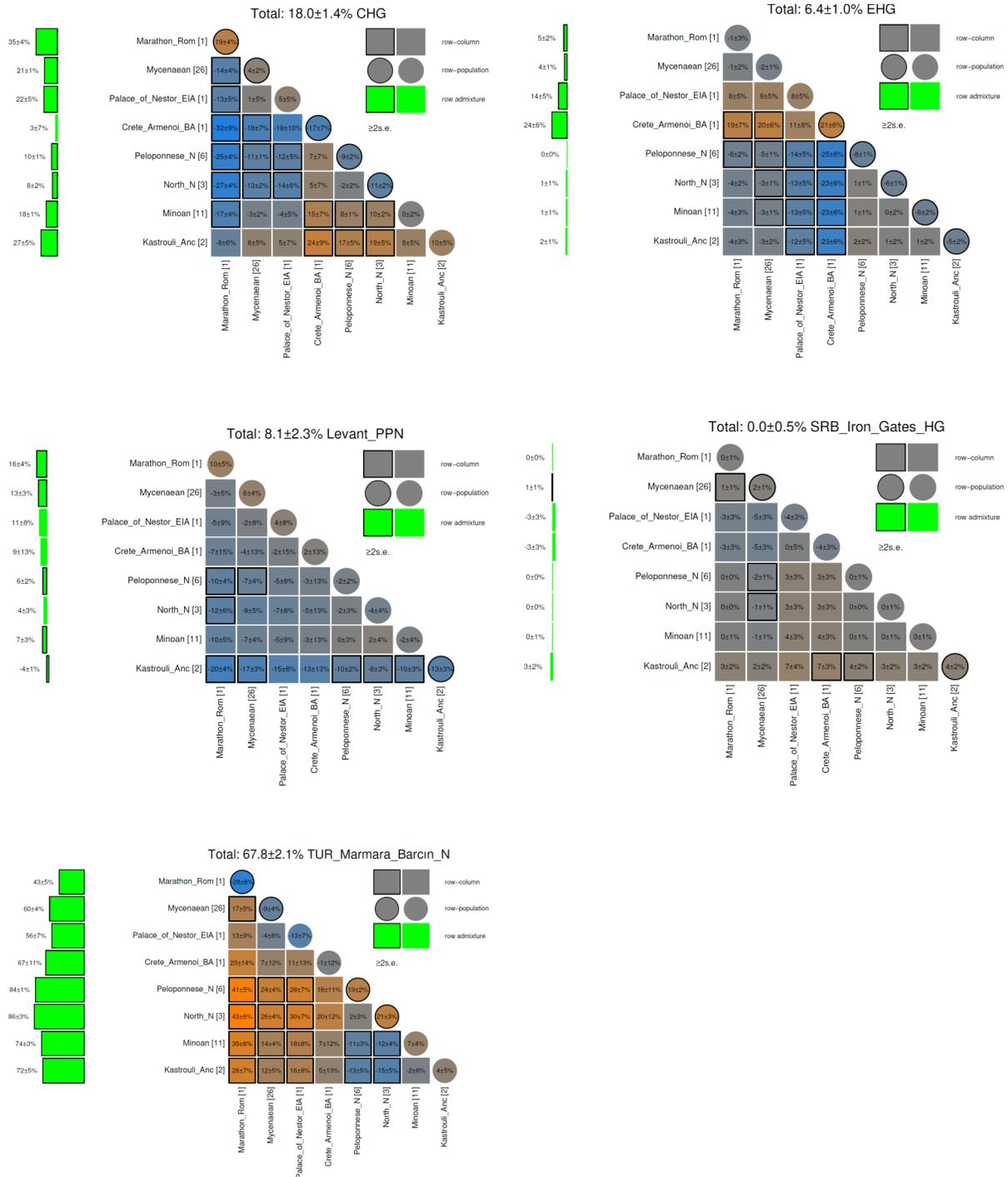


Fig. S 41 Greece

Greece

In the overview of Greece (Fig. S 41), Neolithic Greece, on the basis of available samples, is composed of primarily Anatolian Neolithic-related ancestry as previously inferred.(9, 421) We confirm the presence of some “eastern” CHG-related ancestry in the Peloponnese Neolithic,

although we infer that it was also present in the Neolithic of northern Greece(421), and also in the Neolithic-to-Chalcolithic samples from Albania previously discussed. In the Peloponnese it was accompanied by a small but significant ($6\pm 2\%$) amount of Levantine ancestry. The joint presence of CHG/Levantine ancestry suggests that this non-Anatolian related ancestry may be derived from a CHG/Levantine cline of which we have already seen the Mesopotamian Neolithic was a part.

In the Bronze Age we group individuals into broad Minoan and Mycenaean groups which are used as convenient labels to indicate Cretan and mainland Greece samples; we will look at individual variation within these broad groups below. Anatolian Neolithic ancestry continues to make up the greater part of the ancestry of the Bronze Age samples of both groups, but there is a stronger presence of the “eastern” CHG and to lesser extent Levantine ancestry. This may reflect a fresh pulse of “eastern” ancestry into the Aegean prior to the Bronze Age samples, as it in Anatolia and the rest of West Asia that CHG ancestry exceeds the low levels that occurred in southeastern Europe in the Neolithic. The proportion of eastern hunter-gatherer ancestry is very small but is nevertheless different(16) in the combined Mycenaean sample at a significant $4\pm 1\%$ with the Minoans at a non-significant $1\pm 1\%$. The EHG ancestry is ~ 3 -fold lower in the Mycenaean samples than in Bronze Age samples from North Macedonia and Albania immediately to the north of Greece and ~ 10 -fold lower than in Moldova on the edge of the steppe. Thus, our results suggest that although steppe-derived ancestry was present in Bronze Age Greece it was quantitatively the weakest discernible component, only a little above the practically non-existent Balkan hunter-gatherer ancestry.

The highest EHG ancestry is found in a previously published(16) low-coverage individual from Armenoi in Crete at $24\pm 6\%$ but this is accompanied by a much smaller $3\pm 7\%$ of CHG ancestry so it is difficult to interpret as being derived from steppe migrations where EHG/CHG components are balanced. We do not overinterpret this Cretan outlier except to note it puts an upper bound on the amount of EHG ancestry observed in the Bronze Age Aegean in a collective sample of 43 individuals. On the basis of this sample, it is justified to claim that while there was variation in EHG ancestry in the Aegean, individuals of very high steppe ancestry such as the ones found north of Greece were not common there during the Middle/Late Bronze Age timeframe of our samples.

Two individuals from Kastrouli near Delphi were from the Archaic age (I17962; 775-542 calBCE, and I17959 800-500 BCE). They were genetically similar to Mycenaean-era samples from Kastrouli but their combined EHG ancestry was not significant ($2\pm 1\%$). They differed from the Mycenaean sample set in having more Anatolian Neolithic and less Levantine-related ancestry; their ancestral composition does not suggest any external influence between the Late Bronze Age and Archaic periods as influence from the north would have introduced more EHG/Balkan hunter-gatherer ancestry, and from the east more CHG/Levantine ancestry none of which are observed for the Archaic individuals. Another individual from the vicinity of the Palace of Nestor of Proto-Geometric/Early Iron Age time (I19368) has $14\pm 5\%$ which is similar to the proportion seen north of Greece, albeit with a high standard error and a proportion that is not significantly higher than the Mycenaean group as a whole. On the basis of these 3 post Mycenaean individuals from Pylos and Kastrouli, it appears that some of the variation that existed in the Mycenaean period persisted into the Iron Age without a sign of external influence.

Finally, we note that a Roman-era individual from Marathon (I7833; 252-392 calCE) is within the range of ancestry for the population of the Bronze Age, although with somewhat more eastern (CHG) ancestry; there would definitely have been an opportunity for such ancestry to

reach Greece in Hellenistic and Roman times, as evidenced also by the study of the population of Rome in Republic and Imperial times.⁽⁴³⁶⁾ On the basis of a single individual we cannot conclude that there was a systematic Roman-era shift of the population in an eastward direction as was proposed for Rome for Imperial times. Nonetheless, such “eastern”-shifted individuals were described also in North Macedonia (above) and Croatia (below), and so may cumulatively suggest that southeastern Europe also participated to some degree in the eastward shift of ancestry that was also observed in Central Italy.

To better understand patterns of ancestry in the main Minoan and Mycenaean clusters, we also plot finer-scale variation diagrams for these two groups (Fig. S 42).

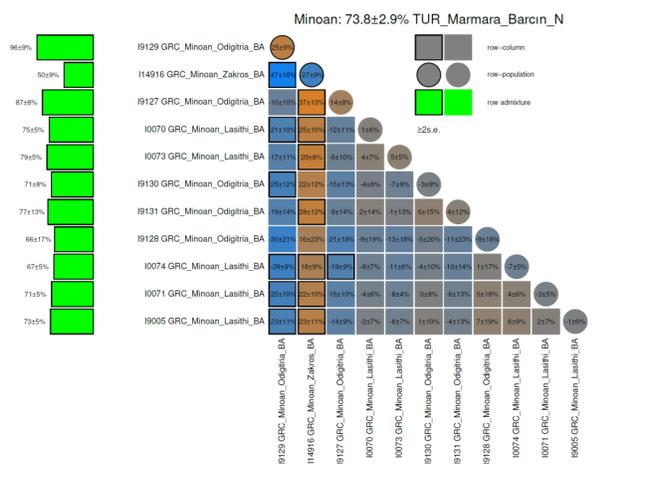
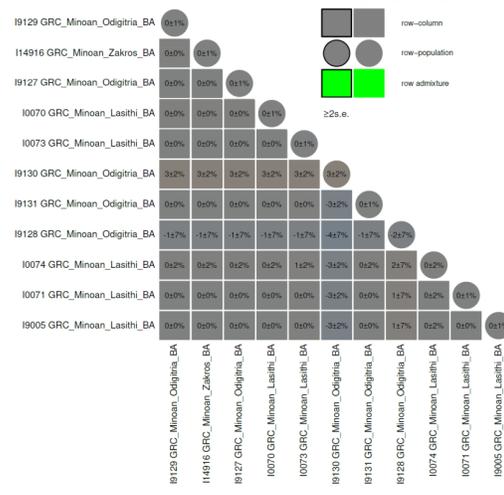
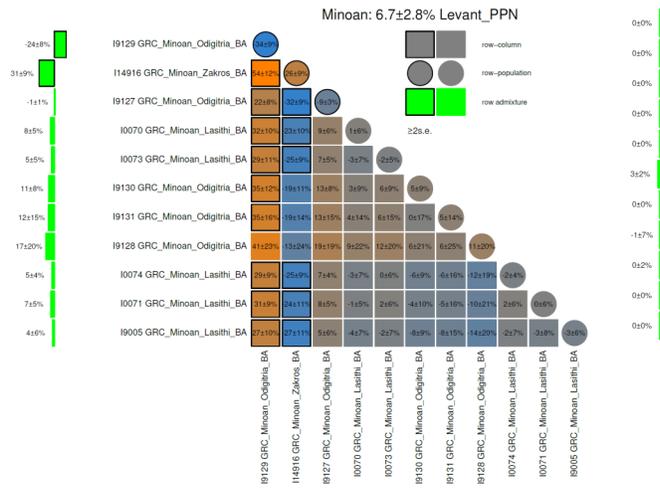
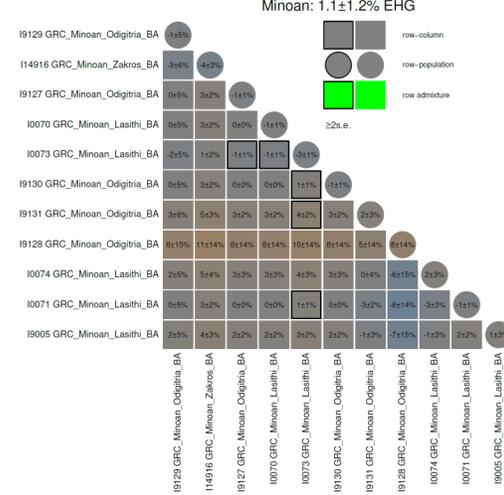
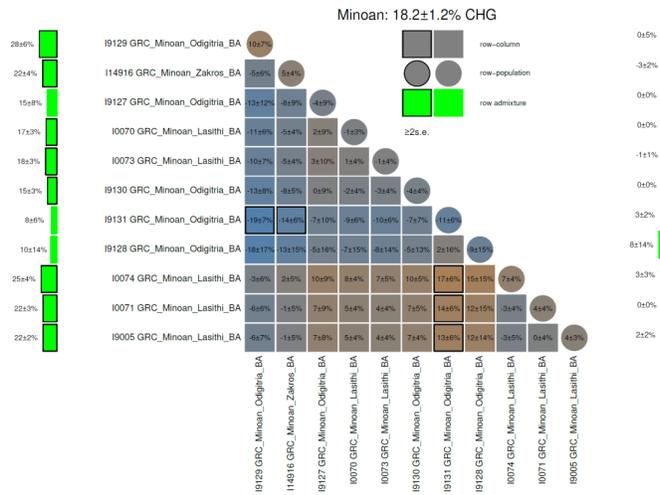


Fig. S 42 Minoan individual variation

The Minoan individuals appear fairly homogeneous with few pairwise differences in ancestry being significant. Two possible exceptions are a published individual(16) from Odigitria (I9129) which is inferred to have more Anatolian Neolithic ancestry than average, and a newly published Middle Minoan individual from Zakros (I14196) which has less Anatolian Neolithic and more Levantine Neolithic ancestry than average.

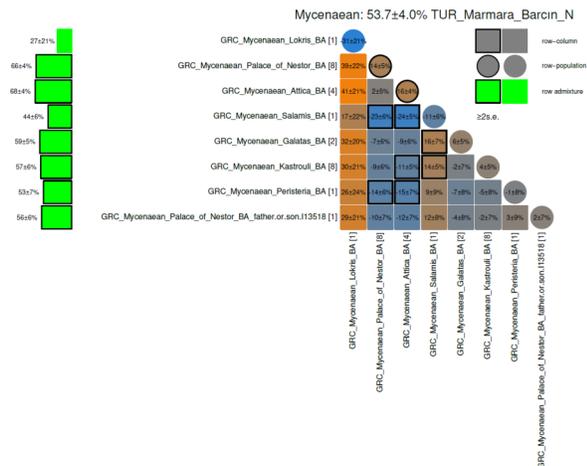
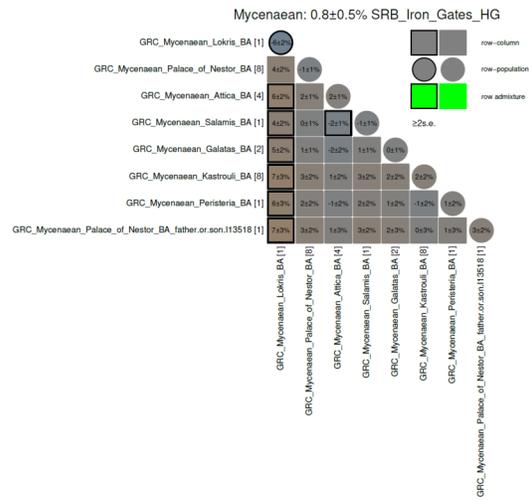
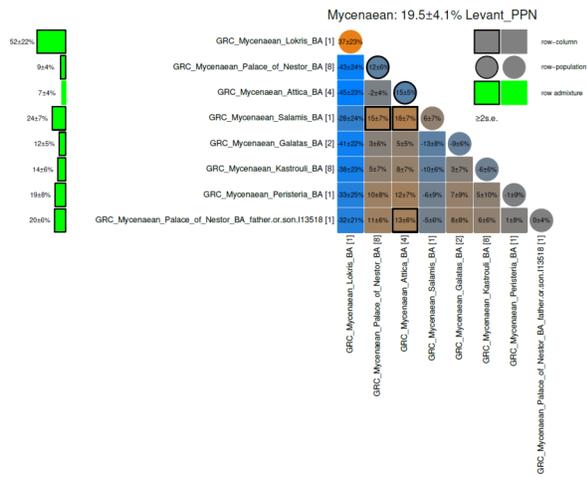
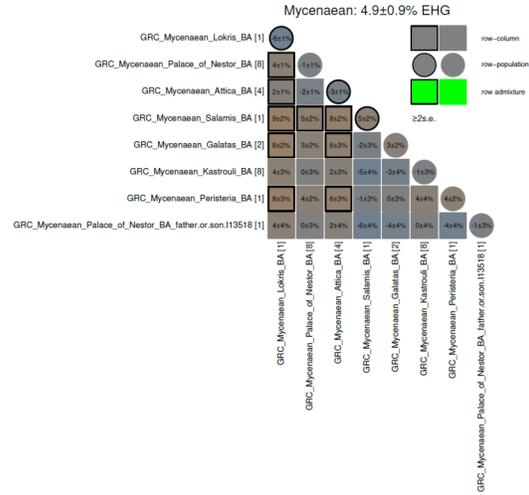
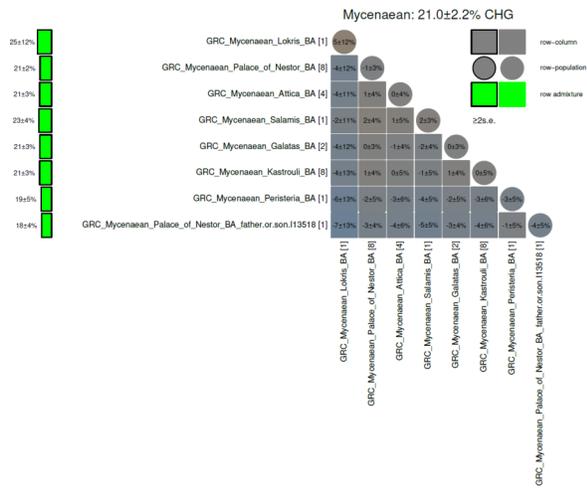


Fig. S 43 Mycenaean regional variation

Examining subsets of the Mycenaean group (Fig. S 43) and focusing on the diagonal we observe that most regional populations do not differ significantly from the population average in the five components. Some notable exceptions are the inferred absence of EHG ancestry in a low-coverage sample from Proskynas IV in Lokris (I6420_d; 1613-1509 calBCE), the less than average Levantine ancestry in Attica with corresponding more Anatolian Neolithic ancestry, and the corresponding $24 \pm 5\%$ greater Anatolian Neolithic ancestry in Attica than in neighboring Salamis. So, while there may have been some variation in terms of ancestry in the Mycenaean world, this seems to be in terms of slightly different proportions of the major sources of ancestry.

We also looked at per-individual diagrams for the two populations with large sample sizes: (Kastrouli, and the Palace of Nestor in Pylos) (Fig. S 44).

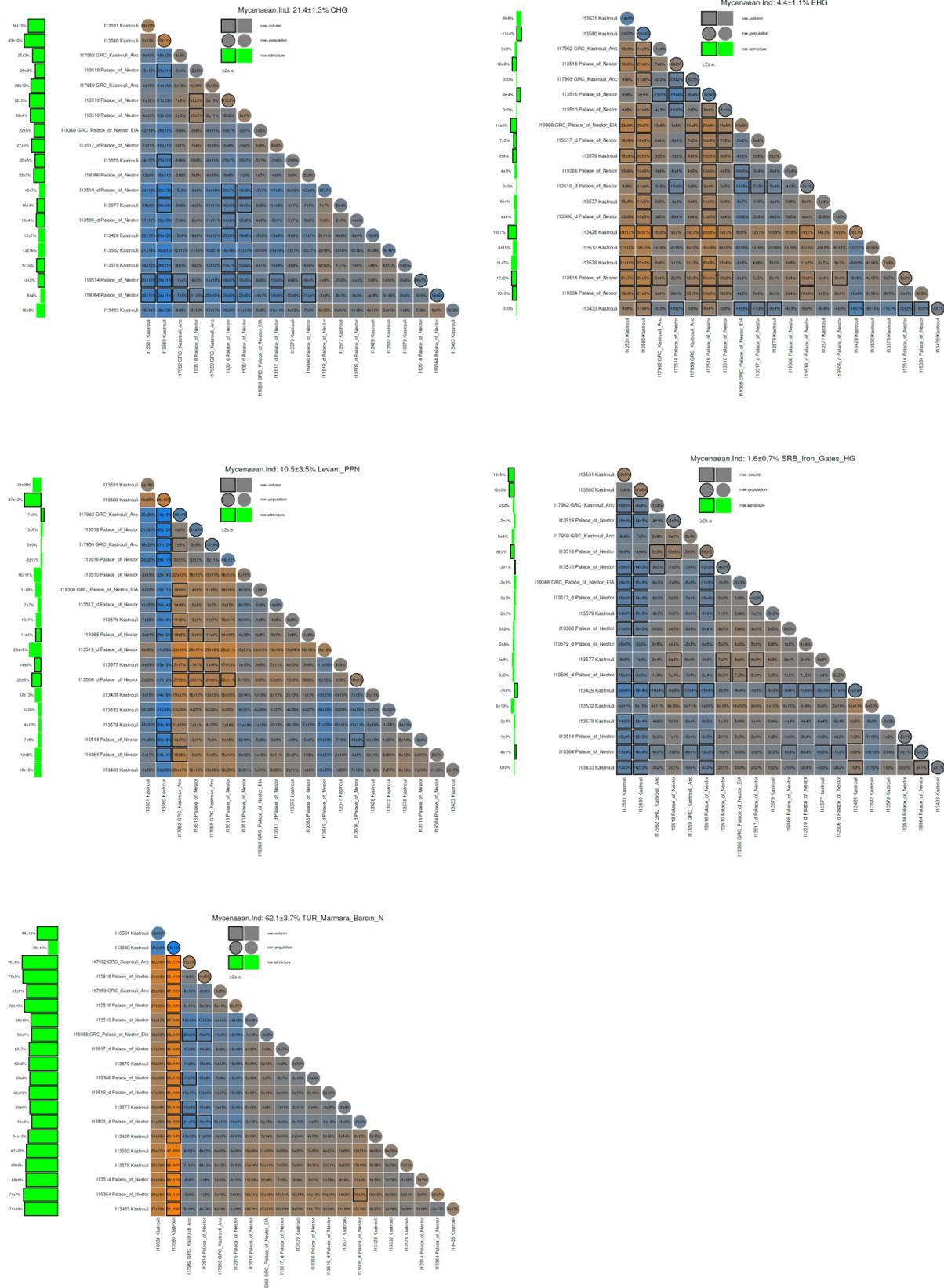


Fig. S 44 Individual variation in Mycenaean from Kastrouli, and Pylos

The individuals from these two sites in the southwestern Peloponnese and central Greece do not form site-specific clusters in terms of their ancestry. Some individuals differ in terms of their ancestral composition from the overall mean or from each other, suggesting some level of ancestral heterogeneity in Mycenaean Greece.

We highlight the case of the “Griffin Warrior(437)”, from the Palace of Nestor in Pylos (I13519_d), a 30-35 year old male buried in a shaft grave with rich grave goods many of which were produced in the Minoan world. The ancestral composition of this individual is unremarkable suggesting that this elite individual did not belong to a genetically differentiated population relative to the population of the Bronze Age Aegean at large, similar to another high status individual from Peristeria(16) (I9033), thus showing no correlation between wealth and ancestry. However, he is estimated as not having EHG ancestry and this is significantly less than the Mycenaean population as a whole, thus lending some plausibility to potential Cretan connections, although he is by no means the only Mycenaean individual to lack evidence of this type of ancestry. In the PCA (6), the Griffin Warrior is near the center of the Bronze Aegean cluster, in-between the Minoan and Mycenaean subclusters and appears to be (a) unremarkable for a LBA individual from the Aegean, and (b) not clearly belonging to either of these two groupings that form the structure of the Aegean population.

To test whether the Griffin Warrior was an outlier for the Palace of Nestor site in terms of his EHG ancestry we computed the difference between each individual of this site and the remaining individuals (Fig. S 45). For the Griffin Warrior this difference is $-5.9 \pm 1.1\%$ which corresponds to a $4.08e-8$ probability that the difference is negative (which remains significant even if we correct it for the 9 individuals considered). For most individuals the difference is not significantly negative, while for I13510 and I13516 it is. Individual I13516 was buried just outside the limits of the town surrounding the Palace of Nestor, while I13510 was buried in a chamber tomb 500m from the Palace of Nestor. Thus, the individuals identified as having less than average EHG ancestry in Pylos were buried in 3 different types of tombs associated with different levels of prestige, and 3 different localities within the area.

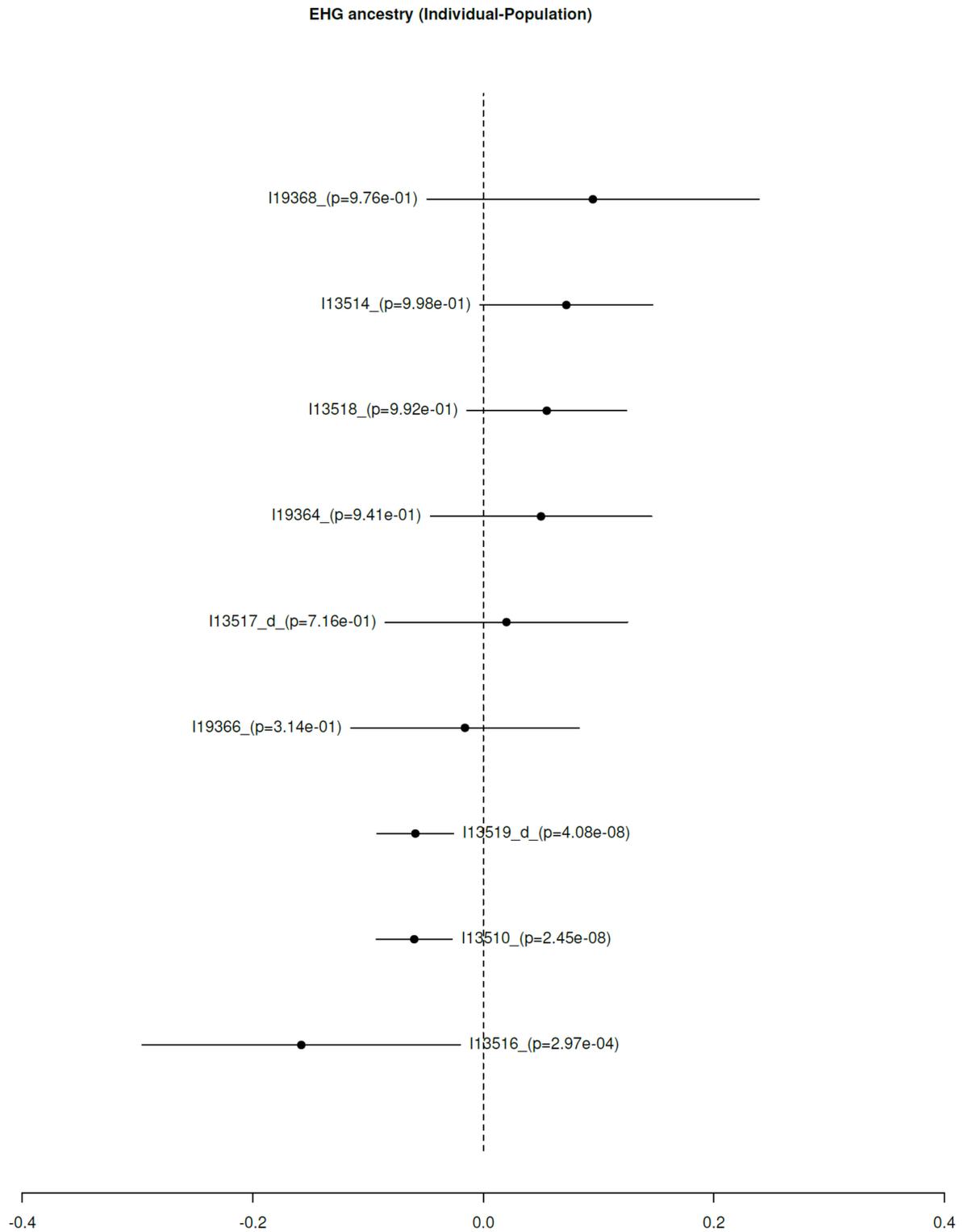


Fig. S 45 EHG ancestry differences between each Palace of Nestor individuals and the remaining individuals. We show ± 3 standard errors of the difference as a bar and list the probability that the difference is negative.

We also computed admixture proportions in our framework on 6 samples from Greece(31) that were published during the course of our analysis and present them in together with other comparative data (Fig. S 46). Estimated admixture proportions for the Minoan sample from Kephala Petras is within 1% of those of the rest of the Minoans. EHG ancestry of the Elati-Logkas MBA samples from northern Greece is high ($16\pm 2\%$) and contrasts with that of the Mycenaean population and reaches levels seen in neighboring Albania at Çinamak. The Logkas samples are separated by a few hundred kilometers and a few centuries from the LBA Mycenaean of Central-Southern Greece and are an important datapoint in the Southeastern European continuum between the low-EHG Mycenaean south and the higher-EHG north.

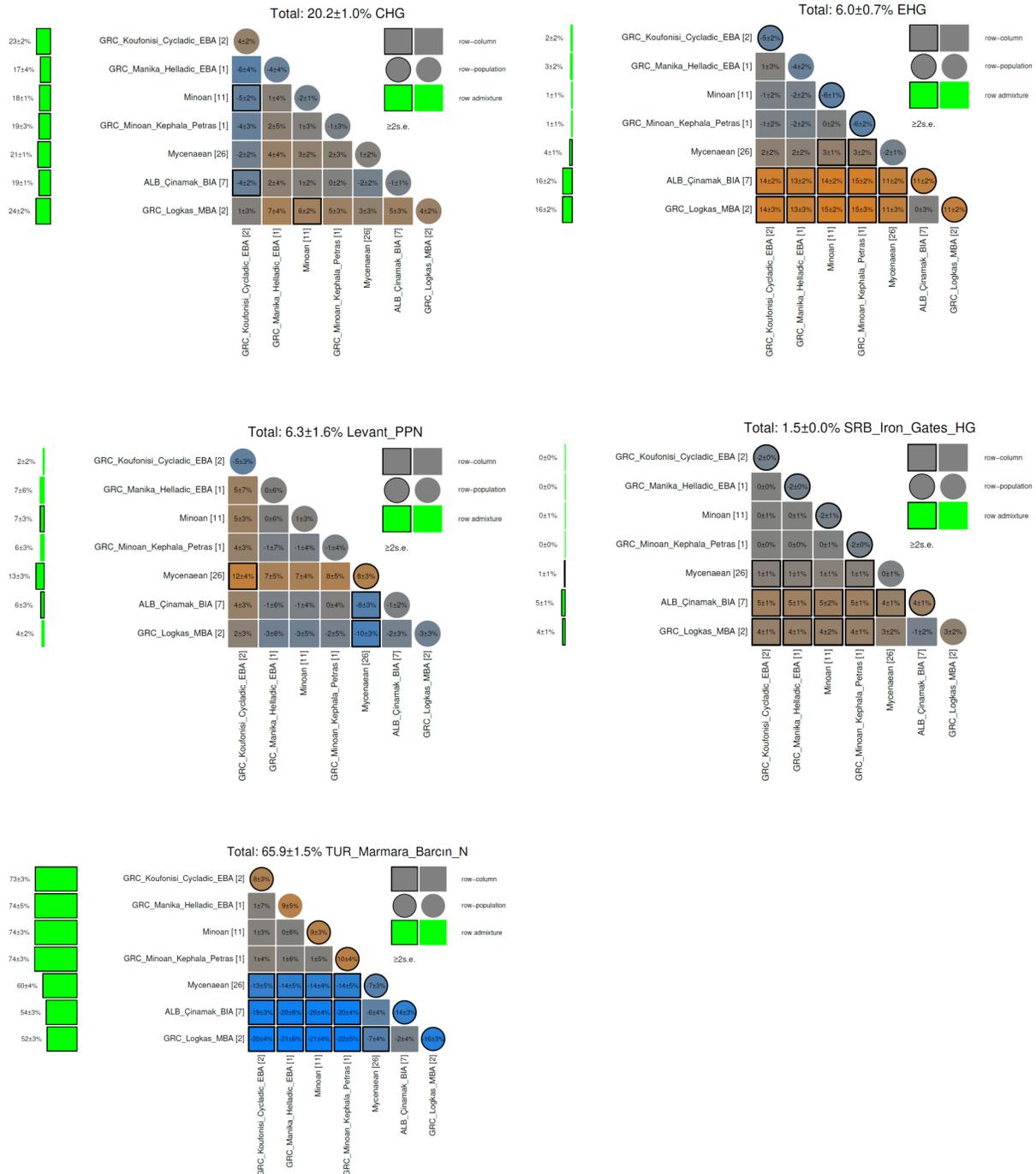


Fig. S 46 Admixture proportions of samples of Clemente et al. (2021)

Serbia

Samples from Serbia (Fig. S 47) include the hunter-gatherers from the Iron Gates who are as expected modeled with them as a source except for an outlier individual(3) (I5232; SRB_Iron_Gates_HG_outlier) who possessed a mix of Anatolian Neolithic and hunter-gatherer ancestry. Neolithic samples from Serbia are primarily composed of Anatolian Neolithic ancestry. Chalcolithic individuals from Podlokanj (4350-4000 BCE) had similar ancestry but with an increase of Balkan hunter-gatherer ancestry to $12\pm 1\%$.

A Yamnaya burial from Vojlovica-Humka (3090-2917 calBCE) had the high percentage of EHG/CHG ancestry typical of steppe individuals but is unique in Serbia compared to the multiple such individuals we already discussed for Moldova. Other Bronze Age samples from Serbia have reduced EHG ancestry; the group labeled SRB_BA (2100-1800 BCE; Mokrin and Ostojicevo) has $\sim 15\%$, similar to levels observed in other Bronze Age groups from neighboring Albania, North Macedonia, and Montenegro. One individual from Ostojicevo was dated to the Iron Age (I16814; 1006-904 calBCE) and is similar to the Bronze Age group. A newly reported Middle Bronze Age sample from Padina in the Iron Gates (I5243; 2462-2299 calBCE) is exceptional in that it has a very high level of $37\pm 3\%$ Balkan hunter-gatherer ancestry, suggesting a great deal of local absorption of hunter-gatherers in the region.

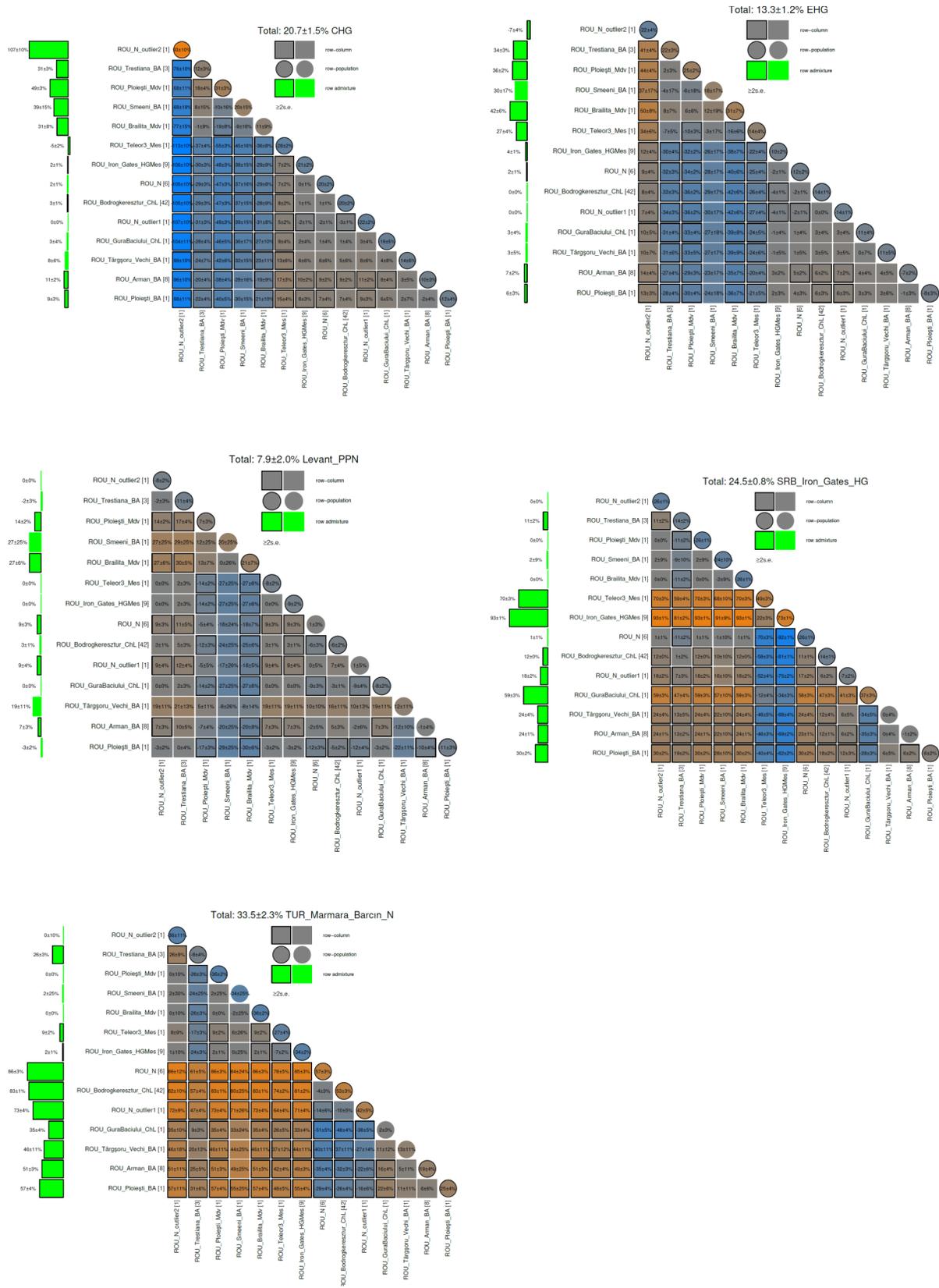


Fig. S 48 Romania

In Romania (Fig. S 48) the Mesolithic hunter-gatherer population from the Iron Gates(3, 438) can be modeled as largely cladal with the Iron Gates hunter-gatherers from Serbia. The Mesolithic hunter-gatherer²³ from Teleor 3, to the east of the Iron Gates in southern Romania, has most of its ancestry from a similar population, but with ~1/4 of its ancestry from EHG, thus being a part of the European cline of differential EHG affinity.(3, 10) The Neolithic population is predominantly of Anatolian Neolithic ancestry as expected, with the exception of two outliers: I7126/ROU_N_outlier1 (5305-5077 calBCE) from Urziceni has 18±2% hunter-gatherer ancestry not observed in the rest of the Neolithic samples. More surprising is I6661/ROU_N_outlier2 which is predominantly of Caucasus-related ancestry. This individual from Carcea has a putative date of 5500-4300 BCE but is otherwise undated.

The Chalcolithic individuals from Bodrogkeresztur (Urziceni) ((3) and new data) ~4,000 BCE, are similar to each other and indistinguishable from the ~1,000-year older Urziceni Neolithic outlier mentioned above. The one from Gura Baciului(438) has much more hunter-gatherer ancestry.

In the Bronze Age the population clusters into two main groups.

The first cluster is made up mainly of individuals from Arman (Cârlomănești) who have very low amounts of CHG/EHG ancestry but substantial (~24%) Balkan hunter-gatherer ancestry as does an individual from Târșoru Vechi (I7152) in the mid-3rd millennium BCE and an individual from Ploiești Triaj (I10494/ROU_Ploiești_B) at ~30%.

A second cluster of samples to which belong individuals from Trestiana of the 2nd millennium BCE and an individual from Smeeni that has high levels of steppe ancestry and low-to-non-existent levels of Balkan hunter-gatherer ancestry.

A medieval individual from Ploiești Triaj (I10495/ROU_Ploiești_Mdv; 982-1021 calCE) also has no detectable Balkan hunter-gatherer ancestry but steppe-level of EHG (~36%) and clusters with the much earlier samples. This individual fails the 5-way admixture model using qpWave ($p < 1e-8$) and has substantial East Eurasian ancestry in ADMIXTURE analysis (11), suggesting that it is in fact has ancestry from medieval nomads from the steppe and thus not derive in a simple way from the earlier people of the region. A medieval individual from Brailita (I17642; 901-1029 calCE) shows a similar pattern to the Ploiești individual.



Fig. S 49 Romania Bronze Age (individual variation)

The by-individual plot (Fig. S 49) shows that the same pattern of high hunter-gatherer vs. high-CHG/EHG ancestry is also applicable to individuals within the mentioned groups. The Arman individuals are from the southeast of the Carpathian Mountains, while the Trestiana ones are from the east, close to neighboring Moldova where we also observe high-steppe ancestry individuals as described above. Brailita and Smeeni, the other two sites of high steppe ancestry, are also on the plains, Smeeni just 30 km southeastward of the burial place of Arman individuals, whereas Brailita 100 km to the east. Ploiești where one high hunter-gatherer individual was sampled is located in the south between the Carpathians and the open plain.

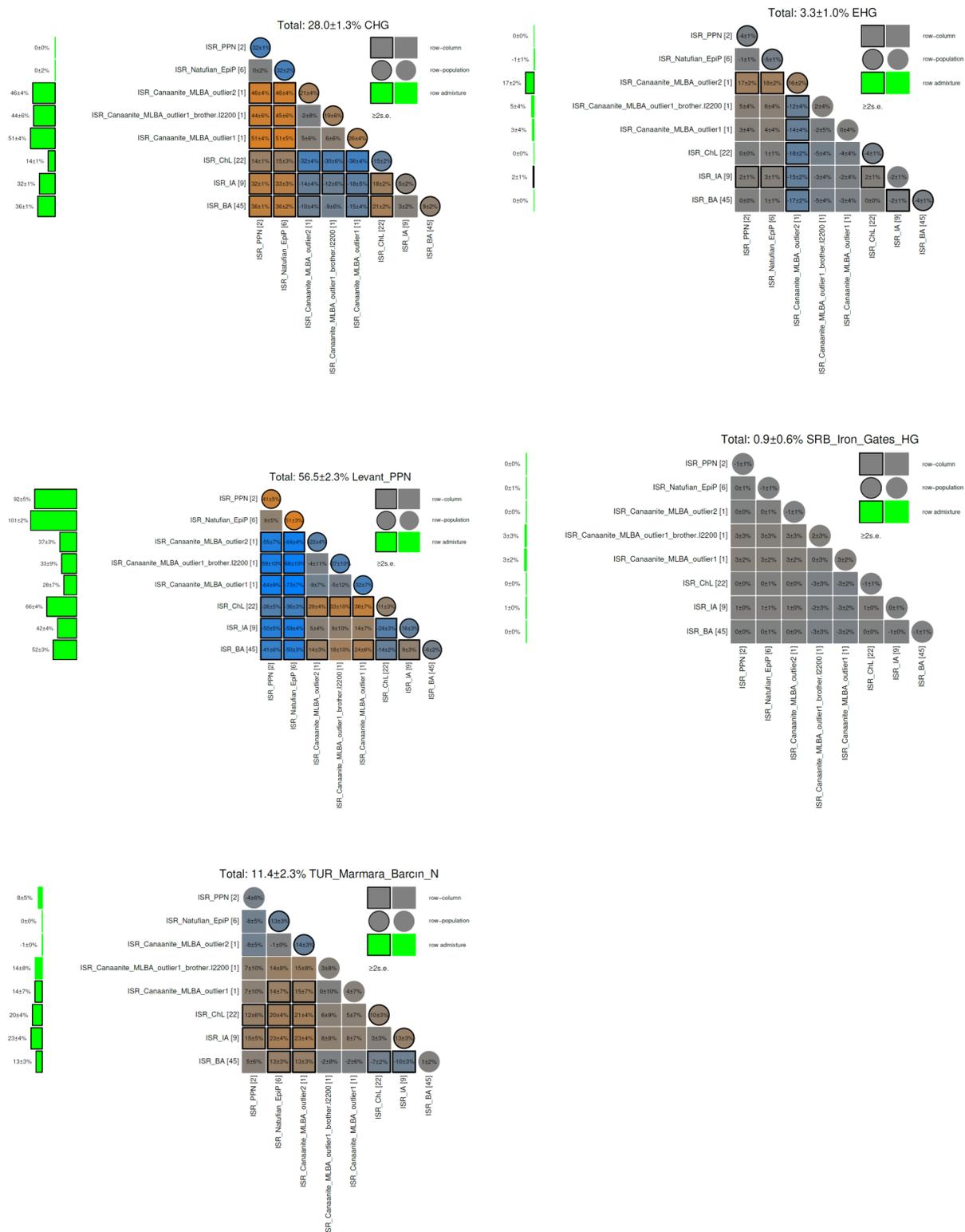


Fig. S 50 Israel

Israel

In samples from Israel ((10, 410, 420, 432, 439, 440) and this study) the Levantine ancestry is the most important one in all periods (Fig. S 50). Note that we model Epipaleolithic Natufians(10) (that precede the Neolithic) as derived from the Levantine Neolithic. It has previously been inferred(441) that these can be modeled as a mixture of the Levantine Neolithic with North African Epipaleolithic.(408) We used qpAdm to confirm that this model fits (P=0.16 with $21.2\pm 2\%$ North African input); in the 5-way model used to model individuals here the North African source is not included and hence Natufians are modeled as entirely Levantine Neolithic.

When we use qpWave to test whether the Levantine Neolithic forms a clade with Natufians the model fails ($p < 1.44e-26$). Examining the statistics of the form (Levant_PPN, ISR_Natufian_EpiP; X, Mbuti.DG) for the different outgroups, this is significantly positive for $X = \text{TUR_Marmara_Barcın_N}$ (0.003824; $Z = 9.0$) and $X = \text{Epipaleolithic of Anatolia (Pınarbaşı)}$ (0.003388; $Z = 4.8$), suggesting that there is shared genetic drift between the Anatolian-related populations and the PPN Neolithic of the Levant that was not shared by Natufians. In (11) we show two opportunities for the establishment of this shared drift: first, that the Levantine Neolithic can be modeled as a mixture of Pınarbaşı and the Natufians (i.e., Anatolian-related influence in the Levant prior to the formation of the Levantine Neolithic; second, that the population sampled at Barcın could be modeled with $12.8\pm 3.3\%$ Levantine Neolithic and $26.8\pm 4.5\%$ Mesopotamian Neolithic ancestry (i.e., Levantine-related influence contributing to the formation of the pottery Neolithic in Anatolia).

To summarize our observations, the data suggests that the Natufian Epipaleolithic is not cladal with the PPN farmers of the Levant but can only be modeled with some North African input. The PPN farmers of the Levant, in turn, share genetic drift with both Epipaleolithic and Neolithic Anatolians which can stem from either admixture prior to their own formation, or a Levantine contribution (via Mesopotamia or directly) to the farming populations of Anatolia.

In the Chalcolithic(420), 3 sources are needed: $\sim 2/3$ of the ancestry is Levantine Neolithic, $\sim 1/4$ Anatolian Neolithic and the remainder ($\sim 1/7$) related to CHG. The CHG ancestry rises to $\sim 1/3$ in the Bronze and Iron Ages. The Levantine ancestry is reduced in each successive epoch reaching $\sim 42\%$ in the Iron Age (of course there is variability in the Iron Age as we will see below). No clear pattern emerges for the Anatolian Neolithic whose temporary dip in the Bronze Age is restored by the Iron Age.

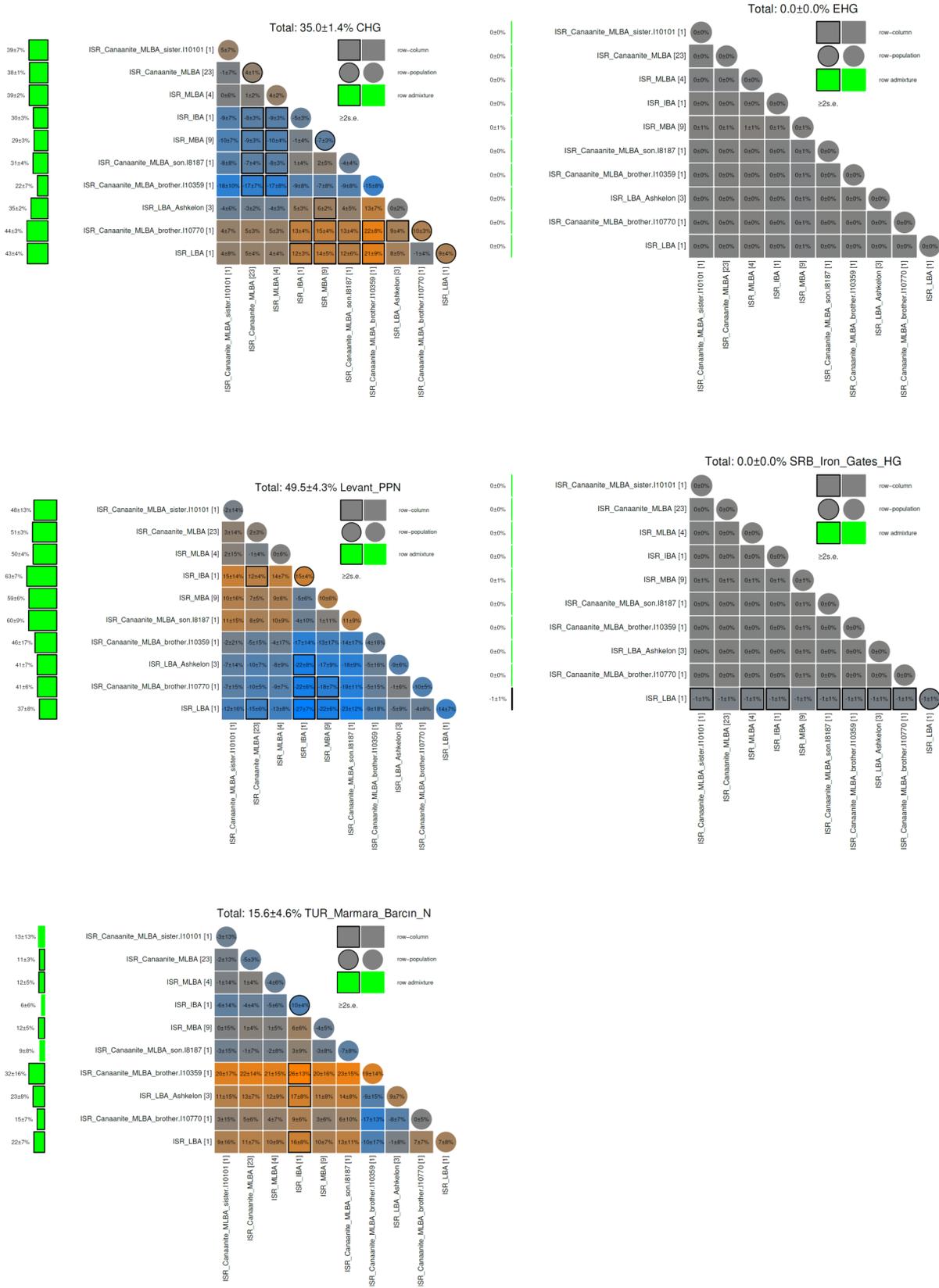


Fig. S 51 Israel (Bronze Age)

We looked at a finer-scale breakdown of Bronze Age populations (Fig. S 51). All of them are made up of the three main components discussed above, except I10100/ISR_Canaanite_MLBA_outlier2, a 1688-1535 calBCE individual from Megiddo(432) whose combination of no Anatolian ancestry but $17 \pm 2\%$ EHG ancestry points to origins in the Caucasus.

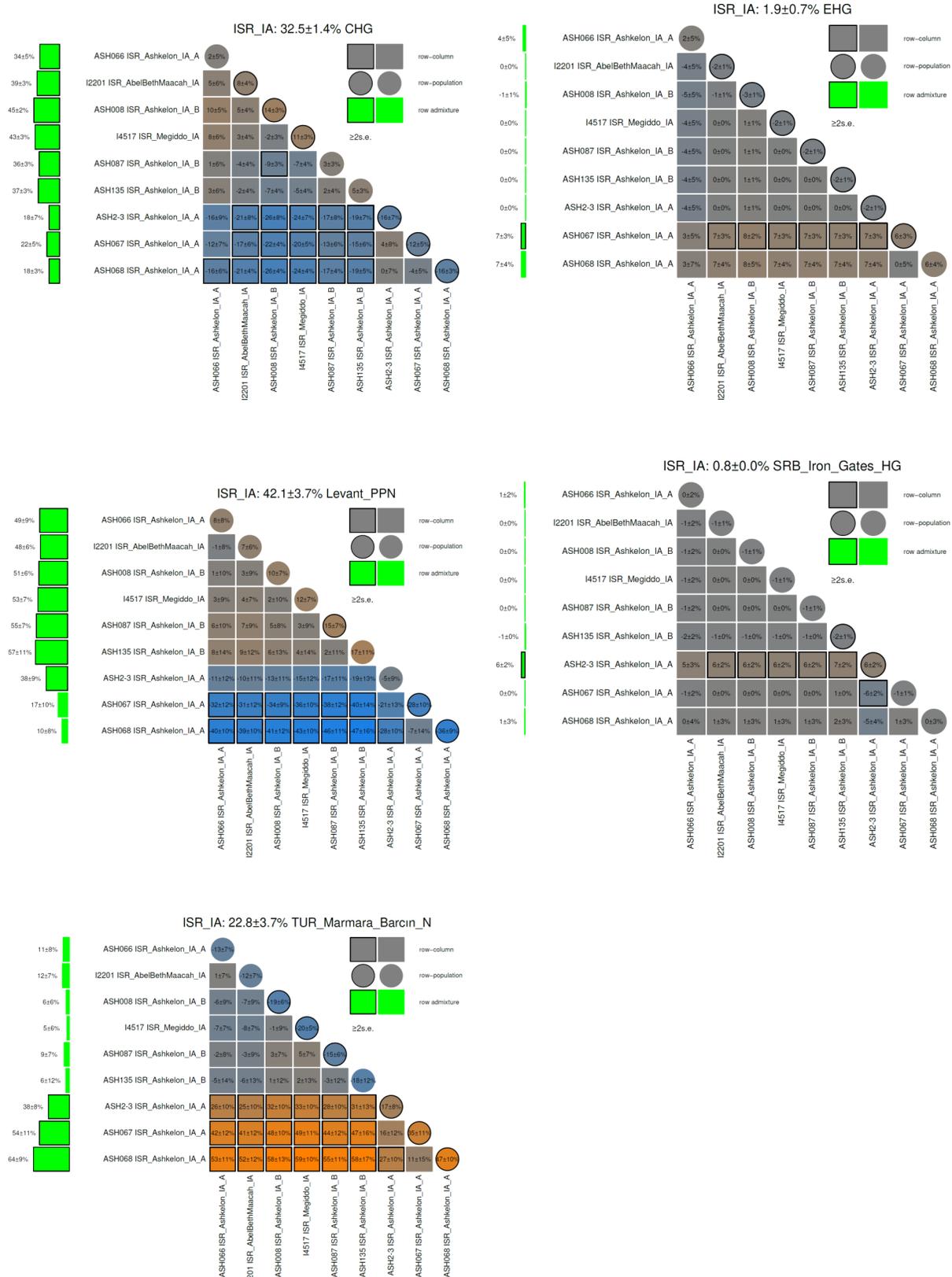


Fig. S 52 Israel (Iron Age)

We also looked at Iron Age variation (Fig. S 52). Our results add to the knowledge about the origin of the more “European” Iron Age Philistine-related outliers from Ashkelon(440) (group ISR_Ashkelon_IA_A). These differ substantially in their Anatolian Neolithic ancestry between ~11-64%. In the original publication these were modeled with Israel Chalcolithic, Iran Chalcolithic, and WHG as sources. ASH066 with a high amount of Levant_PPN/CHG ancestry is the most Near Eastern of the group. ASH067/ASH068 have the most Anatolian Neolithic ancestry and ~7% EHG ancestry and closely resemble Mycenaean samples from Greece as we also observed in (6). ASH2-3 has clearly more Anatolian ancestry than other Levantine Iron Age samples but lower than the Aegean-like samples and no EHG/Balkan hunter-gatherer ancestry. It most resembles in its ancestral makeup samples from the Hatay province of Turkey which we will discuss further down which would account for its additional Anatolian Neolithic ancestry.

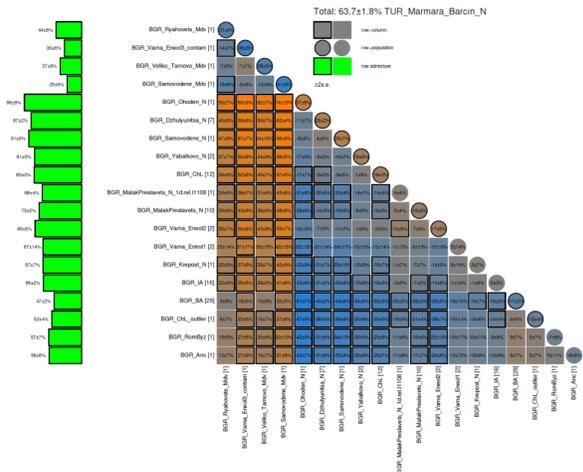
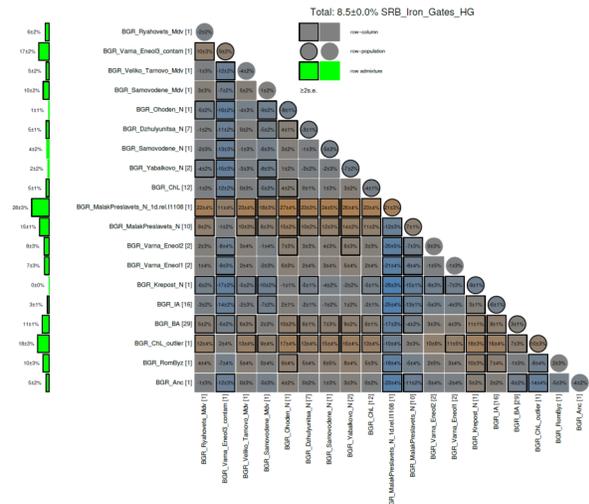
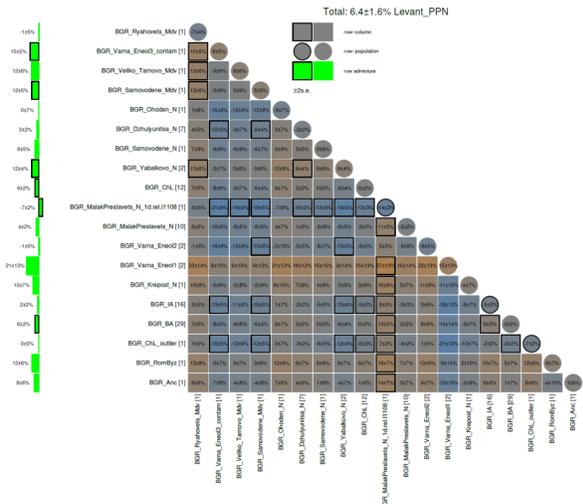
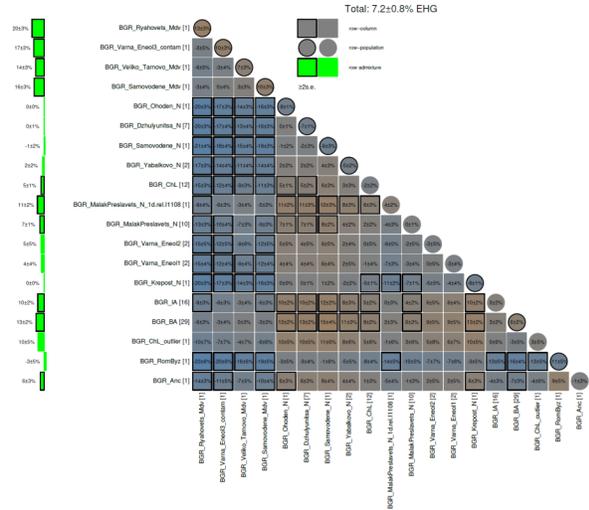
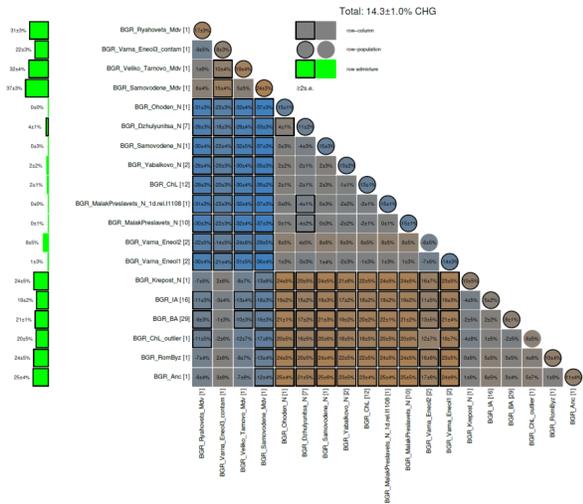


Fig. S 53 Bulgaria

Bulgaria

We have already examined data from all neighboring countries of Bulgaria which is geographically intermediate between the world of the Aegean and the northern Balkans. We will go into finer detail on samples from the Bronze Age and Iron Age which are too numerous to display in the ancestral variation diagram above, but first we examine the broad time-scale picture of variation (Fig. S 53).

The major contrast in this is the presence of early (Neolithic and Chalcolithic) samples of predominantly Anatolian Neolithic ancestry which is then reduced in samples from the Bronze Age and later periods when a portion of Anatolian ancestry is replaced by CHG/EHG ancestry. An outlier within this general pattern is the Neolithic sample from Krepost (5718-5626 calBCE)(3) with $24\pm 5\%$ CHG (but not EHG) ancestry. We have seen above the presence of CHG (but not EHG) ancestry at low levels also in Neolithic Greece, Neolithic/Chalcolithic Albania, and of course in the later Minoans of Crete at a similar $\sim 1/5$ level. This suggests the presence in Neolithic Southeastern Europe of at least two groups: one bearing Anatolian Neolithic ancestry and another one bearing some amount of CHG ancestry. As we will see in our analysis of Turkey, populations of northwestern Turkey (such as TUR_Marmara_Barçın_N used in our paper as a representative of Anatolian Neolithic ancestry) were followed by populations affected by an influx of CHG ancestry by the Chalcolithic. Thus the presence of CHG ancestry in Neolithic Southeastern Europe which we show using the many new samples we have analyzed was not just a phenomenon affecting a single sample is a geographic extension of a process also documented in populations east of the Aegean and Thrace where such ancestry had arrived from the east by the same time. An important topic for future research will be to obtain DNA from additional individuals affected by this process and to understand its archaeological correlated.

We also note that the hunter-gatherer component in the Malak Preslavets Neolithic population(3) includes an EHG component ($11\pm 2\%$) but without CHG ancestry. The joint CHG/EHG ancestry becomes the norm in the Bronze Age as we will see below. For the pre-Bronze Age period we can summarize our results as dominance of Anatolian Neolithic ancestry with some groups (such as Malak Preslavets) affected by admixture with Balkan hunter-gatherer/EHG ancestry and some others (such as Krepost) by CHG ancestry. While the CHG ancestry is most likely reflective of exogenous immigration from Anatolia in this period, the hunter-gatherer admixture in the Malak Preslavets individuals likely reflects ancestry from the local hunter-gatherer population, which remains unsampled in the ancient DNA record in unmixed form. The fact that this hunter-gatherer source has a higher proportion of EHG ancestry than the Iron Gates hunter-gatherers fills in an empty space in the developing map of hunter-gatherer ancestry variation in Europe; further eastward in Ukraine at this time the balance was shifted even more strongly to EHG.(3)

In the Bronze/Iron Age periods the Anatolian component is further reduced and populations of this period have noticeable CHG/EHG ancestry; we will look at these in more detail below.

An individual of Hellenistic times (I19500/BGR_Anc; 300-200 BCE) from Rozovo largely continues the pattern of previous ages. A Roman/Byzantine era sample (I18792/BGR_RomByz; 300-500 CE) from Boyanovo is also similar but with no detectible EHG ancestry. Medieval samples from Samovodene (887-981 calCE) and Ryahovets (800-1400 CE) have the lowest amount of Anatolian Neolithic ancestry (only $\sim 25-30\%$) and the highest amount of CHG/EHG ancestry. This diminution of Anatolian Neolithic ancestry parallels what we have observed in a medieval individual from North Macedonia and so seems to reflect a real pattern in southeastern Europe rather than outlier individuals in either country.

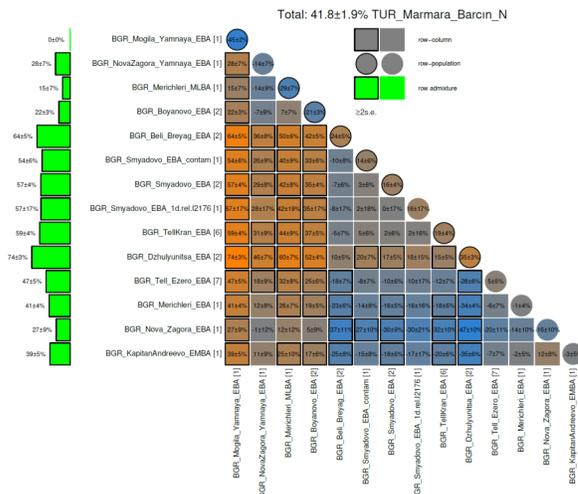
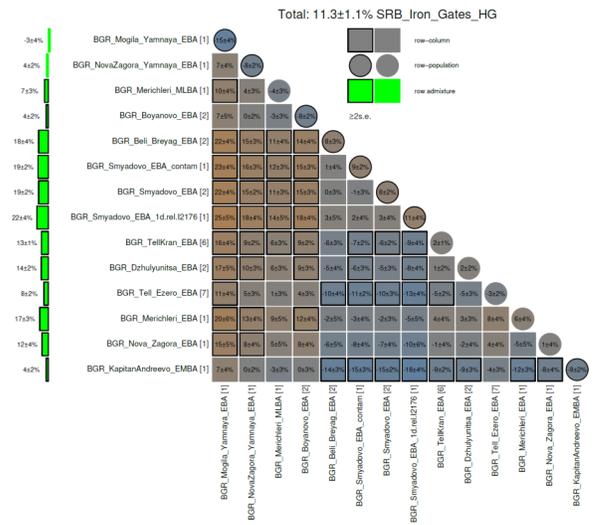
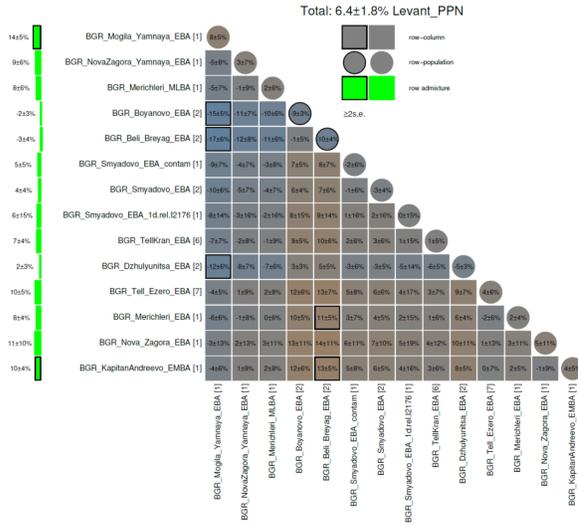
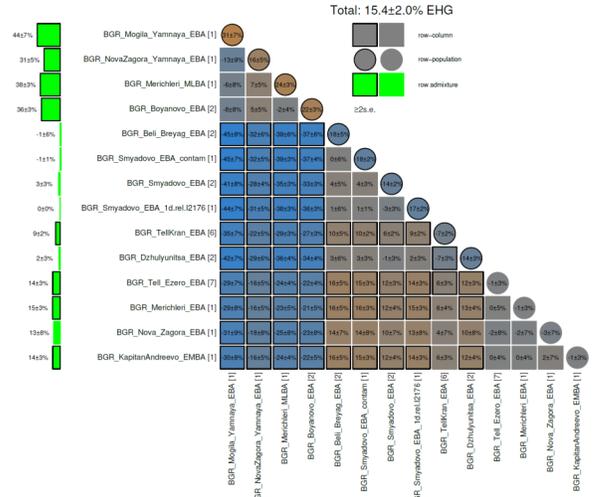
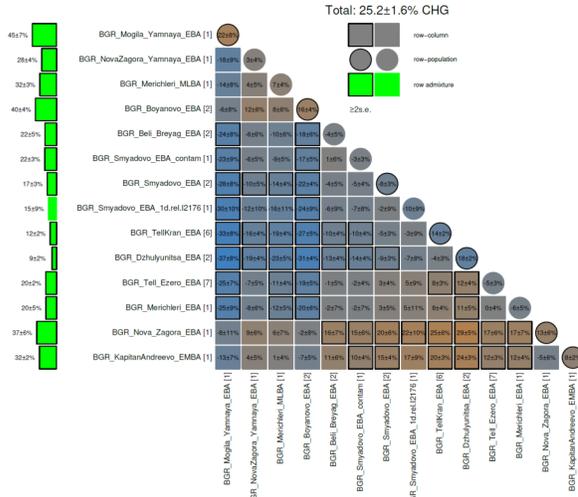


Fig. S 54 Bulgaria (Bronze Age)

We now look at finer detail at samples from the Bronze Age (Fig. S 54). A new Yamnaya individual from Mogila (3000-2500 BCE) has an ancestry profile with the highest CHG/EHG ancestry typical of the steppe and similar to a Yamnaya individual from Nova Zagora (3012-2900 calBCE) and an individual from Merichleri (1750-1625 calBCE).(3) Two individuals from Boyanovo (2500-2000 BCE) also belong to the same “high-steppe” cluster, whose ancestral proportions are reminiscent of the high-steppe individuals from Romania and Moldova and the outlier in Çinamak from Albania.

The existence of these high-steppe individuals thus traces a path Moldova->Romania->Bulgaria of southward steppe intrusion into southeastern Europe; moreover the fact that individuals with high EHG ancestry are found in Bulgaria at the southern end of this expansion suggests that this is not gradual diffusion (in which case it would be diluted over time by admixture with intermediate populations) but was—at least in part—due to migration of individuals of steppe ancestry southward. The presence of these individuals well beyond the geographical limits of the Steppe (as exemplified by the Çinamak EBA sample from Albania), suggests that the high-steppe individuals avoided significant admixture with the local population which would have been expected if the diffusion of steppe ancestry was protracted and gradual.

But the Early Bronze Age in Bulgaria also has examples of a different combination of ancestry in which the majority is Anatolian Neolithic (thus continues with the Neolithic/Chalcolithic) and there is substantial Balkan hunter-gatherer but no significant EHG ancestry. Dzhulyunitsa, Beli Brayag, and Smyadovo are dominated by this second type of mixtures of ancestries.

The high-steppe and high-Neolithic/hunter-gatherer groups we have just described did combine in the territory of Bulgaria, as evidenced by the presence there also of populations of intermediate genetic makeup, notably an Early Bronze Age individual from Merichleri, one from Nova Zagora, several individuals from Tell Ezero, and one each from Veliko Tarnovo and Kapitan Andreevo. All of the above have ~13-15% EHG ancestry or about ~1/3 ancestry from populations like that of the Mogila Yamnaya sample and all of them have some Balkan hunter-gatherer ancestry with intermediate Anatolian Neolithic ancestry between the two contrasting groups.

Thus, we see in the territory of Bulgaria the fusion of two populations: one derived from the steppe and consisting of individuals of very high EHG ancestry, one derived from the local Chalcolithic population with high Anatolian and substantial hunter-gatherer ancestry, and a set of intermediate populations in which the EHG component of the steppe group is reduced and so is the Anatolian component of the Chalcolithic substrate.

Further evidence for the non-gradual nature of the steppe admixture is furnished by analysis of admixture dating of Southeastern European population using DATES(34) (Fig. S8) which leads to an estimate by regression of the admixture time at ~4,850 years ago with a crisp regression line which predicts the generation length of 28 years previously established(54). This adds to our confidence that however the steppe ancestry came into Southeastern Europe, broadly speaking it is consistent with an early arrival coinciding with the westward spread of the Yamnaya culture.

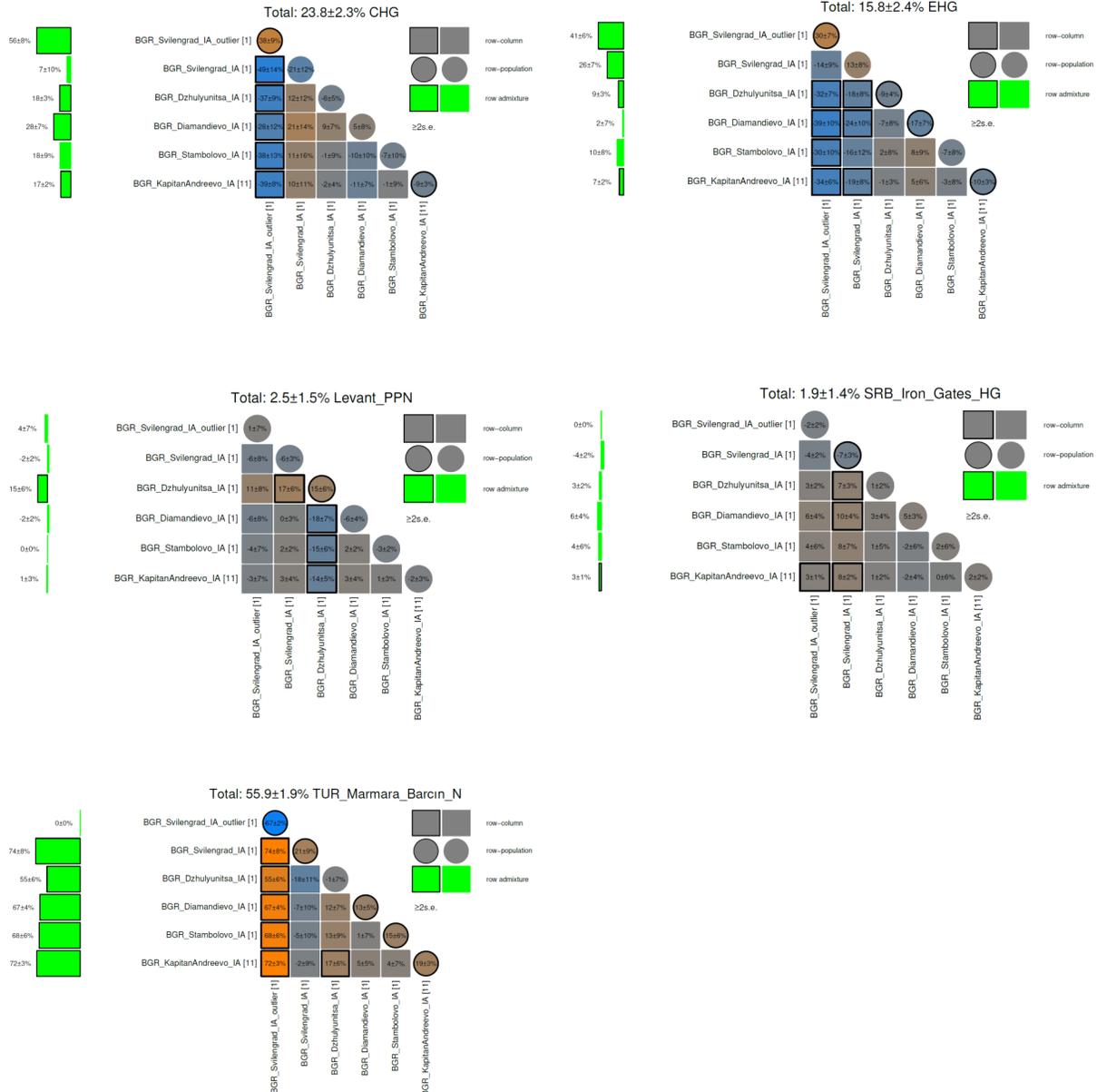


Fig. S 55 Bulgaria (Iron Age)

We next turn to the Iron Age (Fig. S 55). In the Iron Age most sampled populations have $> \sim 2/3$ of their ancestry from the Anatolian Neolithic. A notable exception is an outlier from Svilengrad (I19488/BGR_Svilengrad_IA_outlier) which based on our ADMIXTURE analysis has $\sim 1/7$ East Eurasian ancestry and could represent a steppe nomad (“Scythian”-related) of the Iron Age when such ancestry existed on the steppe.(430, 431)

Neither EHG nor Balkan hunter-gatherer ancestry is high in the Iron Age, although both are present at low levels that are nominally intermediate between samples of the Aegean and further north. A mixture of Anatolian Neolithic and CHG ancestry as in the Aegean are the main forms of ancestry present in our samples from this period.

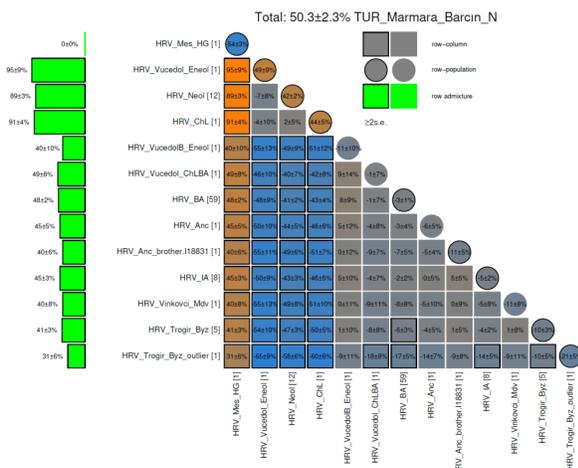
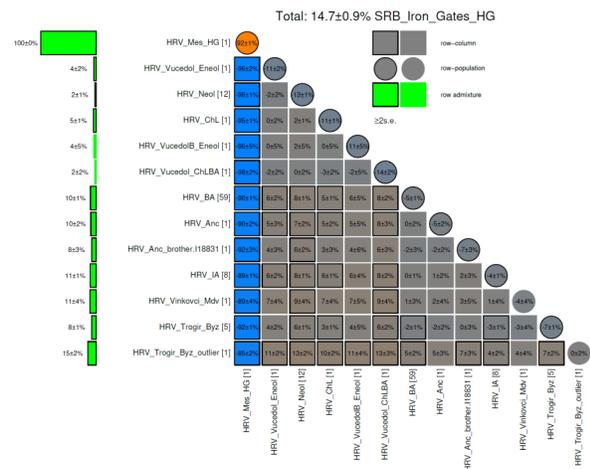
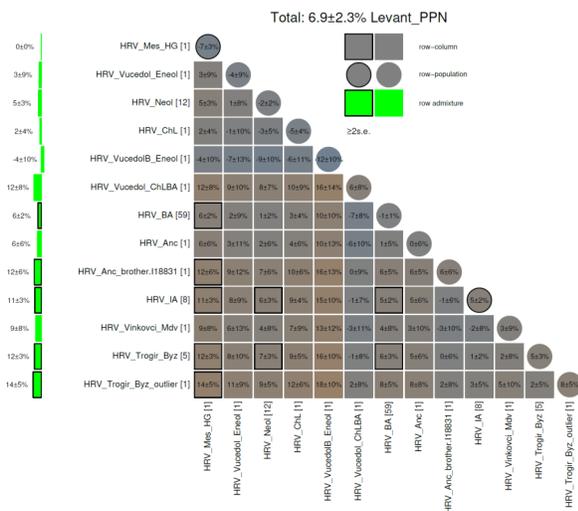
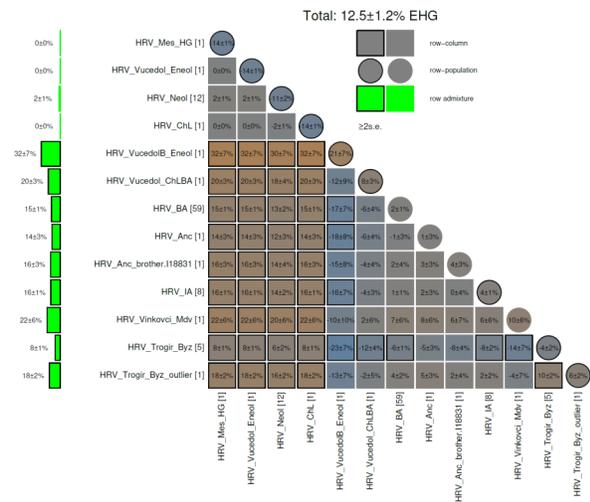
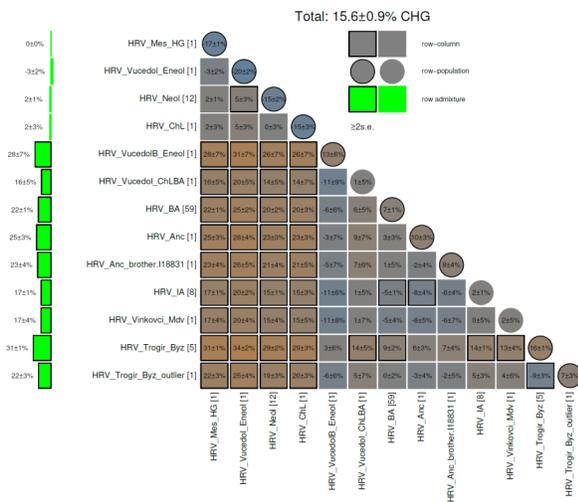


Fig. S 56 Croatia

Croatia

Croatia (Fig. S 56) is at the northwestern edge of the Southern Arc and presents a complete time series from the Mesolithic to the Medieval period. A Mesolithic sample(3) is modeled as a clade with the Iron Gates hunter-gatherer population as a source. The aggregate group HRV_Neol includes samples from (3) and this study (Gornja Vrba and Vinkovci) and has mostly Anatolian Neolithic ancestry similar to groups from southeastern Europe; no major hunter-gatherer ancestry detected. A Chalcolithic sample from Dakovo (5000-3000 BCE) has very similar ancestry. Three published samples from Vucedol(3) differ from each other with one (I2792) being similar to Neolithic groups, one (I4175) having steppe ancestry, and one similar to the other Bronze Age samples.

We will consider the Bronze Age samples in greater detail below, but we note for the time being that they have substantial CHG/EHG ancestry similar to Bronze Age samples elsewhere in southeastern Europe. They contrast to the Neolithic/Chalcolithic population with an overall reduction of Anatolian Neolithic ancestry to $\sim 1/2$, with the same pattern continuing into the Iron Age. The samples from the coastal town of Trogir have high CHG/low EHG, and thus exhibit the opposite pattern of what we saw in Bulgaria and North Macedonia (where EHG increases). However, the pattern should not be generalized to the region as a whole as Trogir (founded as Tragyrium/Τραγύριον by Greek colonists and known as Tragurium in Latin) and the sampled individuals date from the medieval period when the coastal cities of Dalmatia were governed by the Byzantine Empire; thus Trogir may have had its own distinctive population not representative of inland populations.

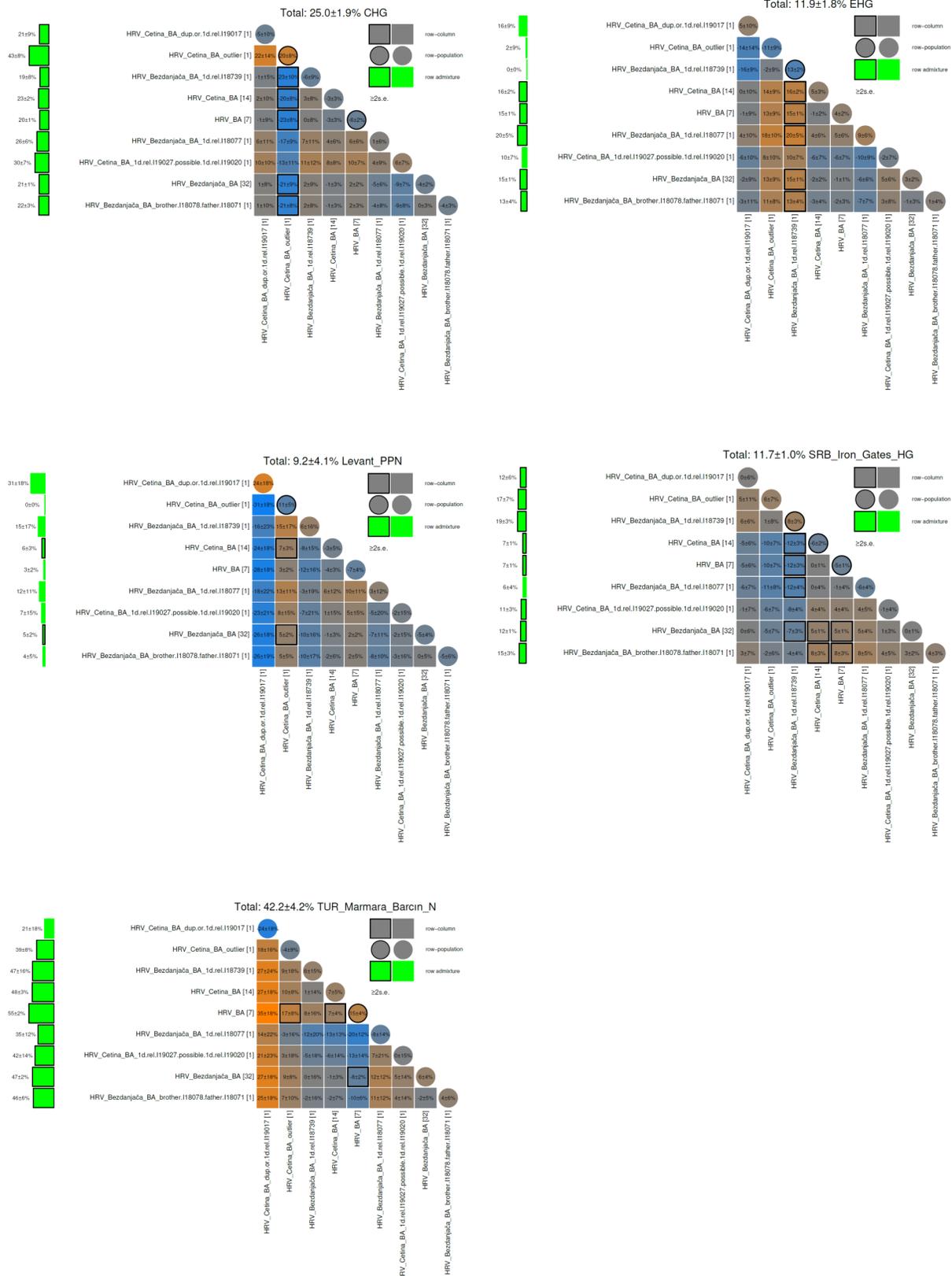


Fig. S 57 Croatia (Bronze Age)

The Bronze Age samples (Fig. S 57) are grouped into three labels:

- (a) HRV_BA which includes two samples from Veliki Vanik(3) and five new samples one from Koprino, Matkovici, Zavojane-Ravca, Bogomolje, and D. Ostrvica-Pasičine
- (b) 19 new samples from Cetina valley from the Middle Bronze Age
- (c) 35 new samples from Bezdanjača Cave from the Middle-to-Late Bronze Age

The three groups are extremely similar in their ancestral makeup which we have discussed above. Of note is an outlier individual from Cetina (I19031/HRV_Cetina_BA_outlier; 1877-1643 BCE) inferred to have substantial CHG but no EHG ancestry. This individual could be related to other such individuals from southeastern Europe we have discussed before, a descendant of the Anatolian Neolithic/CHG mixed population evidenced in Greece and Thrace. We note however that the I19031 individual is of low data quality making its interpretation more tenuous.

Overall, Bronze Age samples from throughout southeastern Europe average ~15% EHG ancestry with ~3× more such ancestry in Moldova, the high-steppe group from Romania and individuals already discussed from Albania, Serbia, Bulgaria, and northern Greece, and ~3× less such ancestry in Mycenaean central/southern Greece.

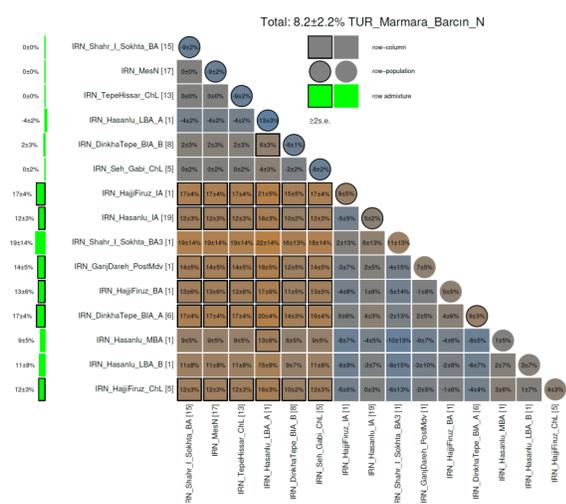
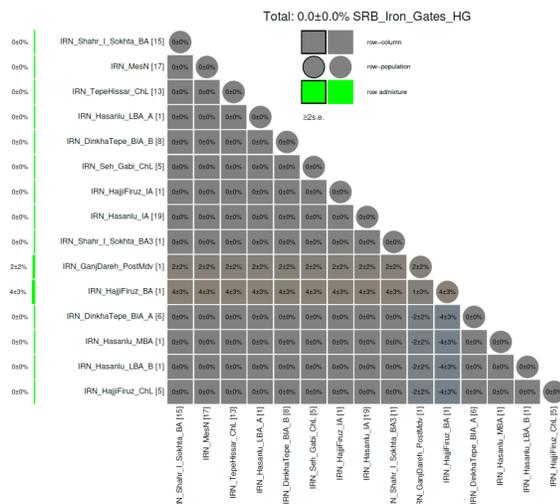
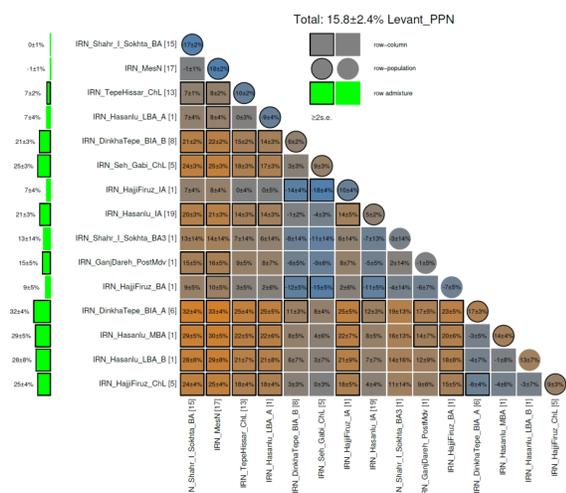
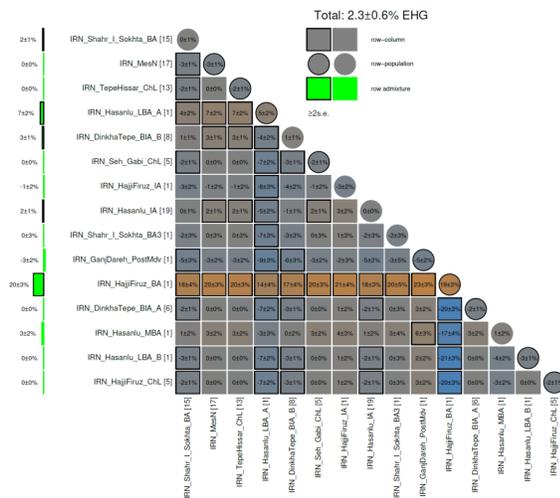
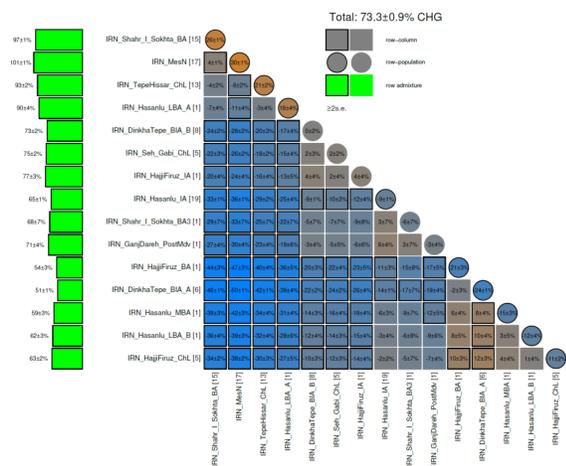


Fig. S 58 Iran

Iran

Samples from Iran (Fig. S 58) are predominantly composed of CHG-related ancestry. It has previously been observed that the Neolithic/Mesolithic populations of Iran were related to the Caucasus hunter-gatherers,(10) so it is not surprising that when CHG are available as a source, the Iran_MesN group which includes data from different sources(2, 10, 34) is composed entirely of CHG-related ancestry.

Bronze Age samples from Shahr-I Sokhta(34) from eastern Iran at the edge of the region we are considering also derive almost all their ancestry from a CHG-related source. These individuals were modeled as having South Asian ancestry, which is not represented in the 5-source model used to model samples from the Southern Arc in our paper.(34) Samples from Tepe Hissar in northeastern Iran ((34) and this study) also have predominantly CHG ancestry but with $7\pm 2\%$ Levantine Neolithic ancestry; the latter could be derived from the CHG/Levant cline of which the Mesopotamian Neolithic was a part.

The Chalcolithic population from Seh Gabi(10) from western Iran has even more Levantine influence of $\sim 1/4$ and a similar population is also one cluster of 8 individuals from Dinkha Tepe in NW Iran (Iranian Azerbaijan) (IRN_DinkhaTepe_BIA_B; new data from this study) spanning the 2nd millennium BCE. All these populations are geographically adjacent to Mesopotamia and the presence of Levantine ancestry there from the Chalcolithic to ~ 1000 BCE suggests contact between the two areas.

The third component that appears in samples from Iran is Anatolian Neolithic ancestry whose spread eastward we will examine below in our study of samples from Armenia and Turkey. This appears in an undated Bronze Age sample from Shahr-I Sokhta (2900-2700 BCE Iran_ShahrISokhta_BA3(34)) and is present at $\sim 13\%$ in Hajji Firuz ((34) and new data) at ~ 6000 BCE in NW Iran (Iranian Azerbaijan) quite close to the aforementioned Dinkha Tepe in which a second cluster (IRN_DinkhaTepe_BIA_A) also possessed it. The differentiation between clusters “A” and “B” at Dinkha Tepe is thus due to the presence of Anatolian ancestry in individuals of “A” but not “B”.

We present new data from Hasanlu in the same region of Iran. Nineteen of the samples are from the Iron Age ~ 1000 BCE, two from the Late Bronze Age (~ 1300 BCE) and one from the Middle Bronze Age (~ 2100 BCE). The two Late Bronze Age samples differ from each other in the amount of Levantine ancestry by $21\pm 8\%$ suggesting some heterogeneity in the population prior to the Iron Age. The Middle Bronze Age sample resembles one of the two LBA ones (with higher $\sim 29\%$ Levantine ancestry). The main group of Iron Age individuals also resembles mostly the high-Levantine ancestry group (with $\sim 21\%$ ancestry).

The low-Levantine ancestry individual at Hasanlu also differs in having $7\pm 2\%$ EHG ancestry, a component that is rare in samples from Iran. At the main cluster of Hasanlu, this component is only $2\pm 1\%$. Only a Bronze Age individual from Hajji Firuz (I4243 / IRN_HajjiFiruz_BA at 2465-2286 calBCE) has $20\pm 3\%$ of such ancestry. The influx of EHG ancestry that affected the South Caucasus (as we will see in our discussion of Armenia), also seems to have had a more minor effect on some individuals at Iran’s Northwestern edge, although by ~ 1000 BCE the great majority of individuals remained minimally affected or not affected at all.

There are some reasons to think that the spread of the steppe ancestry into NW Iran is not associated with the historical Iranian languages: first, its very minor impact; second, its association with the movement of steppe ancestry into the South Caucasus that could plausibly be associated with Proto-Armenian speakers and would thus predict an (Iranian, Armenian)

linguistic relationship rather than the universally accepted relationship of Iranian languages with the Indo-Aryan (or Indic) languages of South Asia. Third, South Asian populations have virtually none of the Yamnaya-derived Y-chromosome lineages, and conversely the samples from Iran included in our study do not have the R-Z93 lineage tracking the spread of steppe ancestry into Central/South Asia.⁽³⁴⁾ Finally, our samples are from the periphery of the Iranian world (NW Iran) and may also predate the establishment of the Median and Achaemenid kingdoms of Iran during the 1st millennium BCE.

We show the individual levels of EHG ancestry at Hasanlu in Fig. S 59.

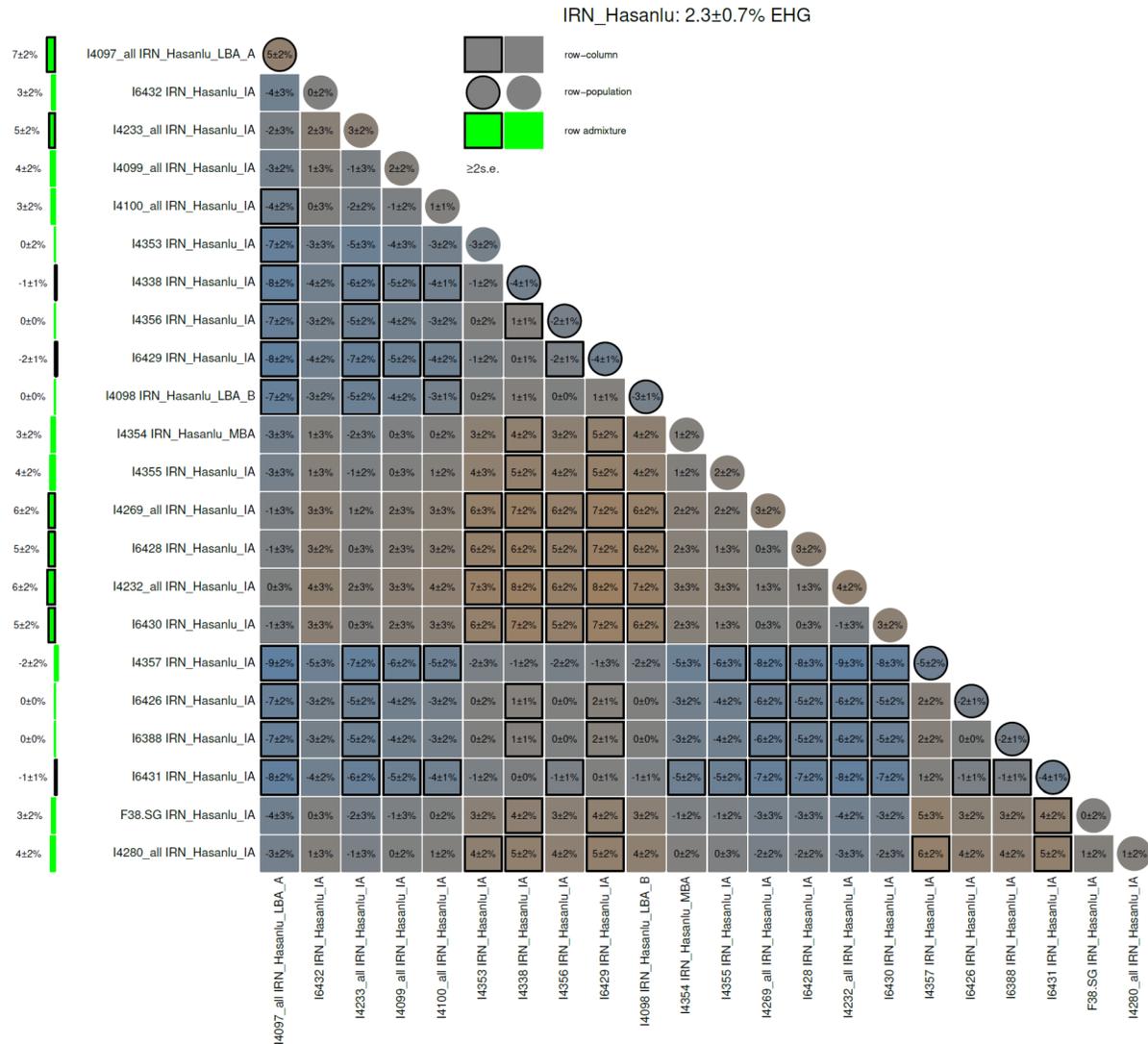


Fig. S 59 Hasanlu (EHG ancestry)

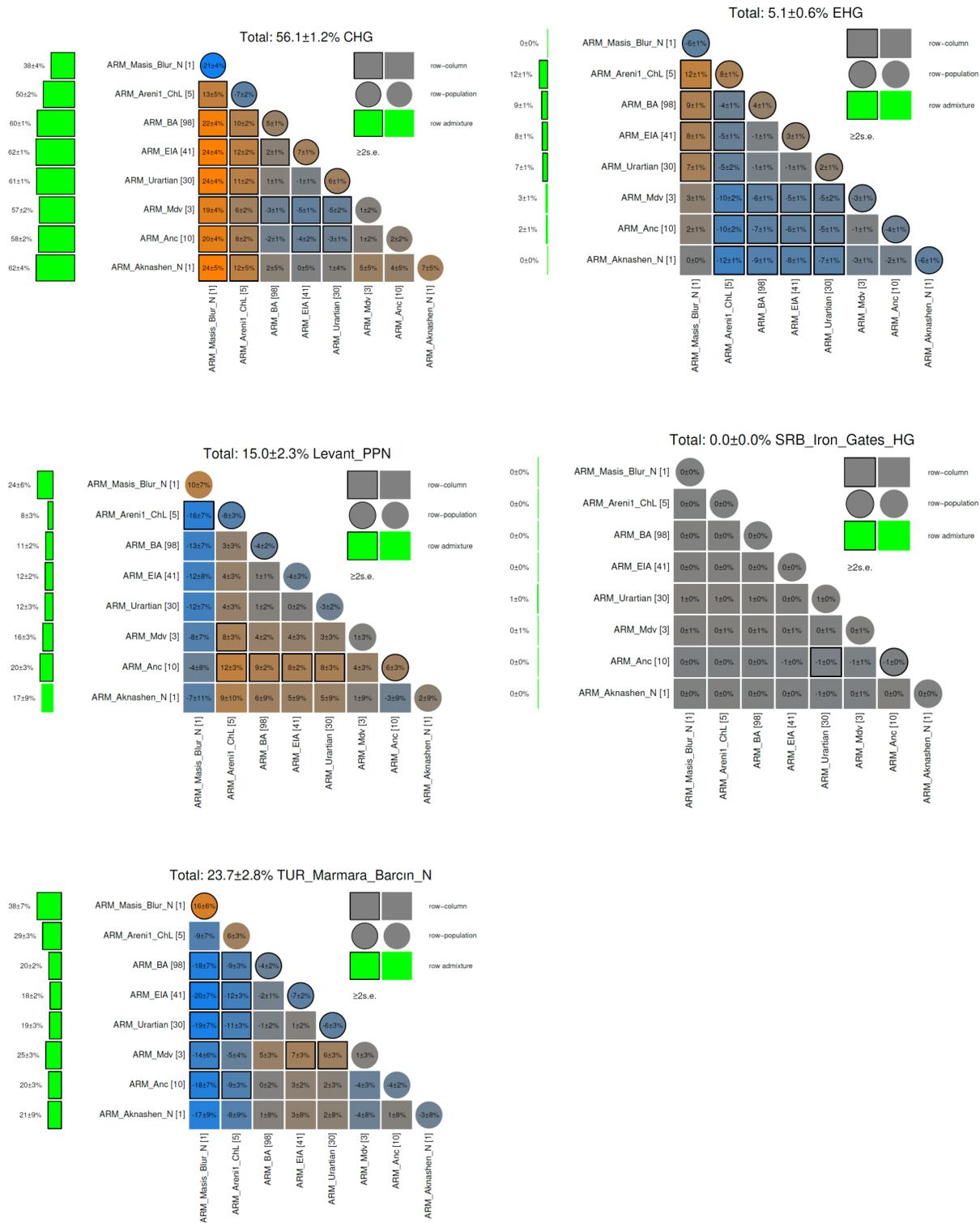


Fig. S 60 Armenia

Armenia

The collection of samples of this study represents a major update to our existing knowledge(4, 10, 17, 431) of the population history of Armenia (Fig. S 60), increasing the total sample size in the time transect from 21 to 195, and filling in many temporal gaps. Two Neolithic samples from Masis Blur and Aknashen are made up of the three West Asian components of ancestry in our model but with contrasting patterns from very low (~38%) to very high (~62%) CHG ancestry which frame the averages for all later periods, with the overall average of ~56% across different periods being on the high end of this range. Corresponding to its minimum of CHG-related ancestry, the Masis Blur individual has a maximum of Anatolian-related ancestry (~38%), a component which exists in all populations. Considering the presence of all three components in Neolithic/Chalcolithic samples from Azerbaijan discussed previously, we can say that in the South Caucasus the population includes Anatolian-related ancestry in contrast to Mesopotamia in the south and parts of Iran to the east where a simpler Levantine/CHG mix is observed, a conclusion also borne out by the analysis of the Neolithic continuum (11). The two localities of the Neolithic samples are within ~20km of each other making geographical structure as the determinant of their contrasting genetic composition unlikely. Temporally, the Masis Blur sample (5634-5544 calBCE) is later than the one from Aknashen (5983-5844 calBCE), which might suggest that the more CHG-related population was earlier in the region, a conclusion that should be considered provisional given that it is drawn from only two individuals.

It is difficult to assess the degree of continuity across the Neolithic transition in the region; areas of early Neolithic development in Anatolia and Mesopotamia were composed of Anatolian/CHG/Levantine ancestry which are precisely the components of ancestry also present in the South Caucasus. The pre-Neolithic population is unsampled but it can be reasonably hypothesized that it possessed at least some CHG-related ancestry. While it is plausible that the Anatolian/Levantine components were introduced together with Neolithization, it is also possible that the population was already present in pre-Neolithic times.

Balkan hunter-gatherer ancestry is absent here and EHG ancestry is absent in the Neolithic samples, appears first at the Areni1 samples(10) at ~12% in the 4300-4000 BCE time frame, and persists in later periods. The amount of EHG ancestry at Areni1 is comparable to the ~15% across a vast swath of Southeastern Europe previously discussed. Note, however, while in the latter case the EHG ancestry is sporadic prior to 3000 BCE, in Armenia it is present at least 1,000 years earlier.

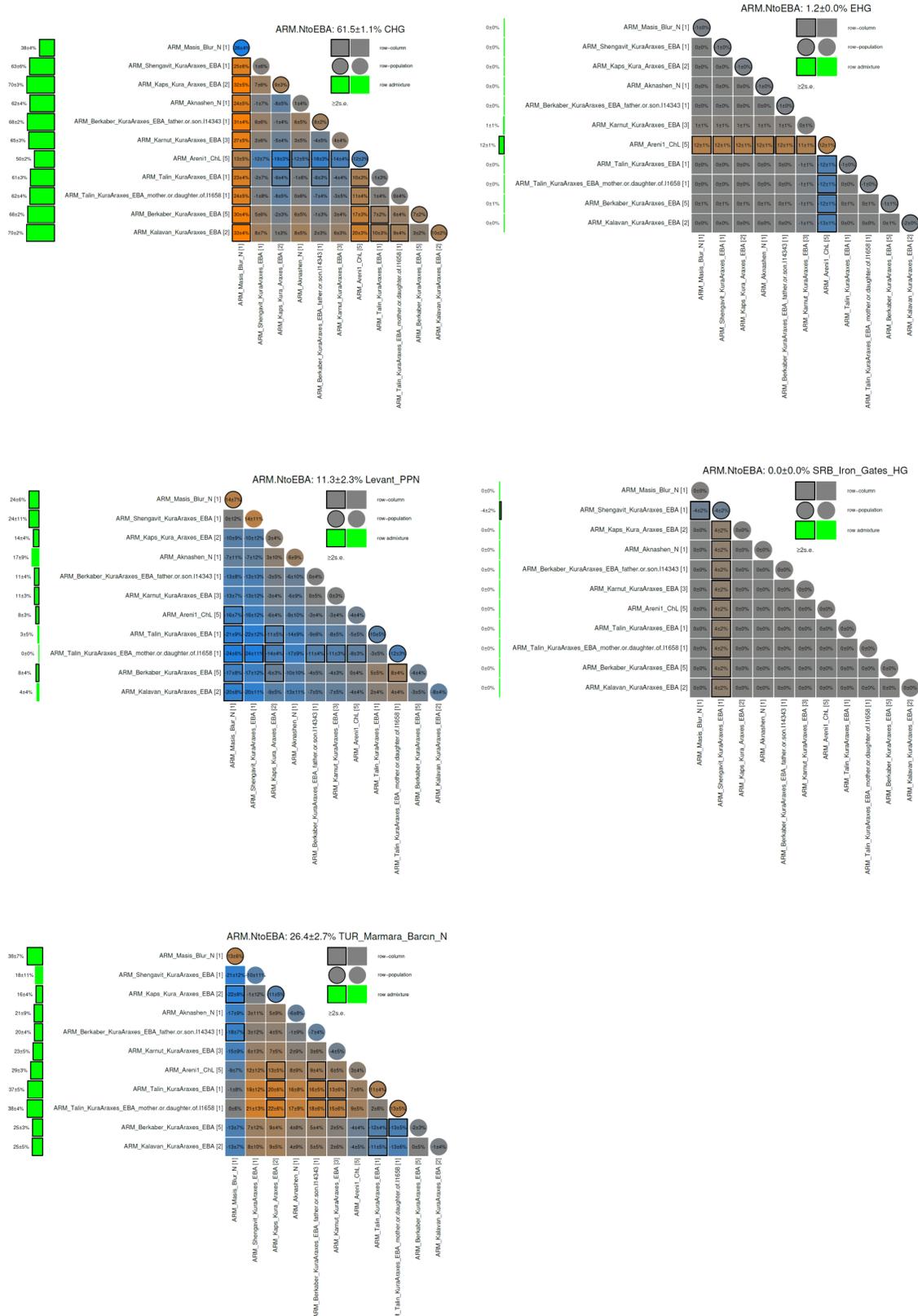


Fig. S 61 Armenia (Neolithic-to-Early Bronze Age Kura-Araxes period)

In the Early Bronze Age Kura-Araxes culture period (Fig. S 61), we observe that CHG ancestry is generally high (Berkaber, Kalavan, Talin, Karnut, Kaps), closer to the high Aknashen end of the Neolithic distribution than to the low Masis Blur end.

Levantine ancestry occurs at low levels in most groups of this period but lower than the Masis Blur maximum; this is plausibly connected to Mesopotamian influence with the spread of the Neolithic economy into the South Caucasus, and there is no evidence for extra Levantine ancestry associated with the Early Bronze Age samples.

In contrast to the two previous ancestral components which had a general and variable distribution, the EHG ancestry is absent in both Neolithic individuals and in all of the Early Bronze Age groups. Thus, steppe ancestry arrived in the South Caucasus in pre-Yamnaya times, as the Arenil samples have been dated to the last quarter of the 5th millennium BCE, and the Early Bronze Age is not associated here with either an increase or pervasiveness of this component in the region as it is in mainland Europe on the west. If anything, the EBA population seems to have none of this component.

The Balkan hunter-gatherer is completely absent in all populations, paralleling the situation in Europe where the CHG ancestry is absent (except in the south). Balkan hunter-gatherer ancestry and CHG ancestry formed a substratum in some of southeastern Europe and the South Caucasus respectively; there is evidence of CHG-related ancestry in southeastern Europe even in Neolithic times but not the reverse.

Anatolian Neolithic ancestry is the second most important component in the populations down to the Early Bronze Age and it occurs at contrasting levels in the two Neolithic individuals, with the high CHG one (Aknashen) having low Anatolian ancestry and the low CHG one (Masis Blur) having higher Anatolian ancestry.

Finally, we note that the Early Bronze Age population of Talin also had higher-than-average Anatolian-related ancestry, but not above the level already observed in the Neolithic at Masis Blur. Thus, the Early Bronze Age in the region does not appear to be necessarily associated with major migration from outside as the EBA population possesses the same composition of ancestry and is within the pre-existing variation, although we cannot be certain whether the Masis Blur Neolithic individual represented a wider local population from which the EBA individuals could be derived or a more transient phenomenon (A further important caveat is that migration from genetically very similar populations is not easily detectable by changes in ancestry composition: the only claim one can make is that *if* there was external migration it was from a genetically similar population that did not alter the population drastically in its aftermath).

Summarizing the picture of the Early Bronze Age we note that there is some heterogeneity in ancestral proportions but within the ranges of the Neolithic/Chalcolithic variation and the virtual disappearance of the steppe-related EHG component whose temporary appearance during the Chalcolithic at Arenil cave did not seem to continue into the Early Bronze Age.

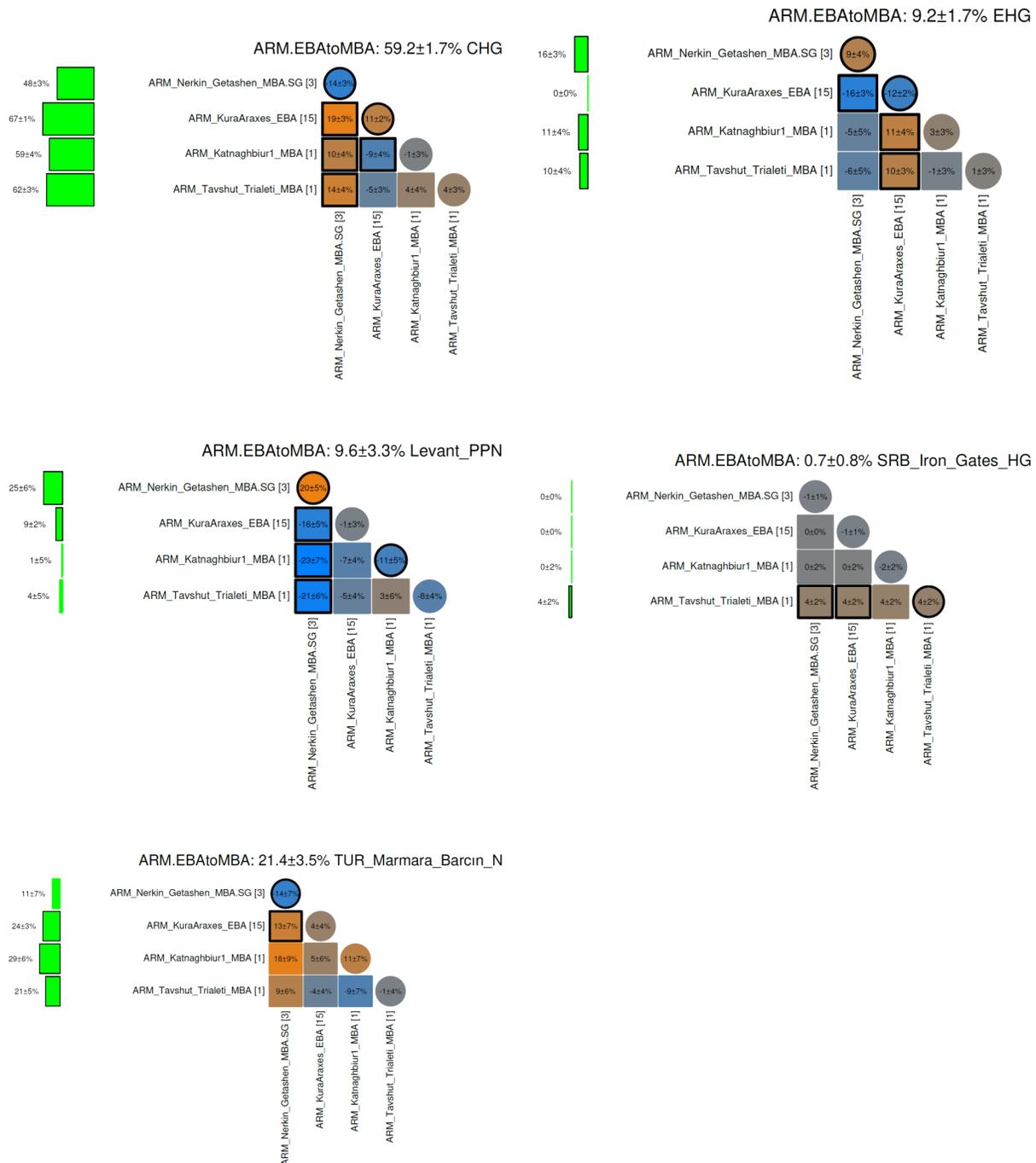


Fig. S 62 Armenia (Early-to-Middle Bronze Age)

None of the Middle Bronze Age samples (Fig. S 62) exceed the amount of CHG ancestry found in the EBA samples. This would have been expected if Armenia had been influenced from other surrounding high-CHG ancestry regions. Published individuals from Nerkin Getashen(4) and Katnaghbiur(10) and a new individual from Tavshut belonging to the Trialeti-Vandazor culture all have significantly more EHG ancestry than the EBA individuals of the Kura-Araxes culture. Thus the disappearance of the EHG ancestry during the EBA after its first appearance in the Chalcolithic is followed by its MBA re-appearance sometime in the 3rd millennium BCE.

How early did this re-appearance occur? Future studies from the early and middle of the 3rd millennium BCE, a period during which steppe migrations were already underway in the rest of Eurasia may help determine whether Armenia had connections to the steppe as early as this period (as suggested by the Early Bronze Age Kura-Araxes individuals analyzed here), or if there were already steppe migrants in Armenia, as suggested by an intriguing discovery of a recently excavated large mound in the Syunik highlands at Gorayak (442).

Our study includes 70 new individuals from the Late Bronze Age in Armenia (Fig. S 63) for a total of 77 individuals from these periods from 15 different sites. A picture of uniformity emerges across the LBA landscape of Armenia; comparisons are tenuous with the previous MBA period which is represented by fewer individuals, but suggestive of a reduction of EHG and increase of CHG ancestry. Regardless of the changes that may have occurred from the MBA to the LBA, the populations of the LBA are characterized by very similar ancestry composition (you may observe the lack of significant differences between any of the populations and the overall average or between pairs of populations). The EHG ancestry that appeared in the MBA continues in the LBA at a ~9% level and with the exception of 1-2 populations (Dzori Gekh and Tekhut) where it is lower than average, is estimated to be in a narrow range of 8-14% around the mean. (The Dzori Gekh individual has a Y-chromosome of Levantine origin and may very well have been a migrant to the region; Supplementary Text S5).

Balkan hunter-gatherer ancestry remains unobserved in Armenia throughout the Bronze Age and Anatolian ancestry shows no increase in the LBA samples compared to the EBA ones. Any western influence, from either western parts of Anatolia or southeastern Europe would have led to an increase of one or both of these components, and thus we can conclude that during the Bronze Age such influence was negligible.

The genetic homogeneity of samples from Armenia from the LBA parallels the homogeneous cultural environment of the Lchashen-Metsamor (LM) culture that appears in the 16th century BCE (Supplementary Text S1) and straddles the MBA and LBA and continues into the Iron Age. Fusion of steppe-derived elements already present in the Trialeti culture and other MBA samples prior to the appearance of this culture is more or less complete and has created a genetically homogeneous set of populations in the LBA in which the EHG ancestry has broadly diffused in society. While not directly measurable, cultural and genetic homogeneity during the LBA and across the LM culture is suggestive that the studied populations may have been linguistically homogeneous as well and may have spoken an early version of the Armenian language, a fusion of EHG-bearing Indo-European speaking migrants of the Middle Bronze Age, of ultimate steppe origin, with local populations south of the Caucasus.

This reconstruction parallels our inference (Fig. S 5) of major mid-3rd millennium BCE steppe admixture in the ancestry of populations of Armenia. Additional sampling from the Middle Bronze Age, and in particular from both the Trialeti culture and the Early Kurgan culture (first stage of the MBA) will disclose whether this admixture took place in situ from steppe migrants that penetrated deep south of the Caucasus and away from the steppe (as in the Balkans); alternatively, the admixture may have taken place north of Armenia, in the North Caucasus bridge joining the Eurasian steppe with the basin of the Kura and Araxes rivers in the south.

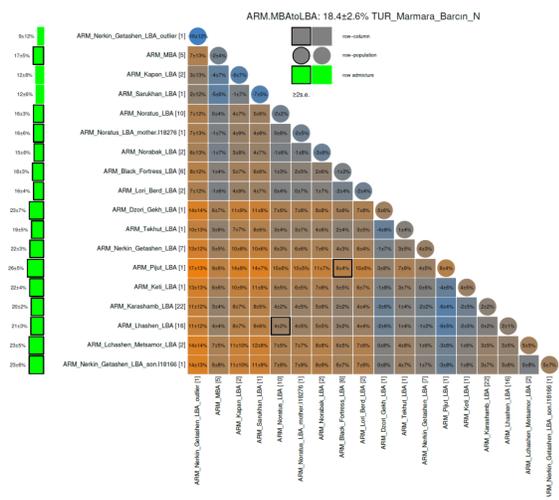
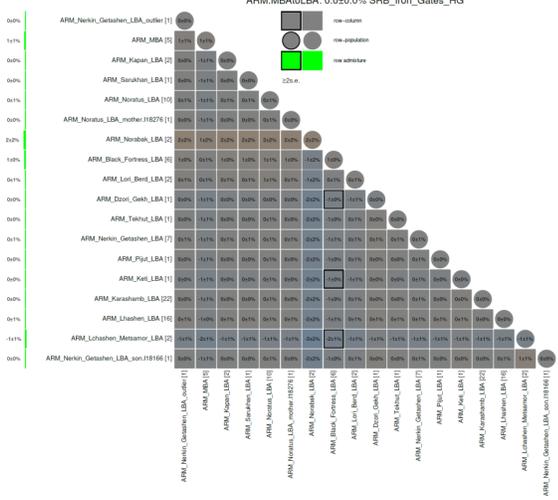
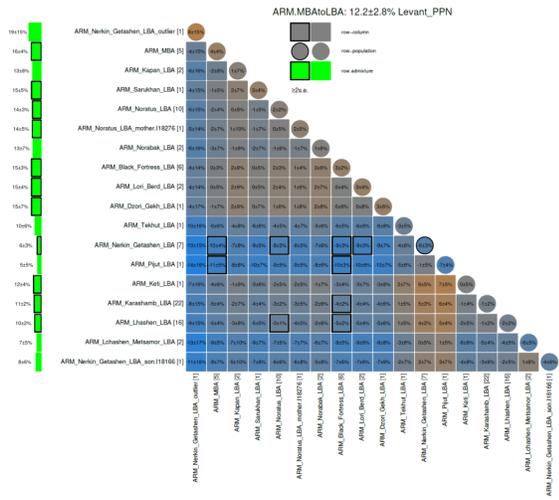
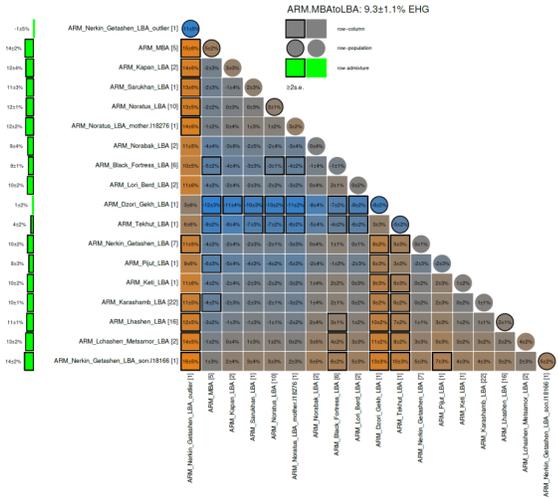
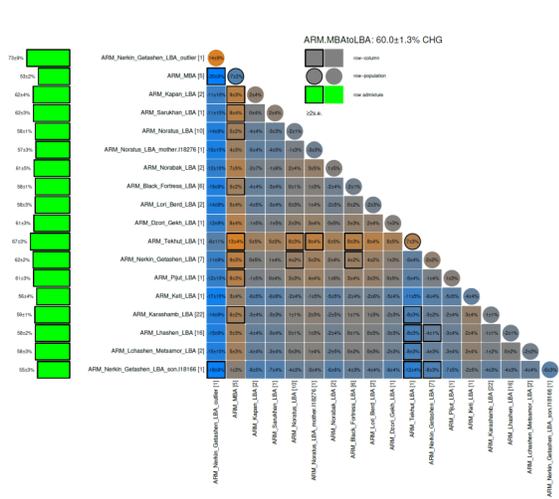


Fig. S 63 Armenia (Middle-to-Late Bronze Age)

Our study includes 41 new individuals from the Early Iron Age in Armenia (Fig. S 64), a few centuries later than the Late Bronze Age just discussed from 9 different sites from which LBA individuals were also sampled; the pattern of ancestry in the EIA is similar to that of the LBA, suggesting that there is no major change of ancestry across the LBA->EIA boundary, indeed the two periods could be combined from the point of view of ancestry. The overall EHG ancestry (Fig. S 60) in the EIA period is ~8%, similar to the ~10% of the LBA, and this is spread across nearly all the sites (except Bragdzor) as in the LBA period and fairly homogeneous across the different sites.

Our estimates of EHG ancestry in the 26 individuals at Karashamb where we have the largest sample size (from both the LBA and EIA) are normally distributed (Shapiro-Wilk test $p=0.36$) with an average across individual estimates of 12.4% and standard deviation of 6.5% and range of [2.9%, 28.4%]. Thus, we detect no presence of population structure at this site, i.e., the presence of high- or low-steppe ancestry subgroups. Thus, not only is EHG ancestry pervasive and homogeneous across different sites but also within the largest size in which any deviations from normality would be most detectible.

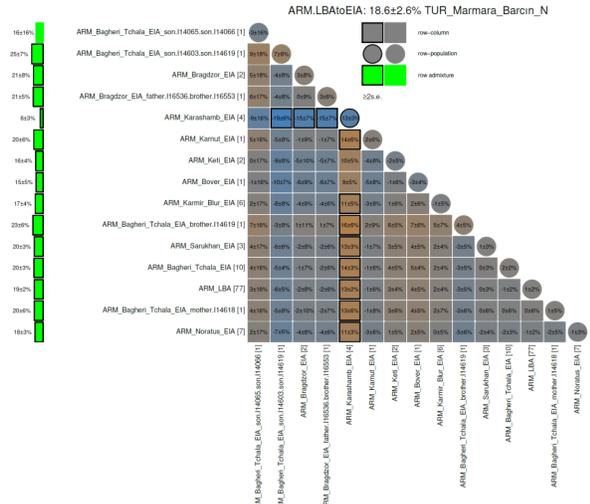
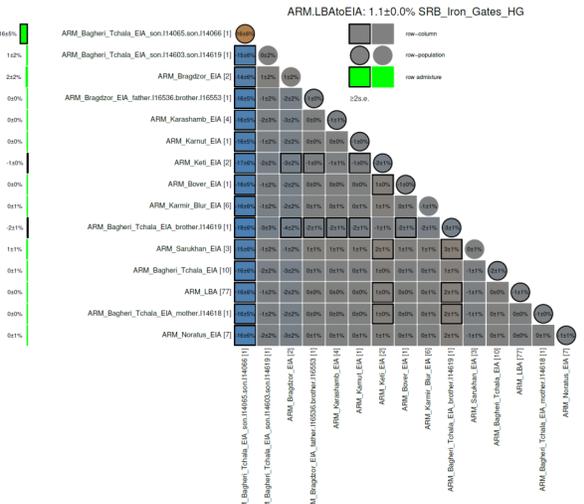
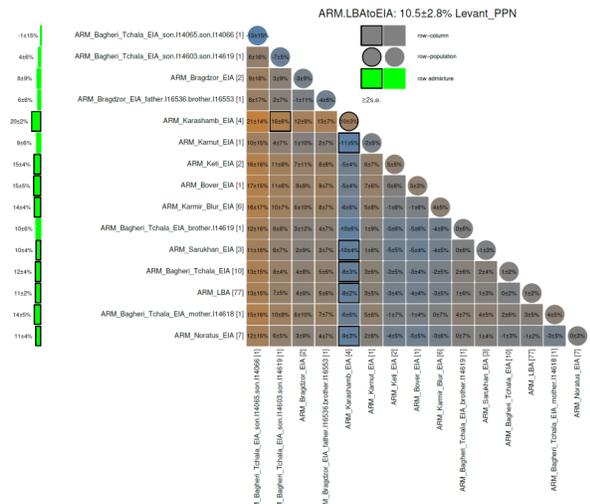
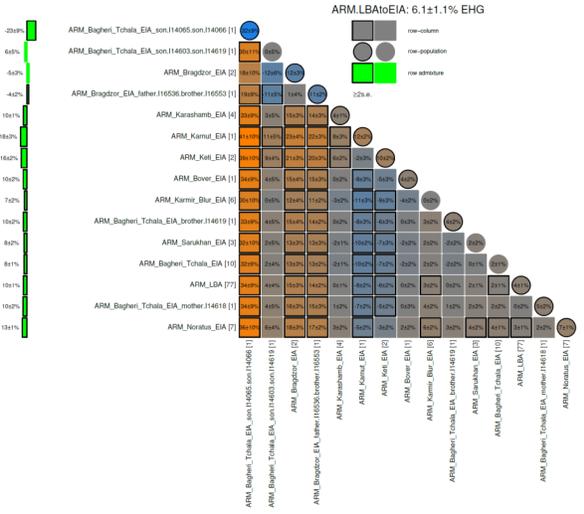
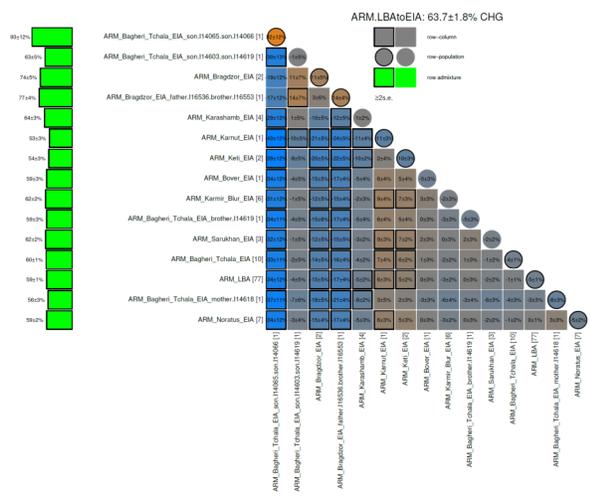


Fig. S 64 Armenia (Late Bronze Age-to-Early Iron Age)

The Early Iron Age is followed by the Urartian period in the 9th-6th c. BCE at the first half of the first millennium BCE (Fig. S 65). During this time, much of Armenia was part of the Kingdom of Urartu whose center was in the Lake Van area of modern Turkey and whose northern extension encompassed modern Armenia. Examining individuals from this period we observe that they have ~7% EHG ancestry, similar to the ~8% of the previous EIA period, suggesting continuity of population, although a couple of outlier individuals seem to lack this component.

In the LBA, EIA, and Urartian period EHG ancestry is general, but the presence of outlier individuals all suggest either survival of non-EHG admixed populations in Armenia, or, alternatively contact between Armenia and neighboring regions in which EHG ancestry had not penetrated. As we will see further down in our discussion of Urartian individuals from Turkey, this was the case in the center of the Van Kingdom of Urartu.

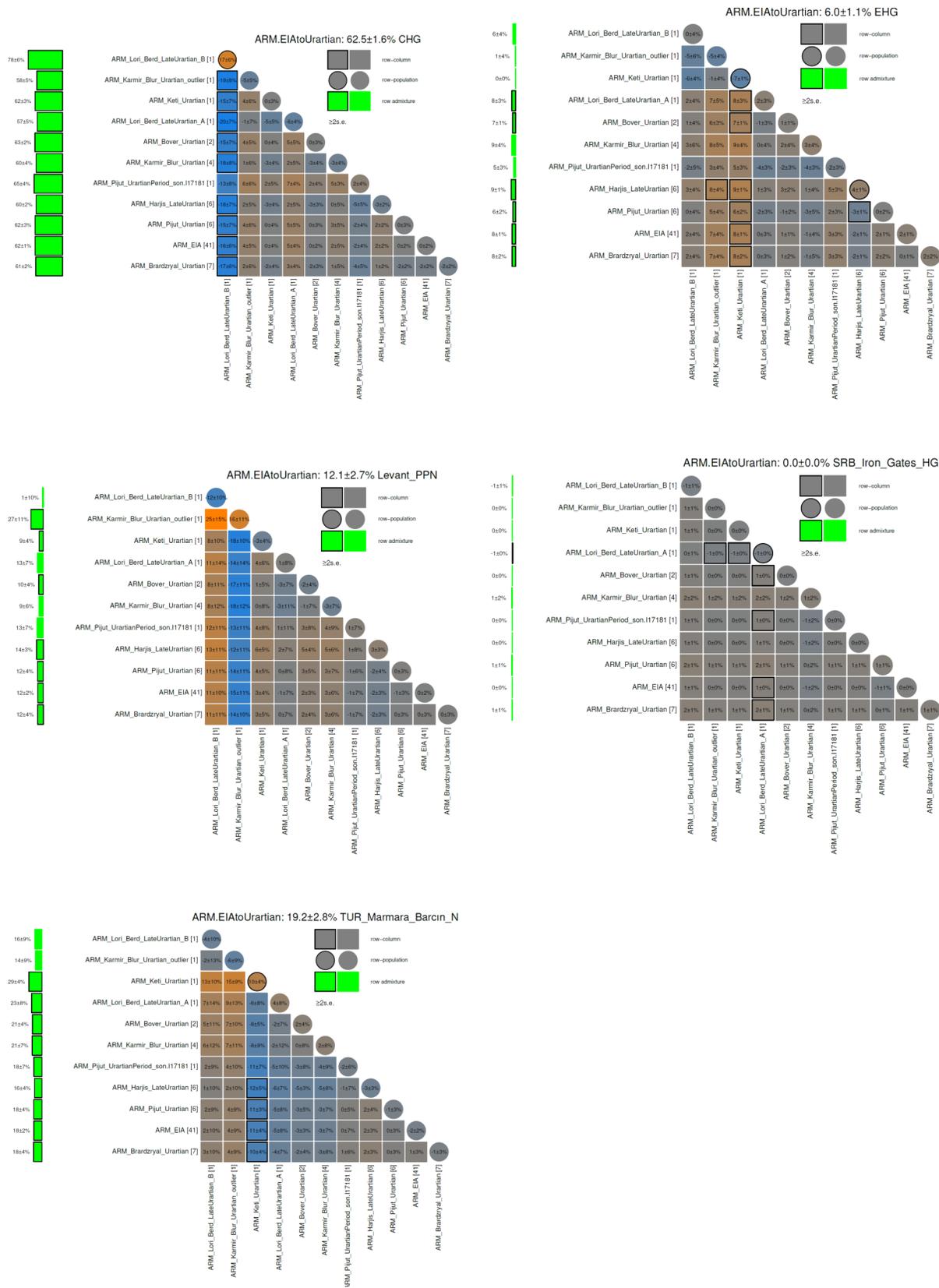


Fig. S 65 Armenia (Early Iron Age-to-Urartian period)

Our time transect of Armenia is concluded by post-Urartian samples from the 2nd half of the 1st millennium BCE and up to the high medieval period at Agarak about 1,000 years ago. Remarkably, the EHG ancestry that has persisted from its ~14% (MBA), ~10% (LBA), ~8% (EIA), and ~7% (Urartian period) is drastically diminished in the post-Urartian period down to ~2-3% (Fig. S 66).

We were concerned that the individuals sampled from the post-Urartian period may have been atypical, so we confirmed the reduction of EHG ancestry in the post-Urartian period also using two present-day Armenians sequenced as part of the Simons Genome Diversity Panel(407) as well as ten present-day Armenians genotyped on the Human Origins array(25). These have reduced EHG ancestry too, with an estimated $3\pm 1\%$ for the larger Human Origins set of present-day individuals (Fig. S 66). When we compare the present-day Armenians to either the Medieval ones from Agarak (~1,000 years ago), or to the ancient ones from several sites (~2,000 years ago), there are no significant differences in ancestry.

The genetic changes we observe in Armenia (Fig. S 67) put constraints on different theories of the origins of Armenians (in the linguistic sense, as Armenian is a language within the broader Indo-European family).

A first possibility is that Armenian language spread was mediated by steppe populations as in parts of Europe(4, 8) and South Asia(10, 34). Steppe influence begins in Armenia during the Chalcolithic and thus before the expansion of the pastoralist Yamnaya culture, but this does not seem to persist or become widespread by the Early Bronze Age, unlike Europe. It becomes generalized during the Middle-to-Late Bronze Age as we have seen.

A second possibility is that the Armenian language may have western origins, related to the historical Phrygians (as suggested by some historical and linguistic evidence(443)). The diminution of EHG ancestry by ~2/3 between the Urartian period and ~2,000 years ago, followed by continuity thereafter implies that dilution of the Bronze-Iron Age population was substantial leaving open the possibility of such a movement. We also note the presence of at least some samples lacking EHG ancestry in the Bronze and Iron Age; these may be early harbingers of this dilution dating to before the historical attestation of Armenians and the Armenian language. However, a relationship of Armenians with populations of the Balkans does not seem to find any parallels in the genetic data as Armenians lack the genetic component (Balkan hunter-gatherer ancestry) of plausible Balkan origin, and thus our data overall favor the first theory—the direct spread of Steppe ancestry—a result also supported by the arrival and wide spread of specifically Yamnaya-associated Y-chromosome haplogroups in this period as discussed in the main text.

Finally, we must note that the dominant component of the population of Armenia at all times is that of Caucasus hunter-gatherer ancestry, and that this ancestry spread both westward (by the Neolithic-Chalcolithic period it had reached southeastern Europe) and northward (by the Eneolithic in the Eurasian steppe(9)). We will continue the thread of this discussion in the following section where we discuss the genetic results from Turkey whose Anatolian region was home to the earliest attested and phylogenetically basal Anatolian group of languages within the Indo-European language family.



Fig. S 66 Armenia (Urartian-to-Ancient-Medieval-Present)

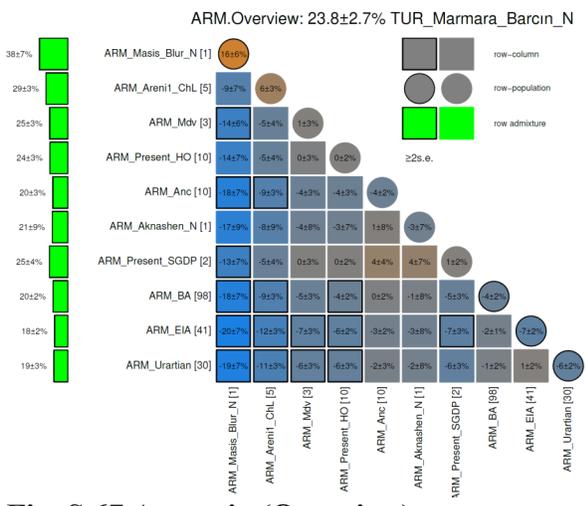
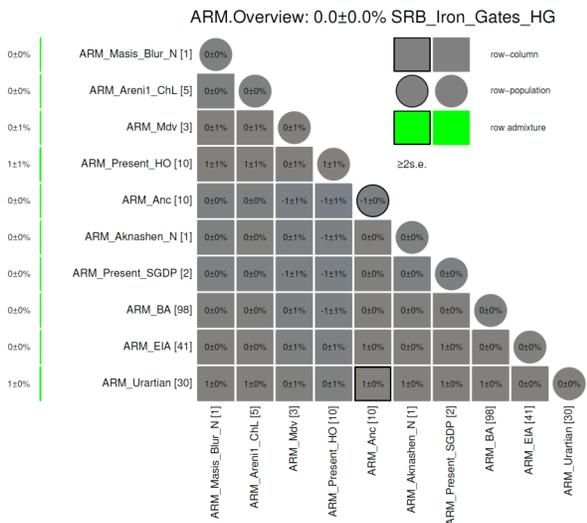
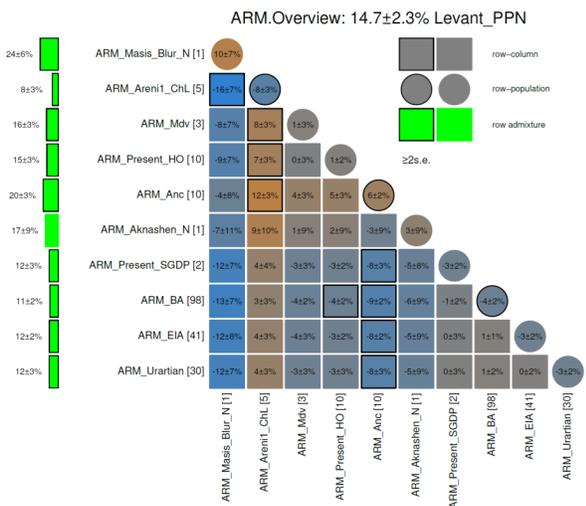
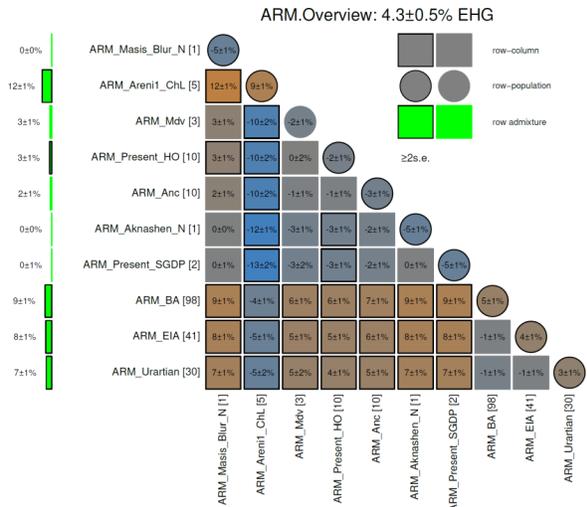
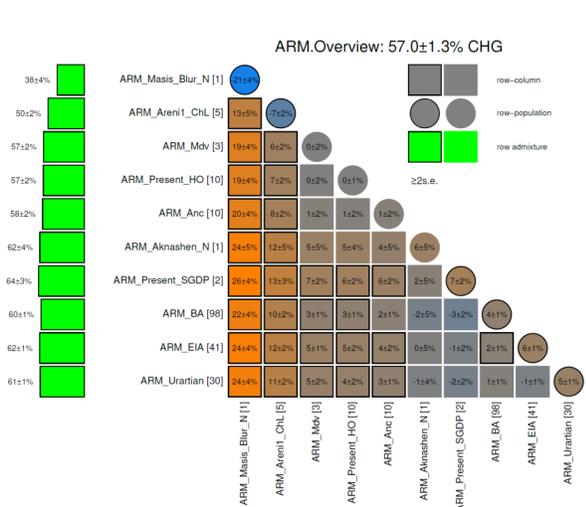


Fig. S 67 Armenia (Overview)

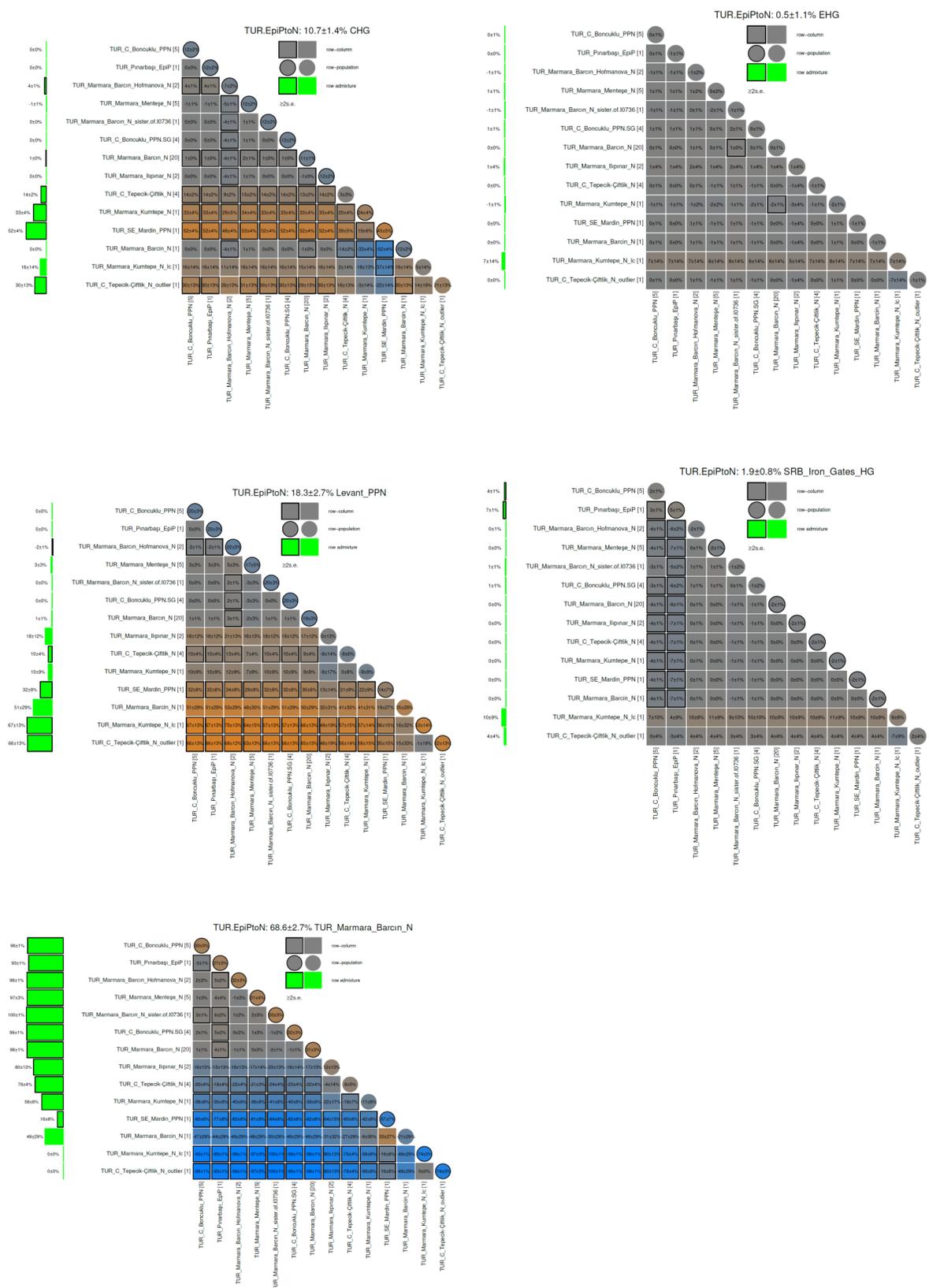


Fig. S 68 Turkey (Epipaleolithic-to-Neolithic)

Turkey

Our samples from Turkey are from Anatolia which borders southeastern Europe by land and sea to the west, and the Levant/Mesopotamia/South Caucasus to the east. Turkey occupies a central position within the geography of the Southern Arc and its great geographical area leads us to adopt both a chronological and a geographical approach to the description of the samples from the country.

Most of the populations of the earliest period (Fig. S 68) can be modeled as deriving their ancestry primarily from TUR_Marmara_Barçın_N, the population with the highest number of samples from NW Anatolia that has been used as one of the five sources in our model and which we colloquially referred to as signifying “Anatolian ancestry” in some of the discussion above. The ancestry represented by this population extended to the interior of Anatolia and to the pre-Neolithic period as PPN samples from Boncuklu(13, 410) as well as the Epipaleolithic hunter-gatherer from Pınarbaşı(410) are also modeled as having the great majority of their ancestry from that source.

(The modeling of Pınarbaşı as mostly Anatolian Neolithic resembles that of the Natufians of the Levant (who are assigned Levant Neolithic ancestry in the 5-way model). The 5-way model, developed in Supplementary Text S2, had the aim of modeling the total population of the Southern Arc as well as individuals from it, and is thus optimized to account for the ancestry of the (mostly Neolithic or later) individuals by having an Anatolian Neolithic source (with Pınarbaşı as a highly informative outgroup). In this section we present the results for all Southern Arc individuals for the sake of completeness. The reader should be cautious in the interpretation of models in which the Test population (e.g., Natufians or Pınarbaşı) antedate the sources of the model. For the Epipaleolithic populations, you may refer to (11) in which these are co-analyzed with Neolithic populations and in which the conclusion is drawn that it is the Anatolian Neolithic population that is drawn from the local Epipaleolithic, with additional ancestry from Mesopotamian/Levantine sources).

At the southeastern end of Turkey, in the region of northern Mesopotamia that borders with previously described samples from Iraq, a Pre-Pottery Neolithic individual from Mardin is modeled as having about half of its ancestry from a Caucasus-related and ~1/3 from a Levantine source, resembling in this respect its geographical neighbors in northern Iraq. It is unclear where the transition between Western/Central “Barçın-like” and Eastern “Mardin-like” ancestry occurred in Anatolia during Neolithic times, how the relative proportions of these two sources shifted over time in this period in each region, and what other components of ancestry may have been present there. However, what we can say is that for the earliest period samples from Turkey both “Anatolian” and “Mesopotamian”/“Levantine” ancestry were present and the latter is expressed as a mixture of “Caucasus” and “Levantine” ancestry in terms of the ancestral components of our five-way model. In the discussion that follows we document changes in these components after the Neolithic, as well as possible introductions of other components into the region.

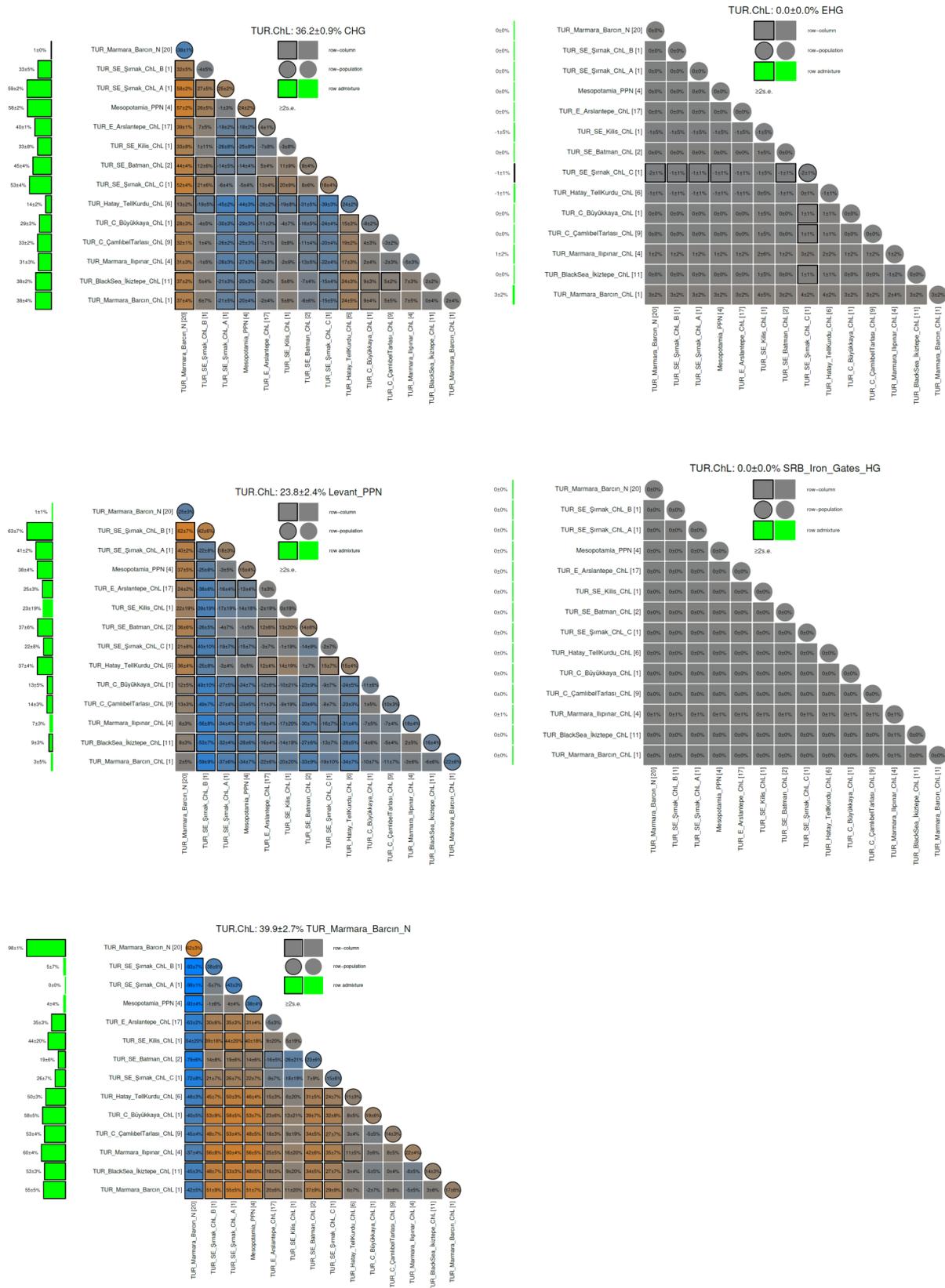


Fig. S 69 Turkey (Chalcolithic)

During the Chalcolithic (Fig. S 69), “Anatolian” ancestry reached the Southeast (Batman, Şırnak cluster “C”; I4480 3369-3104 calBCE) and Tell Kurdu(14) and beyond Turkey in Israel(420), and “Mesopotamian” CHG/Levantine ancestry reached the Northwest (Barcın and Ilıpınar). At Şırnak, the cluster “C” individual that has “Anatolian” ancestry contrasts with the earlier cluster “B” (I4622; 3641-3521 calBCE) that lacks it, documenting this ancestry transition as it was occurring. In both ends of Turkey (NW and SE) during the 4th millennium BCE, the previous ancestral components persist (“Anatolian” vs. “Caucasus/Levantine”) but are complemented by substantial ancestry (especially in the NW) from the opposite end of the region.

We cannot claim that the westward spread of CHG/Levantine ancestry is associated entirely with the formation of the Chalcolithic across Anatolia, as this type of ancestry extended further west (in Greece, Albania, and Bulgaria) even during the earlier Neolithic as we have already seen; for example, the Neolithic individual from Krepost in Bulgaria (5718-5626 calBCE)(3) has such ancestry as high as $24 \pm 5\%$ earlier than any individual in our western Anatolian time series does. Yet, for the two geographical regions within Anatolia for which we do have Neolithic samples (Marmara and Central Anatolia regions) there is a definite increase of CHG/Levantine ancestry associated with the Chalcolithic samples. Thus, there was definitely a change in the balance of the Anatolian/CHG/Levantine components within Anatolia leading to the increase of the “eastern” CHG/Levantine components in parts of Anatolia. The inference in (11) that the Neolithic of NW Anatolia was derived from the local Epipaleolithic with additional Mesopotamian/Levantine Neolithic ancestry raises the possibility that founder Neolithic populations in Southeastern Europe were derived from populations with slightly different balances than those represented by the NW Anatolian Neolithic. One of which was the pottery Neolithic at Çatalhöyük(12) which presents a pottery Neolithic population from Central Anatolia and which we analyze in SI5 showing that it had a different ancestral mix than the NW Anatolian Neolithic, with more Mesopotamian/Levantine-related ancestry.

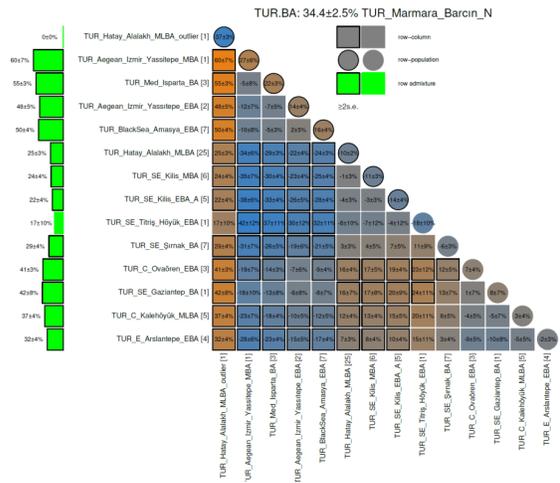
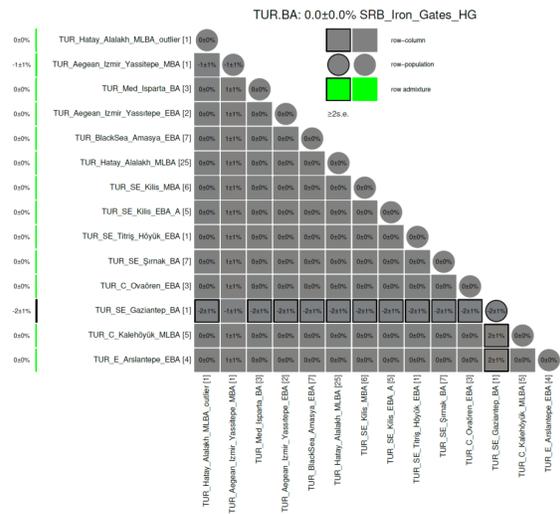
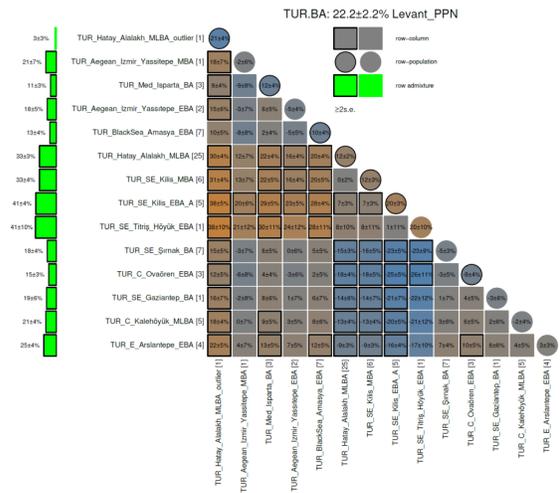
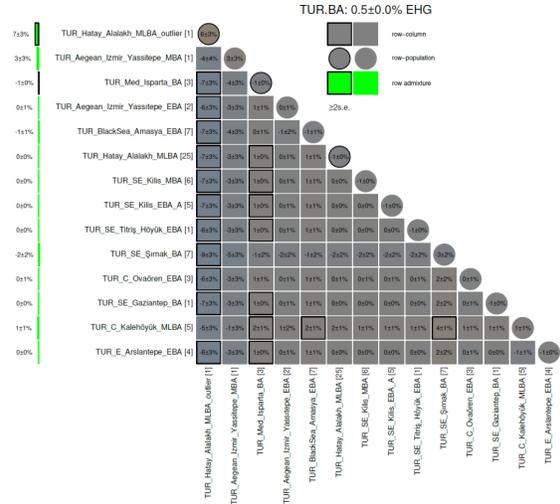
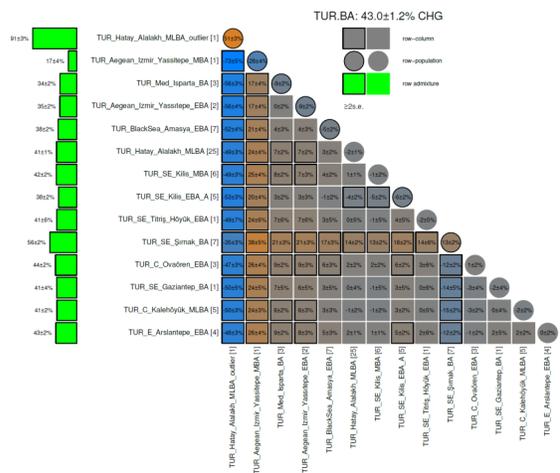


Fig. S 70 Turkey (Bronze Age)

CHG-related ancestry is general in the Bronze Age (Fig. S 70), extending to the westernmost regions of Anatolia (Marmara, Aegean, and Med regions). Levels found in the Early Bronze Age there (at Yassitepe and Isparta) are as high as Kilis in the Southeast (about $\sim 1/3$). Şırnak, the easternmost set of Early Bronze Age samples possesses the highest amount ($\sim 56\%$) of CHG-related ancestry other than an outlier from Alalakh in Hatay region (14) in the Middle-to-Late Bronze Age. While more sampling could also be helpful in order to understand the extent of CHG ancestry in the early Bronze Age, its Bronze Age presence in the west, northeast (at Amasya), central, and southeast regions in a sample size of 71 individuals spread over 14 sites give us confidence that it encompassed the entirety of Anatolia by this time.

Our samples from Devret Höyük (Amasya) from the Early Bronze Age (~ 3300 -2400 BCE) complement previously published ones from the Chalcolithic of İkiztepe (14) from near the coast of the Black Sea (~ 160 km to the north) and a few centuries earlier. Admixture estimates at the two sites are highly similar, documenting a substantial degree of population homogeneity between the Black Sea littoral and interior and also across the Early Bronze Age transition during which no influx of new ancestry is detected. Surprisingly, the samples from Northeast Turkey do not show elevated levels of CHG ancestry compared to those from elsewhere in Anatolia, despite being geographically more proximate to the Caucasus ($\sim 38\%$ at Amasya compared to $\sim 60\%$ in the Bronze Age of Armenia previously discussed). About half the ancestry at Amasya during the EBA was derived from an Anatolian Neolithic source. More ancient Neolithic samples are needed to determine the earliest (pre-Chalcolithic) population local to the region and how it may have placed within the continuum between the Northwestern Anatolian Neolithic and the Neolithic samples of the Caucasus and northern Mesopotamia. What we can say is that after the Chalcolithic and Bronze Age population stability continued until at least the 1st millennium BCE, when samples from neighboring Samsun (the modern name of ancient Amisos) bear close resemblance to those of İkiztepe and Devret Höyük. By that time we also detect a few outlier individuals in the Black Sea region that will be discussed below.

Bronze Age Southeast Turkey contrasts with other regions in terms of the Levantine-related ancestry where the high levels present since the Chalcolithic persist and contrast with lower levels in other regions. Notice that in terms of the ratio of CHG/Levantine ancestry this is fairly balanced in the Southeast but tilts in favor of CHG elsewhere. Very high proportions of CHG/Levantine ancestry were also observed at Ilıpınar during the Chalcolithic in the northwest. We can conclude that while migration brought both “eastern” components (Caucasus- and Levant-related) westward, the former predominated.

EHG ancestry is not present in Anatolia during the Bronze Age except in the aforementioned outlier from Hatay region ($6.5 \pm 2.8\%$; $Z=2.3$), , and very tentatively at $2.9 \pm 2.6\%$ ($Z=1.1$) at Yassitepe in the Middle Bronze Age (15737; 2033-1920 calBCE) out of 71 individuals representing every region of Anatolia. While we cannot exclude the presence of some such ancestry in the Bronze Age in a yet-to-be sampled site, we can conclude that such ancestry was rare (the overall averaging over the Bronze Age populations is 0.5% , driven by the aforementioned outlier, or $0.1 \pm 0.2\%$ averaging over the individuals). Bronze Age Anatolia continues the Chalcolithic pattern with populations composed of the same “western” / “eastern” mix of Anatolian/CHG/Levantine ancestry. In this respect, Anatolia contrasts with both the Aegean in the west (where EHG ancestry was more prevalent at $\sim 5\%$ in Mycenaean samples but with the previously discussed variability) and with the South Caucasus (where $\sim 10\%$ EHG ancestry was present in contemporary samples from Armenia).

Balkan-related hunter-gatherer ancestry is absent in the Bronze Age, thus excluding any substantial migration from regions of Europe where this ancestry was substantial. The pattern of NW Anatolian-related ancestry is the opposite of the Levant-related one, with samples from the SE having the lowest amounts ($\sim 1/4-1/3$) and those from the rest of the country having the highest ($\sim 1/2$).

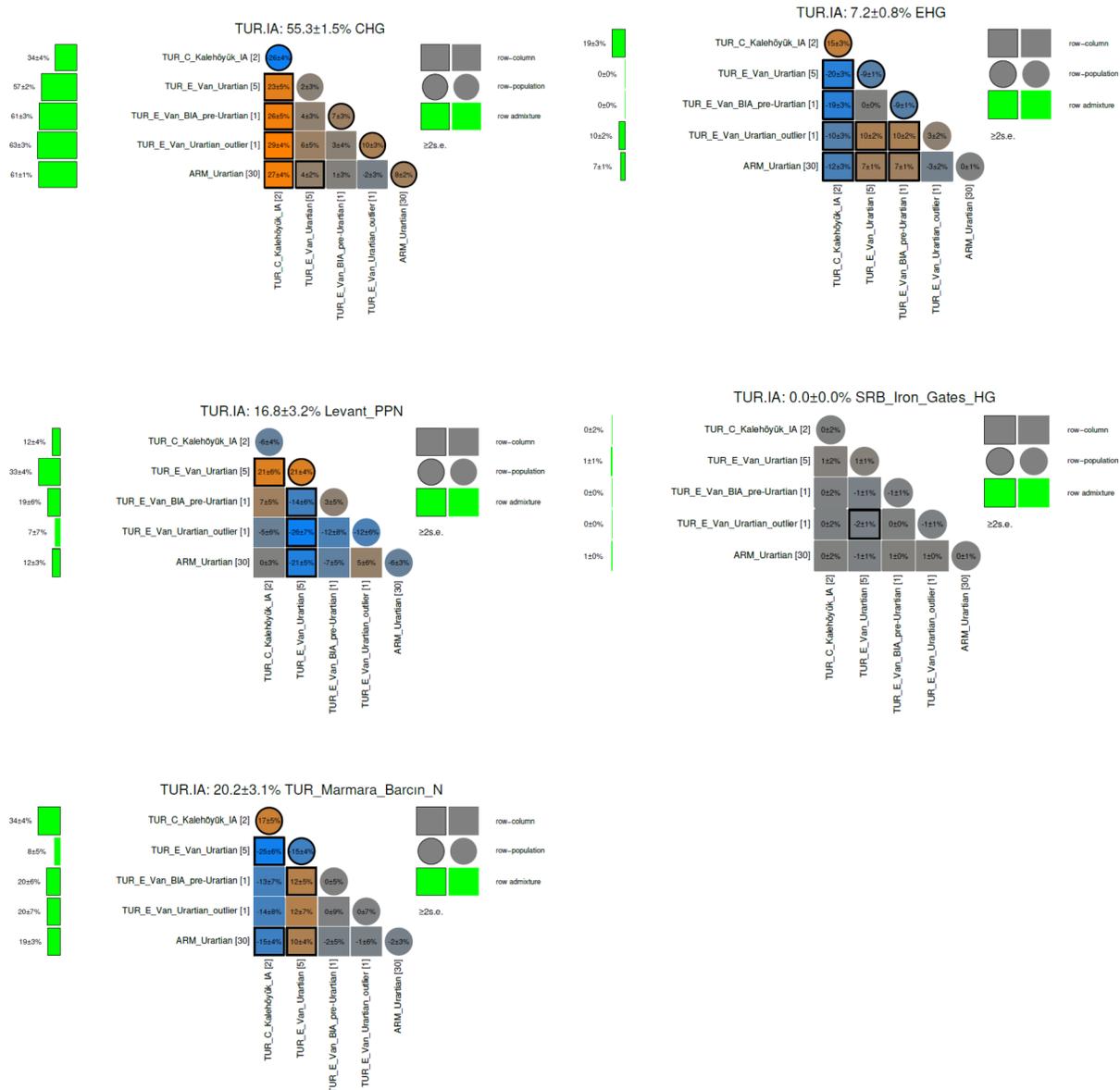


Fig. S 71 Turkey (Iron Age)

The next set of populations comes from the Iron Age (Fig. S 71). The pre-Urartian and Urartian samples from Lake Van (Eastern Anatolia region of Turkey) are fairly homogeneous and possess (as is expected from geography) high levels of the eastern (CHG and Levantine) components. Notice that all but one of them have no EHG ancestry, thus contrasting with Urartian samples from neighboring Armenia which possess such ancestry ($\sim 7\%$) as we remarked

above and which we also include in the plot for comparison. The contrast between the Urartian samples from Turkey and Armenia is also visible in the proportion of Levantine ancestry which is higher in the former. We thus conclude that the Urartian population was not genetically homogeneous in the two locales.

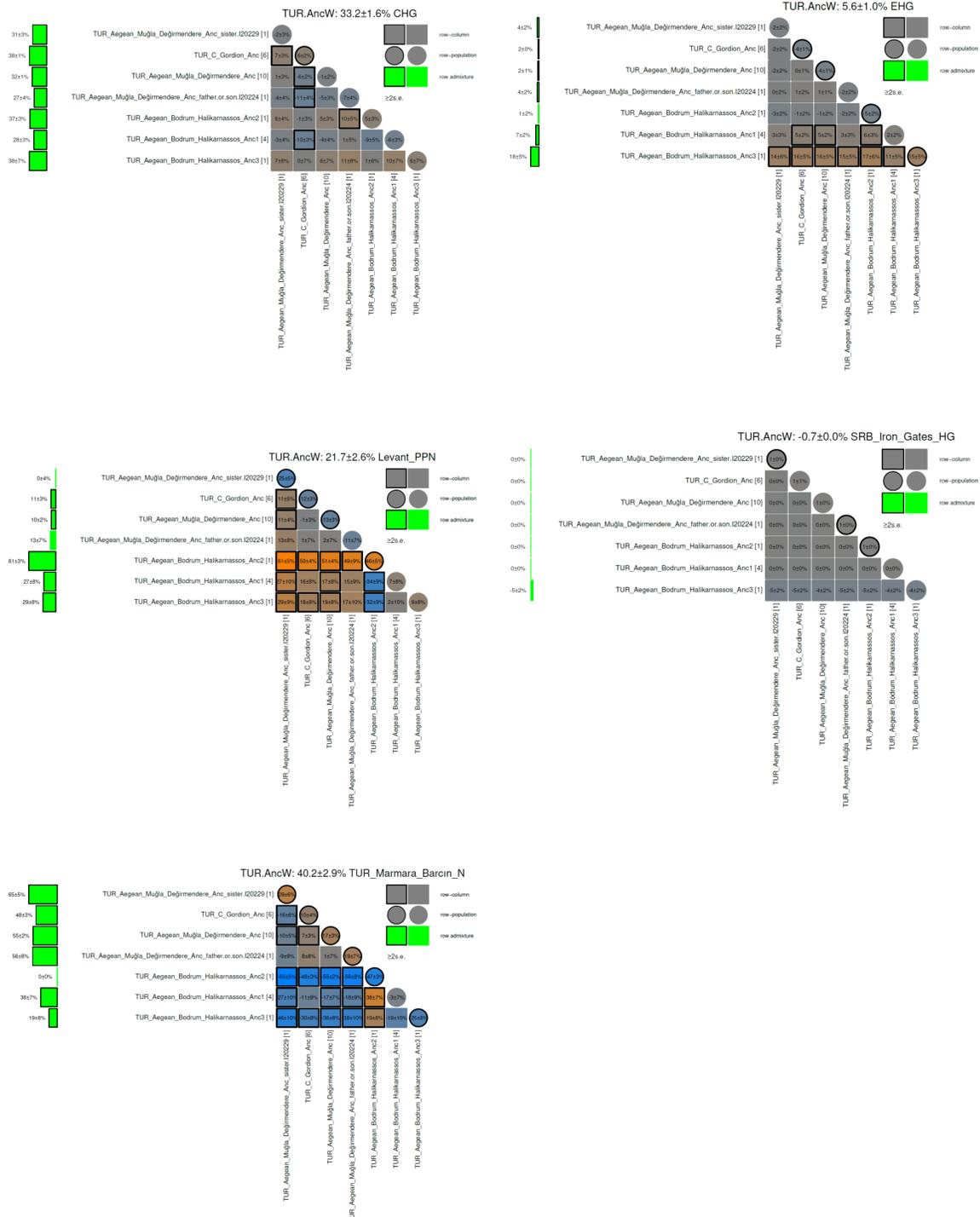


Fig. S 72 Turkey (Antiquity / West-Central)

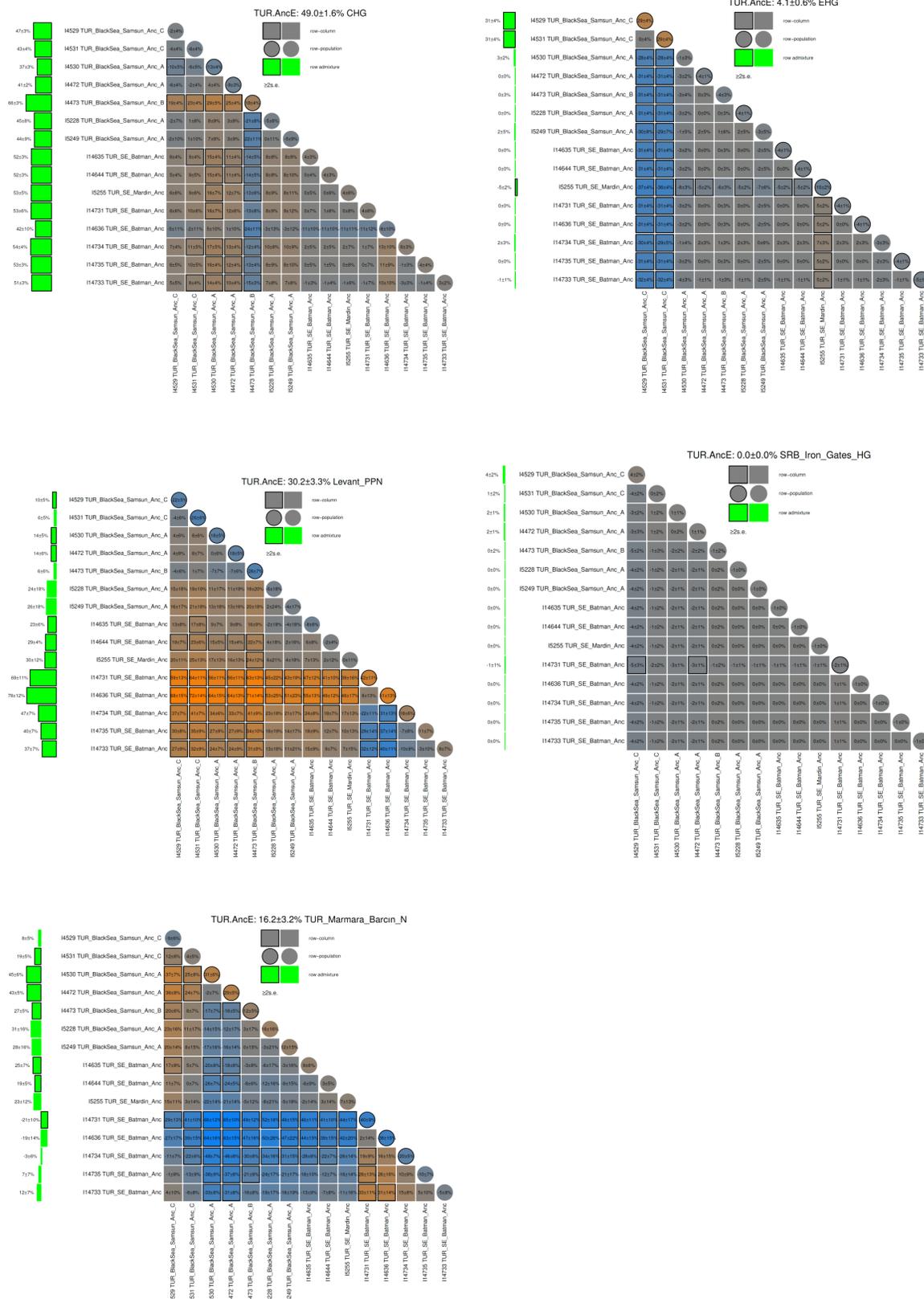


Fig. S 73 Turkey (Antiquity / Northeast-Southeast)

The next set of populations date from the period down to the incorporation of Anatolia into the Roman Empire, a period era of dense history for which we have copious historical sources, including those of Herodotus, a native of Halikarnassos (modern Bodrum) which furnishes some of the samples from this period. Because of the great number of individuals, we split the presentation of the samples into West-Central (Fig. S 72) and Northeast-Southeast (Fig. S 73).

The samples from Gordion, the capital of Ancient Phrygia are made up predominantly of NW Anatolia-related and CHG-related ancestry. Ancient Phrygia was successively incorporated into Lydia, the Persian Empire, and the Hellenistic Empire following the campaigns of Alexander the Great. The samples are centuries apart within this sequence of historical events. Importantly, they are rather homogeneous in terms of their ancestry, so we can be fairly confident that they represent the local “Phrygian” population whatever its origins may have been. The Phrygians were Indo-European speakers thought to have migrated from the Balkans as the Phrygian language is not related to the Anatolian branch of Indo-European which includes such languages as Hittite and Luvian. Importantly, though, the samples from Gordion have only small amounts of EHG ancestry, suggesting that either migration from steppe-enriched Balkan populations was minimal, or that it originated from Balkan populations with little steppe ancestry (such populations existed in the Bronze Age in southeastern Europe as we have seen).

Halikarnassos (modern Bodrum) was a Dorian colony in ancient Caria. The samples are from the Hellenistic period and are varied in ancestry. Some have the expected high NW Anatolian ancestry expected for samples of the Aegean region, but there are others with substantial EHG ancestry (up to $18\pm 5\%$) and one individual with substantial Levantine (I3303: $61\pm 3\%$) ancestry. Thus, they attest to ancestry heterogeneity in a cosmopolitan port city at the border of Europe and Asia, with influences from both West and East together with the local ancestry present in western Anatolia in preceding periods.

The Archaic (sub-Geometric) samples from Değirmendere in the interior of ancient Caria predate the coastal ones from Halikarnassos and have more Anatolian Neolithic and less Levantine ancestry. We may tentatively hypothesize that Levantine ancestry increased in Hellenistic times during the southwest corner of Anatolia from its lower levels during the Archaic period.

In the Southeast, samples from Batman and Mardin continue the CHG/Levantine mix present in the region from Neolithic times with little contribution of the other components, forming a reasonably homogeneous population that lived ~ 2.5 thousand years ago whose composition echoes that of the Chalcolithic population from the same locality thousands of years earlier.

In contrast, in the northeast Black Sea region at Samsun (ancient Sampsous) which was an Ionian colony on the coast of the Black Sea and part of the Kingdom of Pontus most famous for its leader Mithridates VI who threatened the expansion of Rome into Anatolia, a remarkable variety of ancestry occurs. While most individuals exhibit primarily CHG- and NW Anatolia-related ancestry, a pair of individuals have $\sim 31\%$ EHG ancestry differing dramatically from the rest of the population where this ancestry is negligible. The sampled individuals at the time after the demise of the Kingdom of Pontus might perhaps be derived from the preceding period when the Bosporan Kingdom to the north of the Black Sea was briefly part of the Kingdom of Pontus, or the early Roman period when it was a client state of Rome; in any case, these individuals have some East Eurasian ancestry that marks them as outliers and could be of steppe origin.

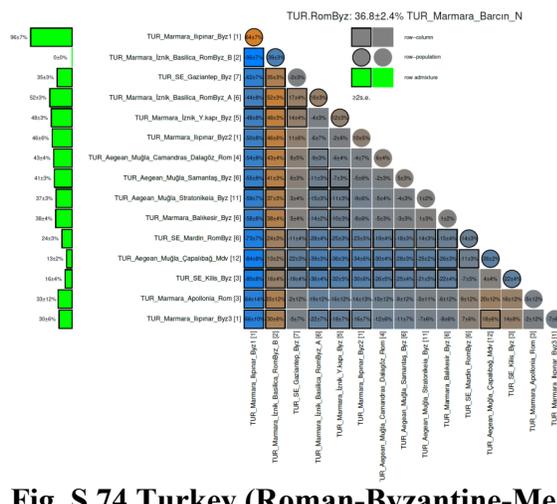
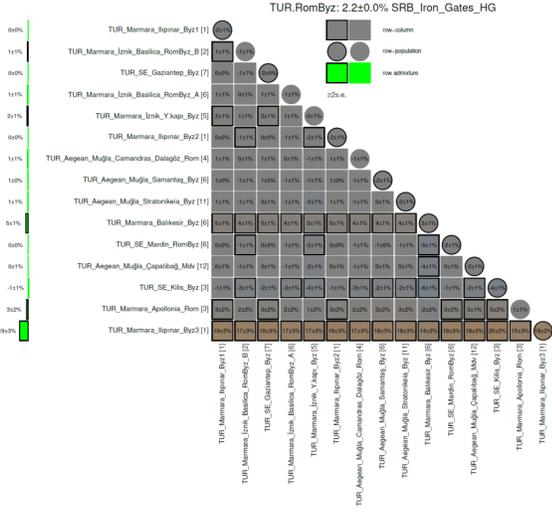
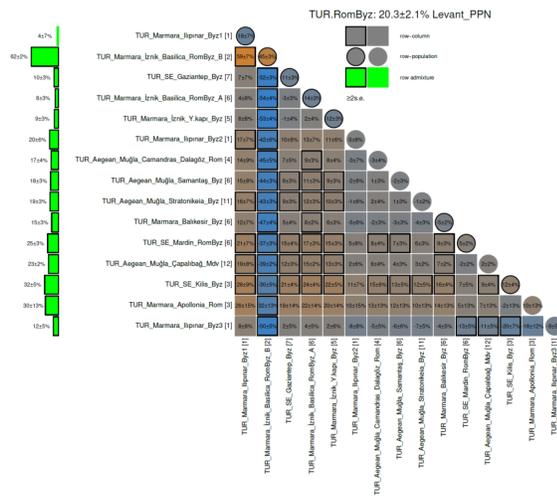
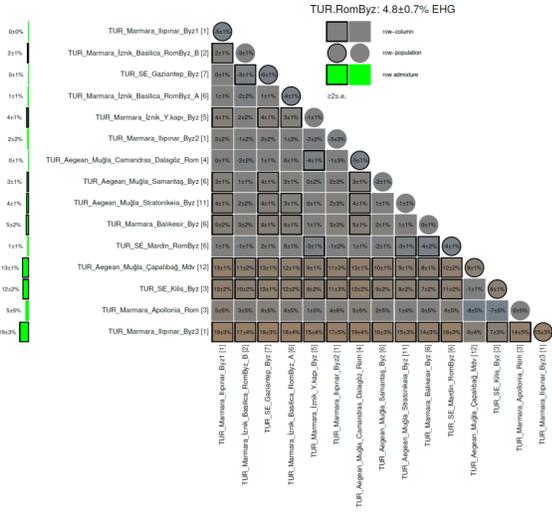
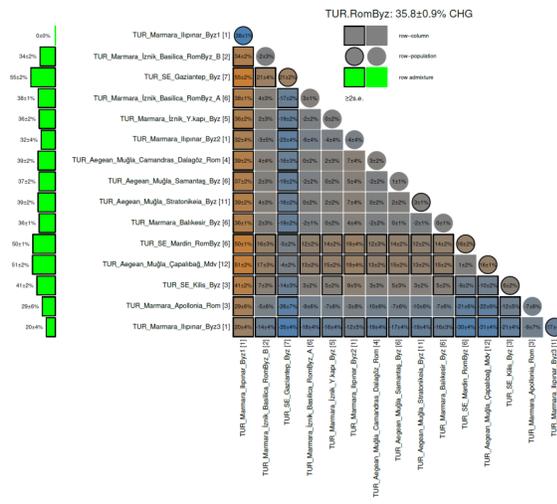


Fig. S 74 Turkey (Roman-Byzantine-Medieval)

We use the conventional periodization into Roman and Byzantine periods, while noting that these did not mark any political change in the history of the Roman Empire in its eastern half whose Late Antique and Medieval period is called “Byzantine”. In Fig. S 74 we present samples from these periods; after the fall of Rome in the West, the Roman Empire continued to have some possessions in both the West and also the Levant and North Africa, but its heartland largely coincided with the geographical territory of the Southern Arc.

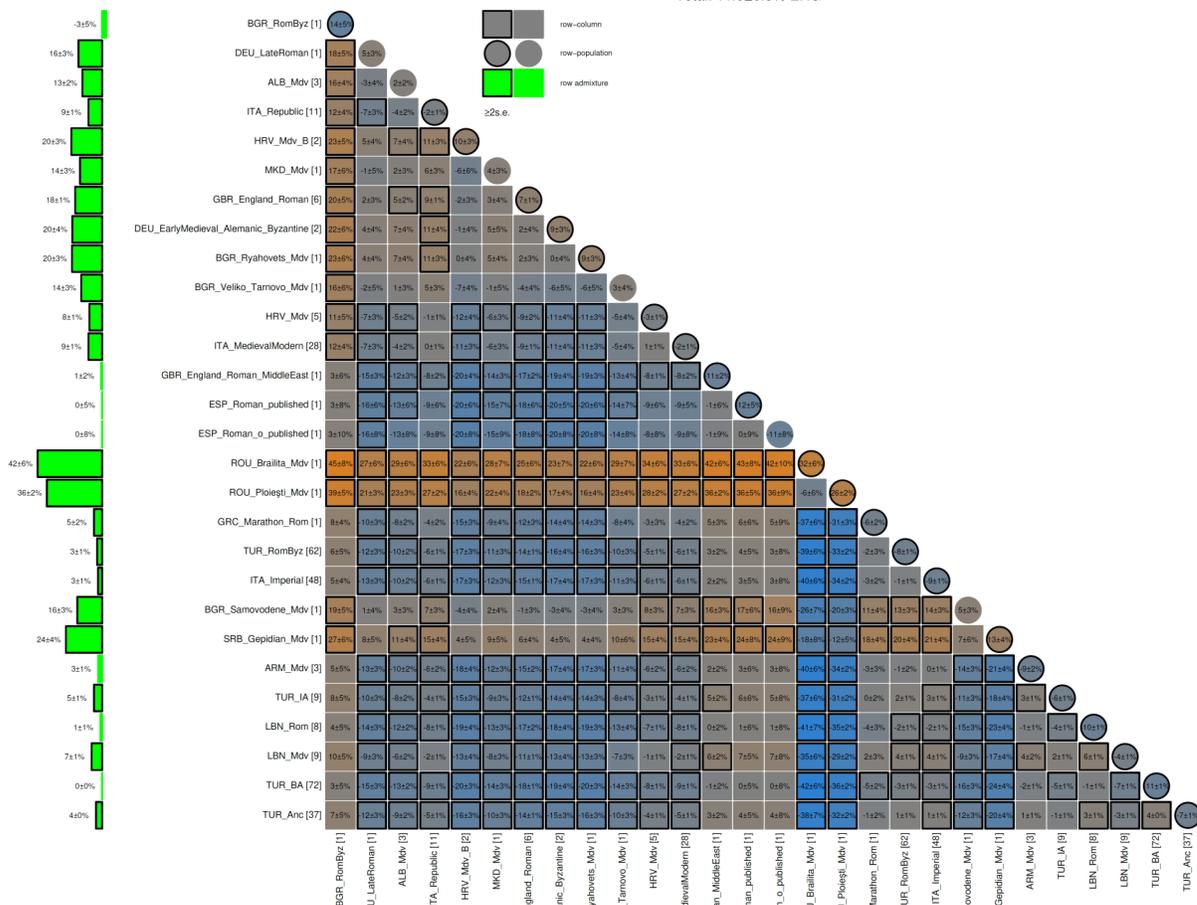
One sample from Ilıpınar of putative Byzantine age (I10429 / Byz1) is almost completely of NW Anatolia-related ancestry. Given the absence of any such populations between the Neolithic and the medieval period we suspect that the age is wrong rather than long-term survival of unadmixed Neolithic ancestry in this particular individual; we do not currently have a radiocarbon date on this individual. The other two individuals from this locality (I10546 / Byz2 and I10430 / Byz3) seem more probably denizens of the Empire of their time, with the former’s low and the latter’s high steppe and European hunter-gatherer ancestry respectively signifying that they stemmed from the Asian and European parts of the Empire. Byz3 has a remarkable amount of Balkan hunter-gatherer-related ancestry ($19\pm 3\%$) and no significant CHG ancestry and could very well also be someone from beyond the borders of the Empire from Europe.

Nine samples are from the remarkable recently excavated Basilica of St. Neophytos in ancient Nicaea (modern İznik) famous as the place where the First Ecumenical Council convened by Constantine the Great was held. The Basilica was perhaps erected following this event and was dedicated to St. Neophytos of Nicaea who according to tradition was killed by Roman soldiers in the early 4th c. CE a few years before the Edict of Milan established religious toleration in the Roman Empire. Most of the samples (group A) have an expected mix of primarily NW Anatolian and CHG ancestry, established in the Marmara region since the Chalcolithic and resemble samples of the same period from Apollonia, Balıkesir, and Yenişehirkapı in the Marmara region and Stratonikea, Yatağan, and Samantaşı in Muğla in the Aegean region (ancient Caria). Two samples from the Basilica (group B) are outliers with high “Levantine” ancestry and could signify migrants from the Levantine or North African provinces of the Empire.

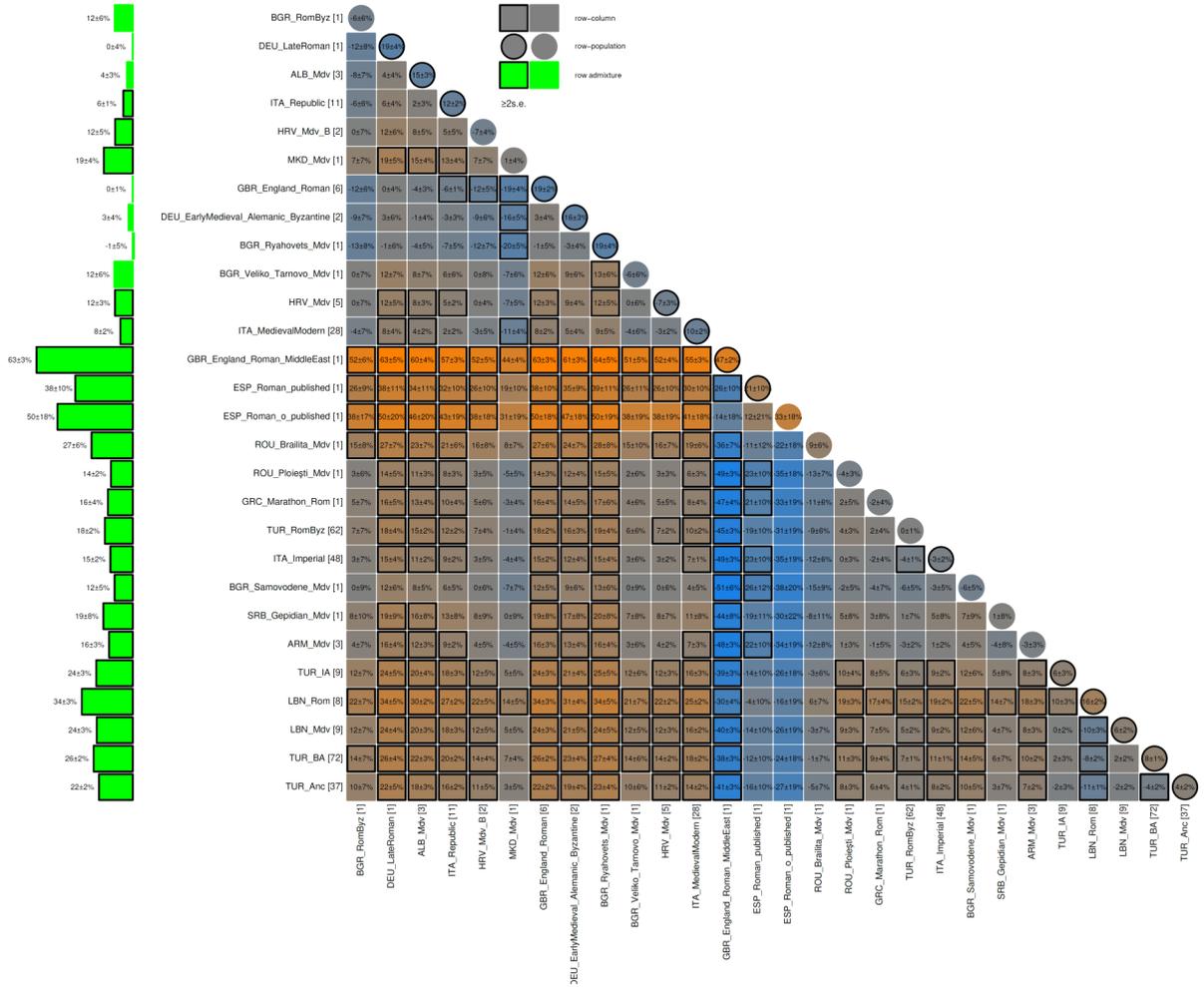
The samples from Mardin and Gaziantep have primarily CHG- Levantine- and NW Anatolian- related ancestry; their Levantine ancestry is reduced relative to levels observed in earlier samples from SE Turkey. The two sites are about ~350km apart and the easternmost one (Mardin) has ~15% more Levantine ancestry than the westernmost one (Gaziantep). But near Gaziantep at Kilis the fraction of Levantine ancestry is ~1/3 and not significantly different than Mardin.

An interesting set of samples from Çapalıbağ at Muğla (1300-1650 CE) have low Anatolian Neolithic ancestry but high ~1/2 CHG and ~13% EHG ancestry. These individuals actually have Central Asian ancestry not accounted for by the 5-way model (Supplementary Text S2) not present in the Southern Arc in general and they date from a period after the establishment of the Seljuq dynasty in large parts of Anatolia, so they may well be descendants of Turkic populations. We date the admixture of these individuals in the main text and also discuss them in (6).

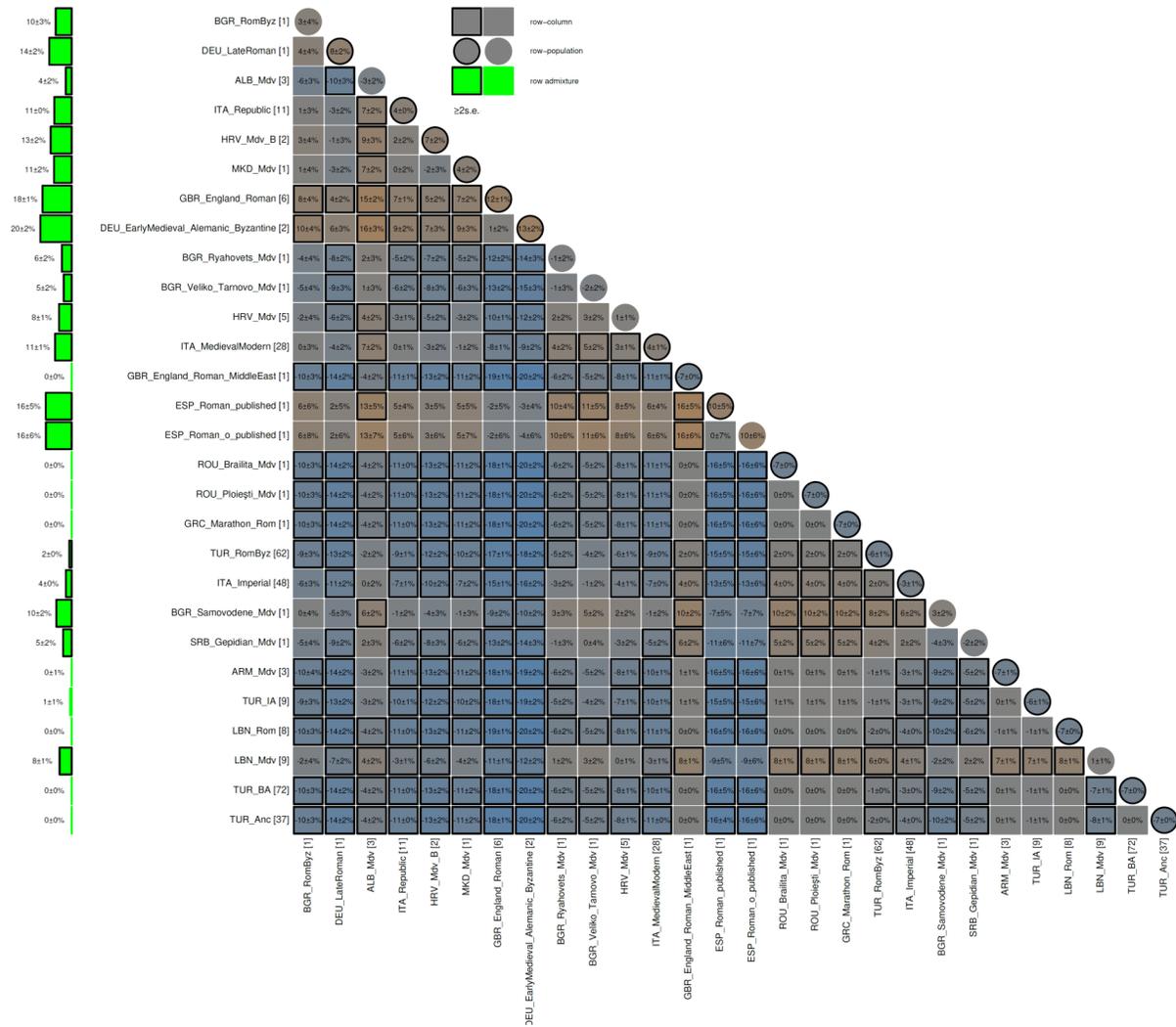
Total: 11.0±0.8% EHG



Total: 18.1±1.7% Levant_PPN



Total: 6.9±0.0% SRB_Iron_Gates_HG



$$\delta_3(X; Y, Z) = \frac{1}{5} \sqrt{\sum_{i=1}^5 (X_i - Y_i)^2} - \frac{1}{5} \sqrt{\sum_{i=1}^5 (X_i - Z_i)^2}$$

If the admixture proportions (X_i) of population X are overall closer to those of Y than to those of Z then this statistic would tend to be negative and vice versa. We estimate $\delta_3(\text{ITA_Imperial}; \text{TUR_RomByz}, Z)$ for Z =all other populations of Fig. S 75 and find (Fig. S 76) that it is nominally negative for all populations, and significantly negative for all populations except the Roman period individual from Attica and the Late Antique sample from Boyanovo in Bulgaria (300-500 CE). The converse statistic $\delta_3(\text{TUR_RomByz}; \text{ITA_Imperial}, Z)$ shows that the Imperial Romans were closer to the Roman/Byzantine Anatolians than many other populations Z were, except, of course, the temporally preceding ancient population of Anatolia.

We were concerned that the population-level similarity of Roman/Byzantine Anatolians and Imperial Romans could be coincidental, and so carried out a clustering analysis of *individuals* (using the `hclust` hierarchical clustering function of R) in the space of F4admix proportions (thus individuals with similar proportions clustered together, without any knowledge of their country of origin or population label). This procedure, whose results are shown in (6), shows an interspersed distribution of Imperial Roman with Roman/Byzantine (and earlier) individuals from Anatolia, as well as other clusters of individuals centered on Southeastern Europe, the Levant, and the South Caucasus. In both Imperial Rome and Roman/Byzantine Anatolia, the bulk of the individuals cluster within the Anatolian cluster, with a few grouping the remaining clusters. Thus, the population-level similarity of the two, described in this section, is not due to the averages of the two distributions being coincidentally similar, but reflects a real overlap of the distribution of individuals, which, while being diverse and including individuals of varied backgrounds, nonetheless centered largely on Anatolia.

Our results should not be interpreted as claiming that a single homogeneous population existed in Roman Italy and Roman/Byzantine Anatolia; we have already discussed the presence of outlier individuals and population structure in the latter. Rather, our results suggest that whatever the heterogeneity was, the average position of the two locales where the Roman Empire was founded ~2,000 years ago (Italy) and the place where it ended ~600 years ago (Anatolia) in the genetic landscape of West Eurasia was virtually indistinguishable, and that it resembled the core Anatolian populations of the Southern Arc.

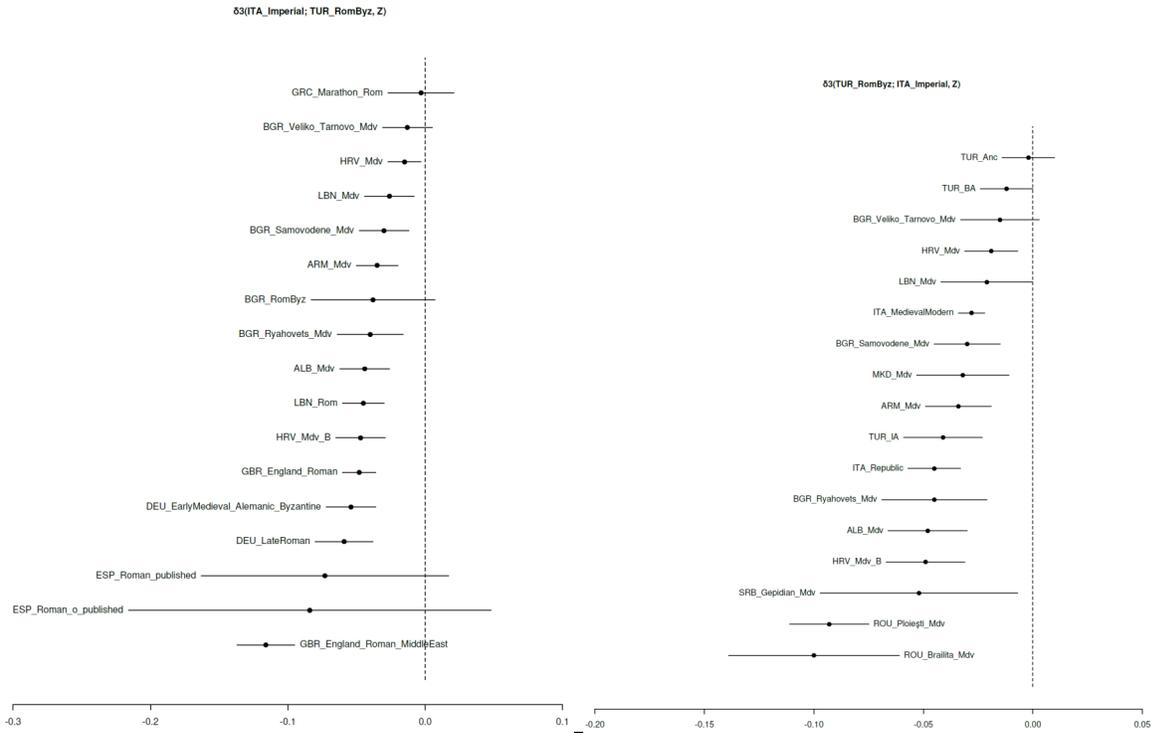


Fig. S 76 δ_3 -statistic. Left: The Imperial population of Ancient Rome most resembles in its composition the Roman/Byzantine/Medieval/Ancient populations of Anatolia and southeastern Europe. Right: The Roman/Byzantine population of Anatolia resembles most the Imperial population of ancient Rome – except for earlier populations of Anatolia and other Roman/Byzantine/Medieval populations of the Southern Arc itself.

S4: Northern and Southern Arc ancestors of the Yamnaya genetic cluster

The mixed origin of the Yamnaya (Pit Grave) steppe pastoralists was first proposed in (8) where it was observed that the statistic $f_3(\text{Yamnaya}; \text{EHG}, \text{Present-day Near Eastern and Caucasus})$ was significantly negative and thus the Yamnaya had ancestry from at least two sources related to Eastern European hunter-gatherers and present-day people from the Near East and Caucasus (such as Armenians). It was estimated that roughly half the ancestry of the Yamnaya was contributed by each of the two sources.

While the EHG predated the Yamnaya and overlapped with them geographically, making them a very plausible source for their ancestry, at the time there were no ancient samples predating the Yamnaya from the Caucasus that could account for the “southern” component, and Armenians and other present-day populations had a potentially complex ancestry that differentiated them from the putative admixing population of >3000BCE. This deficit changed with the publication of the two Caucasus hunter-gatherer (CHG) samples from Georgia(7) which showed that a population with similar ancestry (but not identical) to present-day populations of the Caucasus existed there in pre-Neolithic times, adding to the plausibility of the proposed admixture. Thus, while the CHG proved that a “Caucasus”-related ancestry existed in the region long before both the Yamnaya and the present-day people of the Caucasus, it was also not a good source for the Yamnaya (as it was simpler than the admixing population). The actual historical admixing population’s identification was still in question.

Another major development was the identification of populations that were indistinguishable from the Yamnaya genetically. First, the Afanasievo population from the Altai(4) was shown to be such a population, resolving the question of its origin by proving it was most likely the result of a long-range migration from the west. Second, the later Poltavka culture from the Middle Bronze Age European steppe was also shown to be similar to the Yamnaya(9), as were samples from the Catacomb culture in the North Caucasus(17): all these were genetically simpler than steppe populations that followed them such as the Srubnaya(9), Sintashta(34), and Andronovo(34) cultures, all of which had both Yamnaya-related ancestry and extra ancestry related to European farmers which placed them in Middle/Late Bronze Age cluster of populations that was similar to that of populations of Europe such as the Corded Ware and Bell Beaker groups, as well as the Fatyanovo population(35) of the forest-steppe zone from which the MLBA steppe cluster could arguably be descended.

Another development was the publication of Eneolithic populations of the steppe from Khvalynsk II(9) and Progress-2(17) that predated the Yamnaya and postdated the EHG on the steppe. The genetic mixture of these included both EHG and “southern” ancestry, documenting the spread of the latter into territory previously occupied by the EHG, a process which culminated in the formation of the Yamnaya and its later expansion(4, 8) west and east, presumably as a result for its invention of pastoral nomadism and possibly horseback riding that enabled them to become highly mobile and extract resources from the open steppe in an unprecedented way.(45)

The publication of Eneolithic samples also led to a re-evaluation of the origin of the Yamnaya which were now modeled as having ~1/7 of their ancestry from a NW Anatolian Neolithic-related source, a component that was not present in preceding Eneolithic era populations or the “Steppe Maykop” population of the North Caucasus that also preceded the Yamnaya and was notable for its earlier practice of kurgan burial. Moreover, this publication proposed that Western hunter-gatherer (WHG) ancestry was included in the “farmer” component

of the Yamnaya and so this population may have had ancestry from European farmers (such as the Globular Amphora) in which Anatolian Neolithic ancestry made the major component with the addition of WHG ancestry. Another 3-way model was proposed in another publication in which the Yamnaya were modeled as a mixture of EHG, Iranian Chalcolithic (from Seh Gabi) and CHG ancestry.(10) These various models all agreed in the presence of admixture in the Yamnaya related to surrounding (southern and western) farming populations, but disagreed as to the proximal source of this ancestry.

The problem of inferring the ancestry of the Yamnaya in terms of proximal sources

The data presented in this paper make it possible to seek out additional sources for the “southern” component of ancestry in the Yamnaya as they include Neolithic to Chalcolithic populations from West Asia, including Anatolia, the Caucasus, and Iran, together with other published data from the region that have not yet been evaluated as to their potential as sources. In **Fig. S 5** we infer mid-5th millennium BCE admixture in the Yamnaya, placing it well within the set of available samples of our study.

A major difficulty in modeling the Yamnaya in terms of proximal sources is that neither the “northern” (steppe) or “southern” (Near Eastern/Caucasus) or “western” (European) sources are known precisely: fixing one of these has implications for the remainder of the Yamnaya ancestry as we now explain. EHG ancestry is certainly present in the Yamnaya from the genetic point of view and is entirely geographically and temporally plausible as we explained above. Yet, the samples immediately preceding the Yamnaya (Steppe Maykop and Eneolithic samples from Khvalynsk II and Progress-2) are variable in terms of their ancestry; none of them possess the R-M12149 Y-chromosomes typical of the Yamnaya that would tie them to the emerging population within a recent time frame. Moreover, the EHG occupied a huge territory from Karelia to Samara at least ~8000BCE with a related population of Sidelkino further east,(15) while the sampled Eneolithic populations represent only limited points on that range: presumably there were other, yet to be sampled, Eneolithic populations that could represent the northern source, mediating EHG ancestry to later populations like the Yamnaya.

In the absence of a secure identification of the northern population we may attempt to fit models involving different northern populations, limiting ourselves to sampled ones, but this choice will affect the choice of the corresponding southern one. For example, the published individuals from Khvalynsk are variable in terms of their “southern” ancestry which corresponds to CHG-related ancestry. If the “northern” source had little if any CHG ancestry, then the deficit must be made up by selecting a “southern” source with more such ancestry. Conversely, if the “northern” source is maximally admixed with a CHG-related ancestry then correspondingly less such ancestry must be contributed by the “southern” source.

The issue is further complicated by the possibility of “western” (European) ancestry as in (17) Anatolian farmer ancestry is present in both Europe and the Near East; moreover, in the former case it is variable in terms of its absorption of local hunter-gatherer (WHG or SRB_Iron_Gates_HG-related ancestry): if some Anatolian farmer ancestry is contributed from Europe (to account for the ~1/7 or so estimated by (17)), then a correspondingly “less Anatolian” population must be chosen for the remainder of the Yamnaya’s ancestry.

With these considerations in mind, we proceeded to try to model the ancestry of the Yamnaya with the goal of determining whether any feasible models exist for this crucial population.

We used the following set of outgroups in the qpWave/qpAdm analysis:

Mbuti.DG, ARM_Aknashen_N, ARM_Masis_Blur_N, AZE_N, CHG, EHG, IRN_Ganj_Dareh_N, ISR_Natufian_EpiP, Levant_PPN, MAR_Taforalt_EpiP, Mesopotamia, RUS_AfontovaGora3, SRB_Iron_Gates_HG, TUR_C_AşıklıHöyük_PPN, TUR_C_Boncuklu_PPN, TUR_C_Çatalhöyük_N, TUR_Marmara_Barçın_N, TUR_Pınarbaşı_EpiP, WHG

This is the same set as used in the previous section on the Neolithic continuum, but to which we added Neolithic populations from Anatolia, the Caucasus, Mesopotamia, and Iran, i.e., likely sources of ancestry for the “southern” component that were not available in previous attempts to model it and which will hopefully allow us to have increased power to reject models of ancestry.

We consider the following set of sources of ancestry:

CHG, EHG, WHG, ARM_Aknashen_N, ARM_Masis_Blur_N, AZE_N, IRN_Ganj_Dareh_N, Levant_PPN, Mesopotamia, SRB_Iron_Gates_HG, TUR_C_AşıklıHöyük_PPN, TUR_Marmara_Barçın_N, TUR_C_Boncuklu_PPN, TUR_C_Çatalhöyük_N

This set includes most of the populations of the outgroup set, excluding the Epipaleolithic populations that are most remote from the formation of the Yamnaya (for which the succeeding Neolithic populations, e.g., Levant_PPN instead of Natufians are more realistic sources). Notably the set includes Neolithic populations from across Anatolia, the South Caucasus (defined as Armenia and Azerbaijan), Mesopotamia, and Iran, i.e., different points of the Neolithic continuum, as well as European hunter-gatherers who may have contributed to the Yamnaya either via the local “steppe/northern” component or in mixture with European farmers who had some such ancestry. Also, notably it does not include Chalcolithic/Eneolithic populations as these may have ancestry crossing the steppe-Caucasus boundary prior to the formation of the Yamnaya, such as the Eneolithic populations of Khvalynsk II or the Chalcolithic population at Areni1 in Armenia.(10) We thus want to be able to model here the Yamnaya in terms of northern and southern sources prior to the Eneolithic/Chalcolithic admixture.

Finally, we set the set of Test populations to be:

ARM_Areni1_ChL(10), AZE_ChL(14), RUS_Eneol_Mountains(17), RUS_Eneol_Piedmont(17), RUS_Khvalynsk_Eneol(9), RUS_MaykopCluster(17), RUS_YamnayaCluster(4, 9, 17, 34), RUS_Steppe_Maykop(17), RUS_Steppe_Maykop_outlier(17)

This set includes both the Yamnaya cluster (39 individuals belonging to the Yamnaya themselves, and the aforementioned similar Afanasievo, Poltavka, and Catacomb cultures) as well as Eneolithic/Chalcolithic individuals from the European part of present-day Russia and the South Caucasus.

We try to fit models for each Test population as a mixture of $K=1, 2$ from the sources. In Table S 22 and Table S 23 that follow we list feasible models (mixture proportions within $[0, 1]$ interval and p -value for rank $K-1 \geq 0.01$)

K=1

The Chalcolithic of Azerbaijan in the South Caucasus can fit as a simple clade with the preceding Neolithic populations of the South Caucasus and north Mesopotamia, including the local Neolithic population. The Maykop cluster population can also fit as a clade with the Neolithic of Aknashen in the South Caucasus ($p=0.107$). All remaining Test populations cannot ($p < 1e-4$) fit as simple clades with any of the sources.

K=2

The Chalcolithic population of Areni1 can fit as a mixture of the local Neolithic population and EHG ancestry ($7.5 \pm 1.3\%$), demonstrating that there gene flow from the north to parts of the South Caucasus >1,000 years prior to the formation and expansion of the Yamnaya culture. We note, parenthetically, that the Chalcolithic of neighboring Azerbaijan that fit as a clade with its Neolithic can be modeled as 99.9% AZE_N and $0.05 \pm 2.1\%$ EHG ancestry, so this gene flow can be documented only for the western part of the South Caucasus during the Chalcolithic.

An individual from the Eneolithic of the North Caucasus Mountains (Unakozovskaya)(17) from ~4500BCE can be modeled as deriving its ancestry from the South Caucasus Neolithic with additional CHG-related ancestry ($16.8 \pm 6.5\%$). Thus, there was no simple pattern of ancestry in the Caucasus during the Chalcolithic/Eneolithic period: while EHG ancestry had penetrated to parts of the South Caucasus, individuals in the North Caucasus (geographically closer to the steppe) existed without any or little EHG ancestry.

Finally, 3 Eneolithic individuals from Khvalynsk II in the Samara region of Russia(9) dated to 5000-4500BCE, a territory in which Yamnaya culture would later appear can be modeled on average as having mostly EHG ancestry, but also $21.5 \pm 1.7\%$ CHG ancestry. These individuals postdate an EHG hunter-gatherer from Samara (Lebyazhinka IV)(8) by a thousand years. When we model this hunter-gatherer as a mixture of CHG and the two remaining EHG hunter-gatherers from Karelia(8), the resulting model fits ($p=0.08$) and assigns a non-significant $3.7 \pm 2.4\%$ proportion of CHG ancestry.

The Maykop cluster (which fit a K=1 model with Aknashen Neolithic as a source) also fits 2-way models, all of which involve >90% Aknashen Neolithic ancestry, suggesting that as a first approximation this Bronze Age group of the North Caucasus was highly similar to the population south of the Caucasus from which it may have been ultimately derived. However, it also had some additional ancestry, estimated at $4.3 \pm 1.2\%$ when using EHG as the 2nd source ($p=0.84$).

A plain reading of these results is that there was gene flow into the Eneolithic steppe from a population that had CHG-related ancestry, presumably from the south, although the precise boundary or gradient between CHG/EHG ancestries remains to be determined. Conversely, there was gene flow into the South Caucasus from the north, but not in a generalized manner, as EHG ancestry is lacking in both Unakozovskaya and the Chalcolithic of Azerbaijan. Finally, the Chalcolithic/Eneolithic populations of the Caucasus traced their ancestry to a mixture of CHG ancestry (the most ancient component in the region), and the Neolithic of the Caucasus (dated to the early 6th millennium BCE); there is no evidence that this Neolithic penetrated north as far as Khvalynsk, as we have seen that this population could be modeled without it.

K=3

Only two additional populations can be modeled as a 3-way mixture and that is the Yamnaya cluster, which can be modeled as a mixture of CHG, EHG, and ARM_Aknashen_N ancestry ($p=0.05$), and the Steppe Maykop outlier individuals that can also fit this model as well as some others that all involve CHG or Ganj Dareh, EHG, and Caucasus/Mesopotamia Neolithic sources. In Table S 24 we show fits of the model that fits Yamnaya for all Test populations. The Steppe Maykop outliers are the only other population with a significant ($58.7 \pm 7.5\%$) South Caucasus Neolithic input, showing that this element had already spread into the steppe by their mid-4th millennium BCE timeframe. The populations that fit with fewer sources continue to fit with K=3 sources with the additional source being consistent with zero.

Neither the Steppe Maykop nor the Eneolithic of the piedmont of the North Caucasus (Progress-2) fit the 3-way model. An examination of the outlier f_4 -statistics of the model (“dscore” lines of qpAdm output) indicates that the model underestimates shared genetic drift with both the Levantine PPN ($Z=-5.6$) and the Siberian Upper Paleolithic represented by AfontovaGora3 in the outgroup set ($Z=-3.4$) for the Steppe Maykop population; the same is also true for the Piedmont Eneolithic ($Z=-3.8$ for AfontovaGora3). This suggests the presence of “Siberian” ancestry in the Eneolithic steppe, as previously observed.(17)

K=4

We were curious about the rather low p-value (0.05) for the fit of the Yamnaya cluster itself; this is driven by two outgroups (Ganj Dareh: -2.96 and AZE_N: -2.04). (Note that neither AfontovaGora3-related ($Z=-0.51$) nor Levantine PPN-related ($Z=-1.58$) is significantly underestimated by the 3-way model, and thus the low p-value in Yamnaya is of a different etiology than the rejection of the 3-way model for the Steppe Maykop and Piedmont Eneolithic discussed above). Thus, we also fit 4-way models for this population (Table S 25).

The CHG/EHG combination is invariant in the fitting models, with the EHG proportion in the ~40-50% range in all of them. We note parenthetically that the model of (17) that includes CHG/EHG/WHG/Anatolian Neolithic ancestry fails in our framework ($p<1e-10$), and inspection of outlier f_4 -statistics indicates that it underestimates ($Z<-3$) shared drift with Levant_PPN ($Z=-5.6$), Natufians, Azerbaijan Neolithic, and Ganj Dareh outgroups. We note that Levant_PPN was not used in the set of outgroups of (17) which might be one reason why a successful fit was possible.

A non-significant amount of WHG ancestry ($0.3\pm 1.5\%$) appears in one of the models, which also has a low p-value ($p=0.019$), so there is no clear indication of presence of such ancestry in the Yamnaya cluster; the similar SRB_Iron_Gates_HG ancestry ($0\pm 1.3\%$) is also associated with a small p-value ($p=0.028$). Another model has ancestry from both ARM_Aknashen_N and ARM_Masis_Blur_N, however the proportions of ancestry from each source are poorly estimated (high standard errors $>100\%$) suggesting that the outgroup set is not sufficient to differentiate between these two Neolithic populations of the South Caucasus.

We thus concentrate on the remaining 3 models which have the shared property of being formed by each of the South Caucasus Neolithic sources (Aknashen, Masis Blur, Azerbaijan) and Ganj Dareh, all of which have p-values $\gg 0.01$ and low standard errors. The proportion of the South Caucasus Neolithic source is always significantly higher than zero, while the one from Ganj Dareh is positive but no more than 2 standard errors greater than zero.

The (at least) tripartite origin of the Yamnaya cluster

The results of this section do not fully resolve the origins of the Yamnaya cluster but point to an important new result, the presence of ~35-50% ancestry from the Neolithic of the South Caucasus-Zagros area of the Southern Arc.

As we have seen in our analysis of the Neolithic continuum, the Neolithic populations of the South Caucasus could be modeled as having ancestry from deep (pre-Neolithic) sources of the Near East: CHG, Natufians, and Pınarbaşı. In this section we saw that the Eneolithic population at Khvalynsk II could be modeled as an EHG/CHG mix.

Without precise knowledge of the northern source it is uncertain how much CHG ancestry existed in the Eneolithic northern source that contributed to the Yamnaya.

To see whether the CHG/EHG mix of the Yamnaya could be wholly accounted for by the sampled Eneolithic steppe population, we fit 2 and 3-way models using RUS_Khvalynsk_Eneol as one of the sources (with the remaining ones free to be any of the already considered Sources). 2-way models are rejected ($p < 1e-11$) and none of the 3-way models have feasible ancestry proportions.

As we remarked above, fixing the “southern” population (e.g., ARM_Aknashen_N of Table S 24) has implications about the identity of the “northern” one ($\frac{0.181}{0.181+0.419} = 32\%$ CHG and thus 68% EHG in ancestry). We estimate that in the Khvalynsk Eneolithic the proportion of CHG is 23% (Table S 24), and so the population has less CHG than required: when we examine the outlier f_4 -statistics of the Khvalynsk+Aknashen fit for Yamnaya, we find that indeed the model underestimates ($Z = -3.2$) shared genetic drift with the CHG, consistent with this population having “too little” CHG to be a matched northern source for the southern source of Aknashen.

The Khvalynsk Eneolithic population is visibly heterogeneous in PCA(9), so we applied the CHG/EHG model that fits the population as a whole (Table S 23; $p = 0.099$) to its individuals (Table S 26). Two of these individuals (I0122 and I0433) fit the model comfortably ($p > 0.4$ and standard error $\sim 2\%$), while I0434 does not ($p = 0.001$ and standard error $\sim 4\%$; the model underestimates shared drift with AfontovaGora3, $Z = -2.5$, suggesting that it may have Siberian ancestry as in the Progress-2 individuals). The CHG ancestry in the two well-fitting individuals is 17~24%, lower than the estimated 32% for the “northern” population.

Proximal Eneolithic/Chalcolithic sources

The modeling above has shown that the Yamnaya cluster can be derived from 3 sources: a “northern” mixture of CHG and EHG (which was present in the steppe, but not in the needed proportion in sampled individuals) and a “southern” population, most similar to the Neolithic of the Caucasus. We also tried a set of Chalcolithic/Eneolithic sources to see if a more proximate origin for them could be inferred. We use the following set (which also includes CHG/EHG to ensure that the northern ancestry can be modeled in the absence of a suitable northern source):

ARM_Areni1_ChL, AZE_ChL, IRN_HajjiFiruz_ChL ((34) and this study),
 IRN_Seh_Gabi_ChL(10), IRN_TepeHissar_ChL ((34) and this study),
 RUS_Eneol_Mountains(17), RUS_Eneol_Piedmont(17), RUS_Khvalynsk_Eneol(9),
 TUR_BlackSea_İkiztepe_ChL(14), TUR_C_Büyükkaya_ChL(14),
 TUR_C_ÇamlıbelTarlasi_ChL(14), TUR_E_Arslantepe_ChL(14),
 TUR_Hatay_TellKurdu_ChL(14), TUR_Marmara_Barcın_ChL(10),
 TUR_Marmara_Ilıpınar_ChL (this study), TUR_SE_Batman_ChL (this study),
 TUR_SE_Kilis_ChL (this study), TUR_SE_Şırnak_ChL_A (this study),
 TUR_SE_Şırnak_ChL_B (this study), TUR_SE_Şırnak_ChL_C (this study), CHG, EHG

At $K=2$ no models are feasible; the model RUS_Eneol_Mountains+EHG fails with $p=0.006$. Successful models with $K=3$ include either the Piedmont or Mountains Eneolithic population from the North Caucasus, extra EHG ancestry, and a population of the Southern Arc and are shown in Table S 27.

In Table S 28 we further evaluate the successful models of Table S 27 by adding all their sources into the set of outgroups. Many of the models are strongly rejected when using this set that includes these additional Chalcolithic/Eneolithic outgroups, but four remain all of which

include EHG ancestry, ancestry from the Piedmont Eneolithic at Progress-2, and a Southern Arc source that ranges geographically from the Mountains Eneolithic of the North Caucasus, SE Anatolia, and the Chalcolithic of Azerbaijan (Alkhantepe).

We combined the four sources (other than EHG and Piedmont Eneolithic) in a composite “SouthernArc” population to increase power and fit the 3-way model ($p=0.06$) with estimated $25.9\pm 2.6\%$ EHG, $49.9\pm 4.9\%$ Piedmont Eneolithic, $24.2\pm 2.6\%$ SouthernArc ancestry.

The inclusion of the Piedmont Eneolithic as a source is surprising given its Siberian ancestry. (17) Examining the models of Table S 28 we observe that the five models that do *not* include it as a source all fail ($p<1e-3$) as they underestimate shared drift with this population (Z between -2.98 and -7.3). Thus, at least some component of the Piedmont Eneolithic shares genetic drift with the Yamnaya cluster. Conversely, when we examine the qpAdm output, for the successful 3-way model (EHG+Piedmont Eneolithic+Southern Arc), we see that it overestimates the shared genetic drift with AfontovaGora3 ($Z=3.2$).

These two observations point to the Piedmont Eneolithic having recent common ancestry with the real northern source which differs from it in two respects: first, it has more EHG ancestry, and second, it has less (or no) Siberian ancestry. Moving AfontovaGora3 from the outgroup set to the set of sources results in a very good fit ($p=0.83$) with an estimated $26.4\pm 2.3\%$ EHG, $51.6\pm 7.3\%$ Piedmont Eneolithic, $21.5\pm 2.5\%$ SouthernArc, and $0.4\pm 5.7\%$ AfontovaGora3 ancestry.

We tested this model further by adding (one at a time) 3 additional outgroups. We list the p -value of this model and the Z -score of the fit for each of the added outgroups. First, we added Globular Amphora from Poland(444), a population suggested to have contributed to the Yamnaya(17) ($p=0.42$; $Z=-1.3$). Second, we added a composite population consisting of Neolithic/Chalcolithic individuals from Southeastern Europe ($p=0.66$; $Z=-0.29$).

Finally, we added the Khvalynsk Eneolithic population ($p=0.13$; $Z=2.33$) which is the only one suggestive of not being a true outgroup, but in the direction of *over*-estimating shared drift in our model; thus it is not suggested that this population contributed to the formation of the Yamnaya. In the fitted model, the amount of Piedmont Eneolithic ancestry increases to $63.8\pm 10.6\%$ with a corresponding decrease of the AfontovaGora3 contribution to $-14.2\pm 8.0\%$.

Conclusion

To summarize our results in this section, when we consider Neolithic sources, we can model the ancestry of the Yamnaya cluster as a mixture of a southern source from the South Caucasus and a CHG/EHG-admixed source which does not correspond to any of the sampled Eneolithic populations of the steppe either because they might not have the right balance of CHG and EHG ancestry -which presumably existed in other proportions than those in sampled individuals- or because they have extra Siberian affinity.

The populations of the South Caucasus can be modeled as having both Anatolian and Levantine-related ancestry using the analysis of the Neolithic continuum (11) and in terms of the 5-source model (Supplementary Text S3, Fig. S 3, Fig. 5) and could thus be useful candidates for contributing this type of ancestry to the Yamnaya along the Caucasus genetic bridge (Fig. 3; Fig. S 3). Our modeling suggests that the contribution of the southern population to the ancestry of the Yamnaya was substantial. When we consider more proximal Chalcolithic/Eneolithic sources, the Yamnaya cluster can be modeled with a Southern Arc source that is not geographically well-localized but includes the Caucasus and SE Anatolia and northern ancestry related to the

Eneolithic of the North Caucasus Piedmont but not corresponding to it exactly (having more EHG ancestry than it and no Siberian affinity).

The results of this section move the question of the formation of the Yamnaya cluster (and the related question of Proto-Indo-European and Proto-Indo-Anatolian origins) forward: as they show that there were at least two opportunities for south-to-north gene flow to affect steppe populations: first, the spread of CHG ancestry into the Eneolithic steppe, evidenced in sampled Eneolithic populations which differ from the preceding EHG hunter-gatherers in this respect; second, the spread of ancestry into the ancestors of the Yamnaya themselves, that can be modeled at increasing time depths as: Caucasus/SE Anatolian Chalcolithic, South Caucasus Neolithic, or a mix of Anatolian/Levantine Neolithic ancestry. These two events could be potentially linked to the transfer of language northward along the Caucasus bridge. A mainland European connection is less likely, due to (a) the absence of WHG ancestry in the Yamnaya, the component most diagnostic of mainland Europe, and of any connection with the subsequent Neolithic populations of South-eastern or Eastern Europe, (b) the likely West Asian source of both CHG and South Caucasus Neolithic elements which tethers Yamnaya origins to the east, (c) the implication of Progress-2 in the formation of the Yamnaya and of the outliers of the Steppe Maykop in the earliest appearance of the South Caucasus Neolithic-related ancestry, both of which are immediately north of the Greater Caucasus and which also tether Yamnaya origins to the east rather than the west (the area of the steppe adjacent to mainland Europe).

Open questions that remain include:

- Which was the proximal “northern” Eneolithic source for the Yamnaya with the appropriate CHG/EHG ancestry balance?
- Which was the proximal “southern” Chalcolithic source for the Yamnaya?
- Where did the admixture take place?
- Where did the population ancestral to the Yamnaya, following the admixture, but prior to the set of cultural innovations that launched their successful expansion live?

Some of these questions can only be answered by sampling populations of the north, but as we have shown in this section, “north” and “south” cannot be studied in isolation: the full solution to the story of the formation Yamnaya and, quite possibly, the first chapter in the history of the genetic formation of Indo-European speaking populations, will be written considering both the Southern Arc and its complementary northern counterpart together.

Test	P-value	Source
AZE_ChL	0.983	ARM_Aknashen_N
AZE_ChL	0.032	ARM_Masis_Blur_N
AZE_ChL	0.878	AZE_N
AZE_ChL	0.335	Mesopotamia
RUS_MaykopCluster	0.107	ARM_Aknashen_N

Table S 22 Test populations that fit as simple clades of Source populations

Test	P-value	A	B	Mixture proportions		Standard errors	
				A	B	A	B
ARM_Areni1_ChL	0.244	EHG	ARM_Aknashen_N	0.075	0.925	0.013	0.013
ARM_Areni1_ChL	0.017	EHG	ARM_Masis_Blur_N	0.087	0.913	0.013	0.013
RUS_Eneol_Mountains	0.574	CHG	ARM_Aknashen_N	0.168	0.832	0.065	0.065
RUS_Eneol_Mountains	0.219	CHG	ARM_Masis_Blur_N	0.385	0.615	0.049	0.049
RUS_Khvalynsk_Eneol	0.099	CHG	EHG	0.215	0.785	0.017	0.017
RUS_Khvalynsk_Eneol	0.059	EHG	IRN_Ganj_Dareh_N	0.814	0.186	0.016	0.016

Table S 23 Test populations that fit as 2-way mixtures. For brevity we do not show 2-way models for populations that fit as simple clades in Table S 22

Test	P-value	Mixture proportions			Standard errors		
		CHG	EHG	ARM_Aknashen_N	CHG	EHG	ARM_Aknashen_N
ARM_Areni1_ChL	0.795	-0.126	0.088	1.038	0.048	0.015	0.045
AZE_ChL	0.993	-0.084	0.015	1.069	0.063	0.019	0.055
RUS_Eneol_Mountains	0.881	0.104	0.038	0.858	0.068	0.017	0.063
RUS_Eneol_Piedmont	2.96E-05	0.480	0.438	0.082	0.133	0.023	0.148
RUS_Khvalynsk_Eneol	0.046	0.229	0.790	-0.019	0.085	0.036	0.114
RUS_YamnayaCluster	0.050	0.181	0.419	0.399	0.034	0.011	0.038
RUS_Steppe_Maykop	2.34E-16	1.565	0.683	-1.248	0.324	0.054	0.363
RUS_Steppe_Maykop_outlier	0.028	0.231	0.182	0.587	0.071	0.016	0.075

Table S 24 A 3-way model that fits the Yamnaya cluster applied to all test populations.

P-value	A	B	C	D	Mixture proportions				Standard errors			
					A	B	C	D	A	B	C	D
0.019	CHG	EHG	WHG	ARM_Aknashen_N	0.188	0.415	0.003	0.394	0.040	0.024	0.015	0.041
0.944	CHG	EHG	ARM_Aknashen_N	ARM_Masis_Blur_N	0.259	0.427	0.081	0.233	0.477	0.053	2.202	1.704
0.445	CHG	EHG	ARM_Aknashen_N	IRN_Ganj_Dareh_N	0.060	0.424	0.462	0.054	0.077	0.011	0.043	0.055
0.028	CHG	EHG	ARM_Aknashen_N	SRB_Iron_Gates_HG	0.192	0.410	0.398	0.000	0.038	0.023	0.039	0.013
0.230	CHG	EHG	ARM_Masis_Blur_N	IRN_Ganj_Dareh_N	0.126	0.435	0.361	0.079	0.073	0.011	0.030	0.055
0.122	CHG	EHG	AZE_N	IRN_Ganj_Dareh_N	0.142	0.514	0.286	0.058	0.076	0.012	0.024	0.062

Table S 25 4-way models for the Yamnaya. Well-fitting models are highlighted in bold.

Test	P-value	Mixture proportions		Standard errors	
		CHG	EHG	CHG	EHG
I0122	0.429	0.236	0.764	0.021	0.021
I0433	0.643	0.166	0.834	0.023	0.023
I0434	0.001	0.435	0.565	0.040	0.040

Table S 26 By-individual modeling of Khvalynsk II.

P-value	A	B	C	Mixture proportions			Standard errors		
				A	B	C	A	B	C
0.017	RUS Eneol Mountains	TUR SE Şırnak ChL A	EHG	0.450	0.082	0.468	0.037	0.033	0.011
0.101	RUS Eneol Mountains	CHG	EHG	0.425	0.122	0.453	0.044	0.043	0.011
0.051	RUS Eneol Piedmont	TUR BlackSea İkiztepe ChL	EHG	0.656	0.161	0.182	0.036	0.018	0.022
0.017	RUS Eneol Piedmont	TUR C Büyükkaya ChL	EHG	0.705	0.134	0.161	0.035	0.017	0.023
0.018	RUS Eneol Piedmont	TUR Hatay TellKurdu ChL	EHG	0.748	0.107	0.146	0.031	0.013	0.022
0.077	RUS Eneol Piedmont	TUR SE Batman ChL	EHG	0.590	0.205	0.205	0.041	0.022	0.023
0.038	RUS Eneol Piedmont	TUR SE Şırnak ChL B	EHG	0.630	0.202	0.168	0.040	0.023	0.022
0.013	RUS Eneol Piedmont	TUR SE Şırnak ChL C	EHG	0.605	0.205	0.190	0.045	0.025	0.024
0.013	TUR SE Batman ChL	TUR SE Şırnak ChL B	EHG	0.508	0.029	0.463	7.197	8.134	0.946
0.126	AZE ChL	RUS Eneol Piedmont	EHG	0.247	0.534	0.219	0.027	0.046	0.023
0.063	IRN Seh Gabi ChL	RUS Eneol Mountains	EHG	0.136	0.385	0.479	0.037	0.042	0.011
0.062	IRN Seh Gabi ChL	CHG	EHG	0.421	0.044	0.535	0.039	0.046	0.011
0.330	IRN TepeHissar ChL	RUS Eneol Mountains	EHG	0.127	0.402	0.471	0.026	0.029	0.011
0.017	RUS Eneol Mountains	RUS Eneol Piedmont	EHG	0.407	0.228	0.364	0.065	0.115	0.052

Table S 27 Modeling of Yamnaya cluster with Chalcolithic/Eneolithic sources

P-value	A	B	C	Mixture proportions			Standard errors		
				A	B	C	A	B	C
6.34E-05	RUS Eneol Mountains	TUR SE Şırnak ChL A	EHG	0.528	0.001	0.471	0.047	0.040	0.013
9.59E-04	RUS Eneol Mountains	CHG	EHG	0.427	0.111	0.462	0.051	0.050	0.011
2.54E-03	RUS Eneol Piedmont	TUR BlackSea İkiztepe ChL	EHG	0.651	0.162	0.187	0.035	0.017	0.022
4.45E-03	RUS Eneol Piedmont	TUR C Büyükkaya ChL	EHG	0.689	0.143	0.168	0.032	0.015	0.021
1.31E-03	RUS Eneol Piedmont	TUR Hatay TellKurdu ChL	EHG	0.736	0.111	0.153	0.030	0.013	0.022
5.19E-02	RUS Eneol Piedmont	TUR SE Batman ChL	EHG	0.572	0.213	0.215	0.038	0.021	0.021
1.91E-02	RUS Eneol Piedmont	TUR SE Şırnak ChL B	EHG	0.591	0.224	0.185	0.036	0.021	0.020
2.48E-03	RUS Eneol Piedmont	TUR SE Şırnak ChL C	EHG	0.566	0.227	0.207	0.044	0.025	0.023
5.38E-03	TUR SE Batman ChL	TUR SE Şırnak ChL B	EHG	10.413	-11.425	2.011	16.544	19.063	2.528
1.37E-01	AZE ChL	RUS Eneol Piedmont	EHG	0.259	0.510	0.231	0.024	0.041	0.021
2.36E-05	IRN Seh Gabi ChL	RUS Eneol Mountains	EHG	0.024	0.502	0.475	0.049	0.059	0.015
6.88E-13	IRN Seh Gabi ChL	CHG	EHG	0.312	0.154	0.534	0.031	0.036	0.010
6.91E-04	IRN TepeHissar ChL	RUS Eneol Mountains	EHG	0.103	0.413	0.484	0.028	0.033	0.011
5.92E-02	RUS Eneol Mountains	RUS Eneol Piedmont	EHG	0.412	0.222	0.366	0.060	0.104	0.046

Table S 28 Modeling of Yamnaya cluster with Chalcolithic/Eneolithic sources [adding sources of Table S 27 as outgroups]. Four models, involving EHG, RUS_Eneol_Piedmont, and a SouthernArc source remain plausible.

S5: Y-chromosome variation in the Southern Arc

In this section we describe the distribution of Y-chromosome haplogroups in populations of the Southern Arc. For purposes of comparison and to avoid nomenclature differences we also recalled Y-chromosomal haplogroups in West Eurasian samples outside the Southern Arc.

Methodology for Y-haplogroup calling

We used the YFull YTree v. 8.09 phylogeny,⁵ obtaining information about SNPs from ISOGG YBrowse⁶ and lifting coordinates from hg38 to hg19 using liftOver and intersecting with the SNPs present in the v. 8.09 tree.

The 1240K capture enriches for targeted SNPs of which 32,670 are on chrY. However, the sequenced libraries also include sequences covering other (non-targeted SNPs) many of which are also phylogenetically informative. Thus, we pulled down from the same BAMs used to pull down pseudo-haploid random alleles for our main analysis, with the difference that we chose the majority allele for each SNP (since for a haploid locus in a sample with low contamination the most frequently observed allele will most often be the true one).

We describe below our automated procedure for haplogroup calling which aims to be resilient to different sources of error such as: ancient DNA damage that may flip the ancestral/derived state of a SNP; contamination that may introduce the wrong state at a SNP which may propagate to the majority allele for low coverage samples; sequencing errors; possible errors in the phylogeny in which the ancestral/derived polarity of the SNP might be given opposite to its truth; and recurrent mutations.

Ideally, a sample will be derived for SNPs at haplogroups from the Root up to a most-derived node TERMINAL and ancestral for SNPs for all haplogroup descendants of TERMINAL or collateral branches not belonging to the Root->TERMINAL path. Missing data in any of the nodes of the path are possible and consistent with the TERMINAL designation; however, ancestral alleles are not as a sample cannot be derived for a node downstream of one for which is ancestral. However, because of the possible errors enumerated above, it is possible that this may sometimes happen.

Our procedure first lists the possible “Candidate” TERMINAL designations of a sample by enumerating all haplogroups for which it is derived. Each haplogroup is associated with a “Level” (number of steps from the Root) and candidate sets are scrutinized in reverse order of Level. An alternative approach would be to begin at the root and execute a standard search examining branches that are either derived or have missing data. However, the problem with that approach would be that entire subsets of the tree might be excluded if there is an ancestral state at their root due to one of the different problems we enumerated.

We consider a candidate haplogroup secure if it is supported by either 3 different mutations of any kind or 2 mutations that are not C>T or G>A. For candidate haplogroups that are less strongly supported, we examine all their ancestors to the root. During this traversal of the ancestral path we keep track of the following counts:

1. *Support* is the number of upstream nodes of the candidate haplogroup for which the sample is derived. A haplogroup designation with a large number of supporting upstream nodes

⁵ https://github.com/YFullTeam/YTree/blob/master/ytrees/tree_8.09.0.json

⁶ https://ybrowse.org/gbrowse2/gff/snps_hg38.csv; accessed Oct 18, 2020

is more likely to be genuine than a “fluke” haplogroup based on a SNP caused by some form of error and for which no or few upstream nodes show support. We keep track of the haplogroup’s *Support* until we hit an upstream node that is ancestral (or the root), which ends the haplogroup’s support.

2. *Gap* is the number of levels above the candidate haplogroup before we reach an upstream derived haplogroup. For example, if the candidate haplogroup is X and the sample is also derived for the parent of X then the *Gap* would be zero, whereas if the candidate haplogroup is not derived at all for any upstream nodes all the way to the root, then its *Gap* would be equal to the Level of the candidate haplogroup.

3. *Fail* is the number of ancestral nodes of the candidate haplogroup for which the sample has the ancestral state. Intuitively, a sample could be ancestral in some intermediate node between the candidate haplogroup and the root due to a source of error, but if it is so on many such nodes then this reduces our confidence that the sample belongs to that branch at all.

To illustrate these concepts, consider the following path from root to candidate haplogroup

Root-D-D-N-N-A-D-N-D-D-N-N-CANDIDATE

The *Gap* of the sample is 2 (in red), because it has missing data (N) for its two immediate upstream nodes. Its *Support* is 3 (in green), because it is derived for three upstream haplogroups before reaching the first haplogroup for which it is ancestral (in blue). Finally, its *Fail* (in blue) is 1 because there is only one upstream haplogroup for which the sample is ancestral.

We can specify tolerances for these parameters before accepting a candidate haplogroup call. More stringent criteria would result in less derived haplogroup calls, thus missing potentially useful information. In the example above, if we require *Gap*=0 we would reject the Candidate haplogroup and call the sample as the next derived one (underlined). On the other hand, more lax criteria would result in potentially wrong calls if the derived haplogroup mutations are due to an error. This might not only cause us to accept a more derived haplogroup along a given branch but also to call the wrong branch altogether. Below we show our example together with an alternative candidate haplogroup:

Root-D-D-N-N-A-D-N-D-D-N-N-CANDIDATE1

Root-D-D-N-N-A-D-N-D-D-D-CANDIDATE2

In this example, Candidate2 has no gap and greater support (4) than Candidate1, but one lower Level. Depending on how long a gap or how big of a support we require to accept a call we might decide on either designation.

Additional criteria used are to check whether the candidate haplogroup is based on a C>T or G>A SNP (which might be due to ancient DNA damage) and to check whether for the set of SNPs defining them some are ancestral and some derived. If, for example, there are 9 ancestral and 1 derived SNPs for a particular haplogroup, this might mean that the sample is indeed derived for the particular SNP which happened to occur first in the sequence of the 10 SNPs, or, alternatively, that the particular derived SNP is an error.

The procedure described in this section was adopted as a way to automate the manual inspection of haplogroup calls which becomes very difficult for large number of samples and also subjective as there is no clear way to decide between alternatives that differ in some of the metrics we have described. Additional information might be contained in noting the date of the sample and comparing it to the inferred age of a candidate haplogroup: if a haplogroup inferred to have been formed in the last 5,000 years is found in a 15,000 year old context, this might cast

doubt on the accuracy of the call or the dating of the sample. The geographical and population context might also convey information: an outlier sample could be a real genetic outlier (and hence an interesting find), but it could also indicate a haplogroup miscall.

Our automated haplogroup calls use the following threshold parameters: 3 mutations or 2 non-C>T/G>A ones to consider a haplogroup call certain; a *Gap* of at most 10 (lax) or 5 (standard); *Support* of at least 1 (lax) or 2 (standard); *Fail* no more than 2; we reject haplogroup calls that are a mix of ancestral and derived SNPs; we allow C>T or G>A SNPs in the candidate haplogroup. We generally choose the “standard” thresholds for a haplogroup call and only use the “lax” ones if no haplogroup call can be made with the “standard” thresholds.

Our approach in interpreting the Y-chromosome data is twofold: we trust a pattern if it is supported by many samples that consistently belong to a particular clade of the phylogeny. If an interesting pattern is supported by a few individuals we manually examine their haplogroup calls to see if there was an obvious failure of our automated procedure.

We applied our Y-haplogroup caller on 2,274 male samples, including all West Eurasians and all the Southern Arc samples. A haplogroup call was made for 2,227 individuals (Data S5) which were assigned to 704 different terminal haplogroups. Since each terminal haplogroup implies also the haplogroups on its ancestral path, a total of 1,230 haplogroups were observed. Doubtless many of these will be of potential interest, and in order not to overlook some or focus on others based on our prior knowledge we extracted some interesting patterns using a set of automated procedures.

- (A) Much more frequent outside the Southern Arc than in it
- (B) More frequent inside the Southern Arc than outside it
- (C) Much more frequent in the European side of the Southern Arc than the West Asian and vice versa
- (D) High prevalence but having low time depth
- (E) Geographically dispersed but having low time depth

Haplogroup	# in S.A.	# outside S.A.	Freq. in S.A.	Freq. outside S.A.	Freq. Difference	P-value	TMRCA	Low age	High age
R-L21	1	45	0.1%	2.9%	-2.8%	1.94E-06	4200	3700	5300
R-S461	1	47	0.1%	3.1%	-2.9%	6.67E-07	4500	3700	5300
I-Y3721	2	60	0.3%	3.9%	-3.6%	7.11E-08	10100	8900	11200
R-Z2124	2	69	0.3%	4.5%	-4.2%	3.71E-09	4400	4000	4900
I-CTS595	3	52	0.4%	3.4%	-3.0%	8.61E-06	18300	16500	20400
R-Z94	3	80	0.4%	5.2%	-4.8%	1.02E-09	4500	4000	4900
R-Z93	4	97	0.6%	6.3%	-5.7%	3.94E-11	4500	4400	5400
R-Z645	9	154	1.3%	10.0%	-8.7%	5.22E-15	4900	4700	6100
I-P37	11	127	1.6%	8.3%	-6.7%	2.90E-10	18400	19300	22800
R-M198	13	202	1.9%	13.2%	-11.3%	3.54E-18	8600	12500	15700
R-M417	13	190	1.9%	12.4%	-10.5%	9.45E-17	5400	7400	9900
R1a	14	214	2.0%	14.0%	-11.9%	7.06E-19	17300	20500	25100
R-M459	14	211	2.0%	13.8%	-11.7%	1.87E-18	14100	15400	19200
R-P312	14	180	2.0%	11.7%	-9.7%	7.07E-15	4500	4300	5300
R-L151	16	229	2.3%	14.9%	-12.6%	1.72E-19	4800		
R-L52	19	249	2.7%	16.2%	-13.5%	7.27E-20	5700	5100	6400
R-L51	23	263	3.3%	17.1%	-13.8%	3.03E-19	5700	5500	6800
I-L460	48	297	6.9%	19.4%	-12.4%	4.84E-12	21000	19900	23200
I2	79	322	11.4%	21.0%	-9.6%	2.33E-06	21500	25200	29800
I	85	359	12.3%	23.4%	-11.1%	2.33E-07	27500	40300	45700
R1	141	638	20.3%	41.6%	-21.2%	8.93E-13	22800	25900	30500
R-Y482	147	661	21.2%	43.1%	-21.9%	6.33E-13	28200	25900	30500
R	148	662	21.4%	43.2%	-21.8%	7.04E-13	28200		
P-P226	153	692	22.1%	45.1%	-23.0%	1.83E-13			
P-P284	153	692	22.1%	45.1%	-23.0%	1.83E-13			
P-P337	156	697	22.5%	45.4%	-22.9%	3.18E-13	30700	29300	31900
K2b	157	699	22.7%	45.6%	-22.9%	3.48E-13	44300	41400	49600
P1	157	699	22.7%	45.6%	-22.9%	3.48E-13	30700	40900	42000
P	157	699	22.7%	45.6%	-22.9%	3.48E-13	41500	43000	45400
K2	159	712	22.9%	46.4%	-23.5%	1.69E-13	45400	41400	49600
K	201	745	29.0%	48.6%	-19.6%	1.15E-08	45400	44600	49700

Table S 29 Haplogroups frequent outside the Southern Arc present in at least one individual of the Southern Arc. Empty cells indicate no age estimate in YTree 8.09. Times are in years BP. We list haplogroups with P-value<0.00001 (Fisher’s exact test)

Haplogroups more frequent outside the Southern Arc than in it

Table S 29 shows a variety of patterns ranging in time from the first modern human settlers of West Eurasia to the Bronze Age. (All times are taken from the estimates of Yfull.com based on next generation sequencing data(80) and are included in the downloadable version of their tree.) We focus our discussion on the lowest frequency haplogroups in the Southern Arc.

R-L21 (within **R-S461**) is present in a medieval sample from Lebanon (SI-53.SG)(434) but the overwhelming (41/46) instances are from samples from Britain, Ireland, and Iceland, with a presence in Polish Corded Ware, and Czech and British Beaker samples(36, 445-450) It is thus quite likely to be descendant of a medieval Crusader as suggested before, also on the basis of his autosomal ancestry.(434)

Haplogroup **I-Y3721** is found in a hunter-gatherer (I4878) and Middle Bronze Age individual (I5243) from the Iron Gates in Serbia, suggesting continuity within the region over the millennia. It is abundant in Neolithic/Megalithic Ireland(451, 452) and Britain(36) but also found in Sardinia(453) and France.(452) Thus, it may plausibly track the migration of European farmers across the Mediterranean and along the Atlantic coast to the British Isles from an ultimately west Balkan source.

Haplogroup **R-Z2124** is found in a Roman period individual from Samsun (I4531; 227-337 calCE) and a Byzantine individual from Mardin (I4475; 675-774 calCE). It is abundant in Bronze Age steppe samples such as those of the Sintashta culture,(34) with its earliest occurrence at Potapovka(9) (I0432) in the first half of the 3rd millennium BCE, but also more temporally recent steppe “Scytho-Sarmatian” nomads from present-day Russia and Kazakhstan.(429, 431, 454) Thus, the two Anatolian individuals may well be patrilineal descendants of steppe nomads who found themselves in the ancient Kingdom of Pontus and then the eastern Roman Empire.

Haplogroup **I-CTS595** is found in a hunter-gatherer from the Iron Gates in Serbia (I5236) a later Bronze Age individual also from Serbia (I17916) and a Chalcolithic sample from the Bodrogkeresztur culture in Romania (I15621). Its presence in Neolithic Portugal and Spain(9, 30, 36, 449, 455) suggests that it too may have been involved in European farmer migrations westward from the Balkans. On the other hand, it is also present in hunter-gatherers from Latvia,(3) so its presence in European samples need not have been mediated exclusively from a Balkan source, as indeed the high estimated TMRCA (18,300 years BP) would also indicate.

Four samples belonged to haplogroup **R-Z93** (within R1a), a lineage which first achieved prominence on the Eurasian steppe with the Middle to Late Bronze Age Sintashta culture ~2000 BCE and continued to be important for steppe populations in all succeeding periods, including the two aforementioned ones of its subgroup R-Z2124; one of the other two, a Cimmerian sample from Moldova,(429) was derived down to **R-Z94**. An Iron Age sample (I20186; 1100-500 BCE) from Kapitan Andreevo in Bulgaria (Thrace) was assigned to R-Z93, and suggests that the penetration of steppe populations was not limited to the edges of the Southern Arc represented by the Moldovan individual but also expanded further south. This individual was genetically similar to Mycenaeans (6) as were other individuals from Iron Age Thrace, and may thus represent a second link between the steppe and Balkans/Aegean area in addition to an R-PF7562 Y-chromosome in Mycenaean Greece which we will discuss below.

The examples of R-Z93 also should urge caution in interpreting typical “steppe nomad” Y-chromosomes as evidence of historical Scytho-Sarmatian or later influences as in the aforementioned R-Z2124 individuals; while these are plausible, in conjunction with the outlier autosomal genetic profile of the Samsun individual the presence of steppe-related Y-chromosome in Iron Age contexts suggests that these had reached the Southern Arc very soon after the emergence of pastoral nomadism in the Iron Age. We note here that the earliest known R-Z93 is the aforementioned sample from Potapovka. Another sample from Eneolithic Ukraine (I6561; 4045-3974 calBCE)(3) is likely misdated given that (a) its age predates that of 5,400 years BP upper end of the formation of R-Z93, (b) autosomally it is similar to Corded Ware

individuals of the 3rd millennium BCE, and (c) has an ADMIXTURE LD signal of admixture using the software DATES(34) (<https://github.com/priyamoorejani/DATES>) similar to that of Corded Ware individuals.

The parent node of R-Z93 is **R-Z645** which includes the 4 R-Z93 samples as well as 5 more, including a Late Bronze Age sample from Sabatinovka in Moldova (I10438; 1700-1300BCE) and one from Merichleri in Bulgaria (I2163; 1866-1615 calBCE)(3), but also an ancient sample from Armenia (I17308; 394-208 calBCE). The earliest occurrence of this clade is in a Corded Ware sample from Germany (RISE434.SG; 2880-2629 calBCE)(4). We are agnostic whether this clade originated in the steppe and spread into central Europe with the steppe ancestry present in the Corded Ware, or derived from another source. But, it is clear that it became prominent in steppe populations in the Middle-to-Late Bronze Age (as in Sintashta) from which the LBA samples from southeastern Europe could be derived, although obviously the sample from Germany as well as 16 Bronze Age samples belonging to this clade from Estonia(456, 457) would make a northern European origin (without a steppe intermediary) possible as well.

The parent node of R-Z645 is **R-M417** (within R1a) which includes the 9 R-Z645 samples as well as 4 more. These include a Canaanite outlier (I2189) from Israel(432) and undated samples from Moldova and Romania of possible Eneolithic to Bronze Age date.

We also briefly comment on **R-Z282** (within R1a) which also differs significantly in frequency ($p=0.003$) between Southern Arc and outside populations and which occurs in only 3 individuals (a recent one (I15706; possibly Ottoman descendant;(6) from Albania, and Bronze Age ones from Bulgaria I2163(3) and from Trestiana in Romania: I6185 (1873-1630 calBCE). The earliest detected examples of this clade occurred in Corded Ware/Battle Axe related individuals from the Baltics and Scandinavia.(456, 458, 459) R-Z282 and its subclades occur at high frequencies in present-day Eastern Europe with lower but >10% frequencies in present-day Southeastern Europe, dominated by the M558 subclade.(460) M558 belongs within **R-CTS1211** in the YFull phylogeny within which is included the recent sample from Albania and the Bronze Age one from Romania. On the whole these results show that the dominant lineages within R-M417 in present-day populations of southeastern Europe may have become prevalent more recently than the period covered by our sampling, although they were already present, at least at the edges of the Southern Arc by the Bronze Age.

The next set of Y-chromosomes of Neolithic-to-Bronze Age coalescence all belong to haplogroup **R-L51** (within R-M269) and its descendants, a lineage with a very European-centric distribution (263 non-Southern Arc samples are all from Europe) and an estimated Eneolithic-era origin (5500-6800 BP). The two earliest examples of this important European clade we were able to detect were in Late Neolithic Switzerland (Aes25; 2864-2501 calBCE)(461) in an outlier individual with high-steppe ancestry in an otherwise Megalithic context and possibly in a Yamnaya individual (RISE550.SG(4) from Peshany V in Kalmykia), but on the basis of only a single read from a G>A SNP (PF6535(5465148G>A:A)).

A total of 23 individuals from the Southern Arc belong to the predominantly European clade, and most of these are also from Europe except for 5 medieval samples from Lebanon(434), two Byzantine-or-later samples from Balıkesir and Stratonikeia and a Byzantine pair of brothers from the same region (I20140 and I20141; 1031-1158 calCE). The samples from Turkey are from the regions of Marmara and Aegean, which are proximate to Europe.

A total of 8 individuals are from Bezdanjača in Croatia (Bronze Age; 2000-800BCE) and 1 from Cetina (I18752; 2000-1600 BCE), one from the Iron Age (Sv Kriz; individual I5725; 752-

417 calBCE), a Bronze Age (Ostojicevo; I16813; 2131-1942 calBCE) and an Iron Age (Ostojicevo; I16814; 1011-901 calBCE) sample from Serbia, and an Iron Age sample from Çinamak in Albania (I14688; 600-400BCE). The distribution of the samples thus strongly favors the West Balkans, except for one sample from Tell Ezero in Bulgaria (I19458; 2466-2297 calBCE).

Examination of the downstream information of the R-L51 individuals shows that most of the Southern Arc ones can be assigned to the more derived haplogroups along the path R-L51, R-L52, R-L151, **R-P312**. The latter (also known as **S116**) is a prominent clade in present-day Western Europeans,⁽⁴⁶²⁾ but all 8 Bezdanjača samples from Croatia also belong to it, and hence its presence in the Balkans need not have come about in a more recent timeframe than the Bronze Age.

Haplogroup **R-U106** (within R-M269) is another important European clade within R-L51 that has a complementary distribution to R-P312 favoring central-northern Europe.⁽⁴⁶³⁾ It is also significantly ($p=0.004$) less frequent in the Southern Arc than outside it, and we observe it once in medieval Lebanon⁽⁴³⁴⁾ and once in a post-Medieval sample from Balıkesir in the Marmara region (I14823; 1515-1652 calCE). Thus, it appears like a better candidate for a lineage that may have entered the Southern Arc in historical times.

Haplogroup	# in S.A.	# outside S.A.	Freq. in S.A.	Freq. outside S.A.	Freq. Difference	P-value	TMRCA	Low age	High age
R-A12332	10	0	1.4%	0.0%	1.4%	8.99E-06	4000	3700	5000
J-Y2919	16	1	2.3%	0.1%	2.2%	1.05E-07	4200	3900	4900
J-CTS1026	17	4	2.5%	0.3%	2.2%	4.06E-06	17200	16100	20000
J-Z1828	17	4	2.5%	0.3%	2.2%	4.06E-06	8100	15400	19000
J-Z1884	18	2	2.6%	0.1%	2.5%	8.24E-08	4400	4900	6200
J-Z2507	18	3	2.6%	0.2%	2.4%	4.04E-07	4400	3800	5000
T-L162	18	4	2.6%	0.3%	2.3%	1.56E-06	12100	14600	17200
I-Y16649	19	0	2.7%	0.0%	2.7%	2.81E-10	16400	13700	19200
J-Z585	20	3	2.9%	0.2%	2.7%	5.36E-08	4900	4300	6200
J-Z597	20	3	2.9%	0.2%	2.7%	5.36E-08	4400	4200	5700
J-Z615	20	3	2.9%	0.2%	2.7%	5.36E-08	4900	4200	5700
R-Y19434	20	0	2.9%	0.0%	2.9%	8.91E-11	4300	4100	4900
J-Z600	21	6	3.0%	0.4%	2.6%	9.65E-07	5200	4300	6200
J-YSC0000234	22	3	3.2%	0.2%	3.0%	6.97E-09	5500	4600	6700
J-Z2313	22	3	3.2%	0.2%	3.0%	6.97E-09	5700	4600	6700
J-Z622	23	8	3.3%	0.5%	2.8%	1.24E-06	5200	4700	6700
J-L283	25	9	3.6%	0.6%	3.0%	5.73E-07	5700	8400	10600
J-Z2317	27	3	3.9%	0.2%	3.7%	3.99E-11	5700	4600	6700
I-L596	28	11	4.0%	0.7%	3.3%	2.79E-07	16400	19900	23200
R-FGC14590	28	0	4.0%	0.0%	4.0%	9.47E-15	4500	4400	5600
T-M70	29	12	4.2%	0.8%	3.4%	4.15E-07	15900	16500	20300
J-Z1825	30	16	4.3%	1.0%	3.3%	3.08E-06	13500	13800	17200
J-Z2324	30	3	4.3%	0.2%	4.1%	1.74E-12	5700	4600	6700
R-L584	30	0	4.3%	0.0%	4.3%	9.71E-16	4900	4500	5800
T-L206	30	14	4.3%	0.9%	3.4%	6.78E-07	18400	23800	28600
T	31	14	4.5%	0.9%	3.6%	3.19E-07	26100	39700	45500
J-Z2331	35	6	5.1%	0.4%	4.7%	1.58E-12	5700	5600	7400
J-PF5119	36	19	5.2%	1.2%	4.0%	4.28E-07	13900	14100	16800
J-Z534	37	22	5.3%	1.4%	3.9%	1.24E-06	15500	13800	17200
R-Y13369	37	0	5.3%	0.0%	5.3%	3.45E-19	5100	4900	5900
J-PF5116	38	19	5.5%	1.2%	4.2%	6.31E-08	15400	14400	16800
J-Z1853	38	6	5.5%	0.4%	5.1%	8.18E-14	6500	6200	8500
J-CTS9721	42	7	6.1%	0.5%	5.6%	7.34E-15	8300	8000	10300
J-M102	42	23	6.1%	1.5%	4.6%	5.15E-08	15500	24700	29000
J-Z1865	42	6	6.1%	0.4%	5.7%	1.53E-15	7300	6700	8900
J-Z643	42	6	6.1%	0.4%	5.7%	1.53E-15	7800	7200	9500
J-P58	44	7	6.3%	0.5%	5.9%	1.03E-15	9100	10000	12700
J-L136	45	8	6.5%	0.5%	6.0%	1.74E-15	11300	12300	15200
J-PF4816	46	13	6.6%	0.8%	5.8%	3.84E-13	13700	13200	16200
J-L620	47	15	6.8%	1.0%	5.8%	1.33E-12	14700	16100	20000
R-M12149	56	35	8.1%	2.3%	5.8%	6.90E-09	5400	4900	6000
R-Z2103	58	41	8.4%	2.7%	5.7%	6.13E-08	5400	5500	6800
J-PF5087	60	40	8.7%	2.6%	6.1%	9.41E-09	15600	14700	17100
J-Z2215	64	19	9.2%	1.2%	8.0%	3.91E-17	18000	16400	20300
J-Z2217	64	19	9.2%	1.2%	8.0%	3.91E-17	18000	16100	20000
J-L26	68	45	9.8%	2.9%	6.9%	7.85E-10	15900	16400	19000
J1	69	28	10.0%	1.8%	8.1%	3.52E-15	18300	29200	34000
J-PF4610	69	48	10.0%	3.1%	6.8%	1.76E-09	17700	17500	20400
J-M410	79	55	11.4%	3.6%	7.8%	1.43E-10	18900	24700	29000
J2	123	79	17.7%	5.1%	12.6%	1.69E-16	26800	29200	34000
J	201	110	29.0%	7.2%	21.8%	2.32E-29	31600	40300	45700

Table S 30 Haplogroups frequent inside the Southern Arc and infrequent outside it. Times are in years BP. We list haplogroups with P-value<0.00001 (Fisher's exact test) for a frequency difference between the two regions.

Haplogroups more frequent inside the Southern Arc than outside it

Looking at haplogroups common in the Southern Arc and infrequent outside it, we observe (Table S 30) that a total of 10 samples of haplogroup **R-A12332** (within R-M269) were all found in Armenia and in Bronze Age to Iron Age contexts at 8 different sites. Thus, this lineage was likely an important one in the formation of the distinctive Bronze-to-Iron Age population of the South Caucasus revealed by our analysis of autosomal ancestry. The parent node of R-A12332 is **R-Y19434** and has a similar time depth: 6 of the 10 additional samples that are derived for it but not for R-A12332 are also from Armenia. One additional sample is from Hasanlu, Iran in the Iron Age(2), and here we find two more samples belonging to it in the same population. A final example is a “Scythian” from Moldova from the late 1st millennium BCE.(429) Thus, R-Y19434 appears to be a slightly more general late 3rd millennium BCE founder lineage which corresponds to the steppe admixture detected in Armenia and NW Iran in samples from post-dating this period, with R-A12332 representing what appears to be an Armenia-centered sublineage within this group (not detected in 16 Hasanlu males). **R-FGC14590** is the parent node of R-Y19434 and encompasses a sample from Hajji Firuz and three from Hasanlu (all carbon-dated to late 2nd millennium BCE), and four samples from Armenia assigned to the same period. Further upstream, **R-L584** is found in another couple of samples from Armenia of the same period, and its parent node **R-Y13369** in another 7, including 3 from Karashamb.

Thus 36/37 of the samples of this lineage are from Armenia/Iran (excluding the much later “Scythian” from Moldova). The TMRCA of the entire R-Y1336 lineage was estimated at 5,100 years BP and thus matches the appearance and expansion of the Yamnaya culture ~3,000 years BCE. Indeed, when we examine the parent node of the R-Y13369 clade, haplogroup **R-M12149**, which has a TMRCA of 5,400 years BP, just preceding the emergence of the Yamnaya phenomenon, we find not only individuals from Iran and Armenia (47 for the entire clade), but also 8 Yamnaya individuals from Samara, Kalmykia, and Kazakhstan,(8, 9, 431) 9 individuals of the related Afanasievo culture, and 6 of the related Poltavka culture,(9, 34) 3 individuals from the North Caucasus Early Bronze Age and Steppe Catacomb cultures,(17) two Catacomb and one Multi-Cordoned Ware-related individual from Moldova, and an individual from Chemurchek in Mongolia.(464) ENREF_13 All of these individuals are from the late 4th millennium to 3rd millennium BCE and predate the ones from Armenia/Iran. Together with the appearance of autosomal steppe ancestry in the latter samples, it appears probable that R-M12149 Y-chromosomes arose on the steppe in the 4th millennium BCE and had arrived south of the Caucasus in Armenia and Iran by no later than the 2nd millennium BCE. We will discuss alternative scenarios further down.

The expansion of R-M12149 chromosomes also included southeastern Europe as far south as Albania and North Macedonia, being observed in individual I14690 from Çinamak in Albania (1700-400BCE), I7231 (1371-1123 calBCE) from Ulanci-Veles, and I8112 (783-549 calBCE) from Lisicin Dol, Marvinci, Valandovo, North Macedonia. We note that a high-steppe ancestry individual from Çinamak (I14689; 2663-2472 calBCE) was R-M269 without a reading on R-M12149 SNPs, and could potentially be a precursor of this expansion in the early 3rd millennium BCE. Another high-steppe individual from Serbia (I11446; 3092-2915 calBCE) was female. Overall, the picture from the Balkans is that R-M269/individuals with high amounts of steppe ancestry had appeared there by the Early Bronze Age, with the few later-detected R-M12149 Y-chromosomes indicating a connection with the Yamnaya-cluster of populations of the steppes.

Nonetheless, the handful of individuals of this clade in the Balkans contrasts with the plethora of them in the South Caucasus and NW Iran. Indeed, even in the present-day there is a high frequency of R-M269 in Armenians whose lack of the L51/M412 derived allele(462, 465) ENREF 34 suggests that it is probably mostly within the R-M12149 clade. A more recent study that included the Z2103 marker that is immediately upstream of M12149 indicates that Armenian R-M269 Y-chromosomes are predominantly derived for it. (38) R-M269 occurs also in the Balkans and Greece(462, 466, 467) and is also mostly lacking in the L51 allele, although we are not aware of a recent study which tested Z2103/M12149 directly.

J-Y2919 (within J1) is found in 17 individuals, 13 of which are from the Levant (Israel, Jordan, and Lebanon).(432, 435, 440) It is also called for an undated sample from Nemrik in Iraq (I6441; 1500-1200BCE) of the Late Bronze Age. It is also found in SE Anatolia at Kilis (I14762; 1736-1541 calBCE), a sample from Dinkha Tepe in Iran (IRN_DinkhaTepe_BIA_A; I3911; 2000-1000 BCE) which belongs to the more Anatolian/Levantine cluster of that site, and an Imperial Roman (R1547.SG)(436) who genetically falls on the Levantine end of the Southern Arc. Thus, this lineage appears to track fairly well with Bronze Age Levantine populations and their descendants. The parent node **J-Z1884** is called for a Late Antique Roman(436), a sample from Alalakh in Hatay Province of Turkey (ALA026; 1746-1616 calBCE), and a Canaanite from Lebanon(433). The upstream nodes of J-Z1884 are **J-YSC0000234**, **J-Z2313** and are called for two Middle-to-Late Bronze Age samples from Hatay province,(14) two Bronze/Iron Age samples from Israel,(432) and an Imperial-era sample from central Italy (R835.SG).(436) Further upstream, **J-Z2317** is called for two more samples from Alalakh and two more from Bronze Age Israel. One non-Levantine sample from Dzori Gekh (I16120; 1500-1380 BCE) in Armenia belongs to this clade. Further up, **J-Z2324** is found in two Bronze Age samples from Jordan and one from Israel,(10, 432) and further up the **J-Z2331** clade is found in 6 individuals from the aforementioned Levantine groups, an early Byzantine era individual (I14824; 432-561 calCE) from Balıkesir and a New Kingdom Egyptian (JK2134).(468) Further up, **J-Z1853** is found in Ebla in Syria (ETM012; 2574-2467 calBCE)(14) and SE Anatolia (Kilis; I14798; 3000-2000BCE) as well as a Canaanite from Israel, and four 2nd millennium samples also from Israel could be assigned to the **J-Z1865**, **J-Z643** upstream nodes,(432) a Late Antique (R130.SG; 300-500CE) Italian to the further upstream node **J-CTS9721**, and two samples from Ebla in Syria(14) further upstream to **J-P58**.

Thus, the entire clade **J-P58** is well-associated with the Levant region, may have expanded beyond it (towards Armenia and Iran), by the Bronze Age, and even more broadly (at least in the Mediterranean world) in later periods. The earliest known examples are from Syria and SE Turkey, consistent with the suggestion(469) based on modern variation that the expansion of this haplogroup occurred from “northeast Syria, northern Iraq and eastern Turkey”. The Bronze Age distribution of this clade in all Levantine countries (Syria, Lebanon, Israel, and Jordan), the inferred recent Neolithic-to-Bronze Age origin of clades within the J-P58 lineage, and the present-day distribution in diverse groups of Semitic speakers(469), all also combine to support its association with the expansion of Semitic languages. The latter has been dated to the Early Bronze Age ~5,750 years ago by Bayesian linguistic phylogenetics,(470) with a first split of West Semitic from Akkadian and a common ancestor of West Semitic languages ~5,400 years ago. All sampled (certain) J-P58 chromosomes postdate this period and could thus be associated with this expansion. We caution, however, that the early splits within the Semitic language family were inferred(470) to have transpired within a millennium and the linguistic affiliation of the ancient individuals is uncertain, although some form of Semitic language is quite plausible

given their time and place, so an association of J-P58 with either the Semitic linguistic family as a whole or any of its daughter languages must be clarified by additional ancient DNA study of diverse ancient populations of known or highly likely linguistic affiliation.

J-Z2507 (within J2) is found in 21 individuals. It is part of haplogroup J-M102 for which it was written in 2004 on the basis of present-day samples that: “J-M12 is almost totally represented by its sublineage J-M102, which shows frequency peaks in both the southern Balkans and north-central Italy”(471) In the ancient data we find it in 3 samples from Rome,(436) with the earliest being R474.SG (700-600 BCE). All remaining samples are from the Balkans and indeed the Western Balkans (Montenegro, Croatia, Albania) and most of them are from the Bronze Age. Thus, J-Z2507 has a peri-Adriatic ancient distribution in agreement with the present-day distribution and may represent a Bronze Age or later expansion in the area. The immediately upstream nodes of J-Z2507 are **J-Z585**, **J-Z615**, **J-Z597** with a similar time depth and include two additional Bronze Age samples from Albania and Croatia, and are thus part of the same pattern. **J-Z600**, the parent node of J-Z585, includes four additional individuals, one of which is from Croatia, and three of which are from the Late Bronze Age Nuragic culture in the island of Sardinia,(20, 453) thus suggesting that this culture included individuals of Bronze Age Western Balkan origin (these might have Italian intermediaries, but we do not detect any J-Z600 in mainland Italy prior to the aforementioned Iron Age sample from Rome).

Haplogroup	# in S.A. (Europe)	# in S.A. (West Asia)	Freq. in S.A. (Europe)	Freq. in S.A. (West Asia)	Freq. Difference	P-value	TMRCa	Low age	High age
I-L596	0	28	0.0%	6.3%	-6.3%	6.30E-06	16400	19900	23200
J-CTS9721	0	42	0.0%	9.5%	-9.5%	2.47E-08	8300	8000	10300
J-L136	0	45	0.0%	10.2%	-10.2%	4.08E-09	11300	12300	15200
J-L620	0	47	0.0%	10.7%	-10.7%	2.28E-09	14700	16100	20000
J-P58	0	44	0.0%	10.0%	-10.0%	7.03E-09	9100	10000	12700
J-PF4816	0	46	0.0%	10.4%	-10.4%	4.35E-09	13700	13200	16200
J-Z1853	0	38	0.0%	8.6%	-8.6%	7.27E-08	6500	6200	8500
J-Z1865	0	42	0.0%	9.5%	-9.5%	2.47E-08	7300	6700	8900
J-Z2324	0	30	0.0%	6.8%	-6.8%	2.17E-06	5700	4600	6700
J-Z2331	0	35	0.0%	7.9%	-7.9%	3.90E-07	5700	5600	7400
J-Z643	0	42	0.0%	9.5%	-9.5%	2.47E-08	7800	7200	9500
J1	1	68	0.4%	15.4%	-15.0%	9.05E-12	18300	29200	34000
J-Z2215	1	63	0.4%	14.3%	-13.9%	5.26E-11	18000	16400	20300
J-Z2217	1	63	0.4%	14.3%	-13.9%	5.26E-11	18000	16100	20000
R-Y13369	1	36	0.4%	8.2%	-7.8%	3.17E-06	5100	4900	5900
J-PF5087	4	56	1.6%	12.7%	-11.1%	3.26E-07	15600	14700	17100

Table S 31 Haplogroups frequent in the West Asian part of the Southern Arc and not in its European one. Times are in years BP. We list haplogroups with P-value<0.00001.

Haplogroups more frequent in the European side of the Southern Arc than the West Asian and vice versa

We next examine haplogroups common in the West Asian part of the Southern Arc and not in its European section (Table S 31). Of the 28 instances of **I-L596** in the Southern Arc, 26 occur in Armenia in a Bronze Age or later context. The other two, however, are two Neolithic individuals from Barcin(9) and Mentese (this study). This haplogroup was not detected in the European part of the Southern Arc, but was found in Mesolithic Scandinavians from Norway and Sweden,(472) and later Neolithic or Bronze Age individuals from Central-Northern Europe.(8, 9, 26, 28, 36) However, the relationship of all these I-L596 Y-chromosomes is potentially distant as they have an estimated TMRCa of 16,400 years ago. A total of 19 of the 28 instances (all from Armenia) are further derived for **I-Y16649** (TMRCa 16,400 years BP), and 7 of these for **I-Y16419** (TMRCa 3,100 BCE). Thus, we cannot document a close relationship between the central-northern European and Armenian Y-chromosomes within this clade. The phylogeography of haplogroup I as a whole together with its abundant sampling in ancient samples strongly suggest its European origin. Whether the examples from the South Caucasus and Northwestern Anatolia represent a long-standing presence of the clade in areas adjacent to Europe, or whether these were introduced there more recently remains to be determined.

The patterns involving haplogroup **J** subclades have already been mentioned in our discussion of differences between the Southern Arc as a whole and populations outside it. The breakdown into European and West Asian frequencies further reinforces the specificity of haplogroup **J1** to West Asia with minimum presence in southeastern Europe. The only **J2** related pattern involves haplogroup **J-PF5087** which includes two Minoans from Lasithi(16) and a

Bronze Age sample from Tell Kran in Bulgaria (I19456; 3000-2000 BCE). The two Minoans belong to the downstream **J-M319** clade which links them to a sample from Arslantepe (ART020; 3362-3105 calBCE)(14) in Eastern Anatolia as well as present-day Cretans where it occurs at a frequency of 8.8%.(467)

Haplogroup	# in S.A. (Europe)	# in S.A. (West Asia)	Freq. in S.A. (Europe)	Freq. in S.A. (West Asia)	Freq. Difference	P-value	TMRCA	Low age	High age
J-Z2507	18	0	7.1%	0.0%	7.1%	1.88E-08	4400	3800	5000
J-Z585	20	0	7.9%	0.0%	7.9%	2.73E-09	4900	4300	6200
J-Z597	20	0	7.9%	0.0%	7.9%	2.73E-09	4400	4200	5700
J-Z615	20	0	7.9%	0.0%	7.9%	2.73E-09	4900	4200	5700
J-Z600	21	0	8.3%	0.0%	8.3%	1.04E-09	5200	4300	6200
J-Z622	23	0	9.1%	0.0%	9.1%	1.53E-10	5200	4700	6700
I-M223	24	6	9.5%	1.4%	8.2%	2.60E-06	14100	15300	18800
I-Y3259	24	6	9.5%	1.4%	8.2%	2.60E-06	11600	12400	16000
J-L283	24	1	9.5%	0.2%	9.3%	9.29E-10	5700	8400	10600
J-M241	25	1	9.9%	0.2%	9.7%	3.72E-10	9500	11000	13900
J-Z1825	26	4	10.3%	0.9%	9.4%	3.76E-08	13500	13800	17200
J-Z593	26	1	10.3%	0.2%	10.1%	1.49E-10	12400	12100	14900
I-M436	31	6	12.3%	1.4%	10.9%	1.78E-08	17000	19300	22800
I-L460	41	7	16.3%	1.6%	14.7%	2.86E-11	21000	19900	23200

Table S 32 Haplogroups frequent in the European part of the Southern Arc and not in its West Asian one. Times are in years BP. We list haplogroups with P-value<0.00001.

We next examine haplogroups common in the European but not West Asian section of the Southern Arc (Table S 32). Haplogroup **I-Y3259/I-M223** is first detected in Mesolithic Italy (R7.SG; 9107-8634 calBCE)(436) and is found also in hunter-gatherers from the Baltic and the Iron Gates in the Balkans.(3) It persists in the Balkans where it is found in a currently undated sample from Bosnia-Herzegovina (I19561), the Chalcolithic in the Bodrogkeresztur from Romania and then at Arman in the Bronze Age and Smyadovo, Nova Zagora, Beli Brayag, and Merichleri in Bulgaria ((3) and this study). All these populations have substantial autosomal Balkan hunter-gatherer ancestry, and I-M223 could well represent a lineage of the hunter-gatherer population that survived into the Neolithic and Bronze Age period. While its Paleolithic TMRCA does not allow one to establish a close relationship between different Y-chromosomes belonging to it, we note that the 6 examples from the West Asian portion of the Southern Arc are a classical period sample from Lebanon (SFI-35.SG; 539-330 BCE), a Hellenistic sample from Halikarnassos (I3311; 323-31 BCE), and three Byzantine or later samples from the Aegean and Marmara regions of Turkey. All of these could possibly be derived from southeastern Europe where I-M223 chromosomes were abundant. However, we also find it in a Middle Bronze Age context in the Aegean region at Yassitepe near Izmir (Smyrna) (I5737; 2035-1900 calBCE), so the later examples from Turkey and Lebanon need not have also arrived in the historical period. Indeed, the I5737 outlier has no detectable Balkan hunter-gatherer ancestry (-0.9±0.7%) or EHG ancestry (2.9±2.6%) and thus does not appear to be a recent migrant from the Balkans.

Haplogroup	# in S.A.	# outside S.A.	Freq. in S.A.	Freq. outside S.A.	Freq. Difference	P-value	TMRCAs	Low age	High age	Log#/TMRCAs
G-PF3378	2	8	0.3%	0.5%	-0.2%	0.733305	5900	8100	10200	0.000390
R-Z2118	3	8	0.4%	0.5%	-0.1%	1	5100	5100	6400	0.000470
R-L48	1	10	0.1%	0.7%	-0.5%	0.189291	4600	4000	5300	0.000521
R-Z2108	4	15	0.6%	1.0%	-0.4%	0.458457	5400	4900	5900	0.000545
E-CTS1273	5	7	0.7%	0.5%	0.3%	0.532568	4500	4100	5100	0.000552
R-S499	1	12	0.1%	0.8%	-0.6%	0.076543	4600	4000	5300	0.000558
R-Z195	2	11	0.3%	0.7%	-0.4%	0.366813	4500	3700	5300	0.000570
J-Y15058	10	1	1.4%	0.1%	1.4%	7.06E-05	4100	3800	5000	0.000585
E-Z1057	8	7	1.2%	0.5%	0.7%	0.090002	4600	4000	5500	0.000589
R-Z2106	7	18	1.0%	1.2%	-0.2%	0.830867	5400	4900	5900	0.000596
R-CTS1211	2	12	0.3%	0.8%	-0.5%	0.249172	4400	4100	5100	0.000600
E-V13	10	9	1.4%	0.6%	0.9%	0.078	4800	6800	8800	0.000613
I-DF29	1	15	0.1%	1.0%	-0.8%	0.030365	4500	4000	5100	0.000616
R-Z280	2	17	0.3%	1.1%	-0.8%	0.07743	4600	4300	5300	0.000640
R-S263	1	21	0.1%	1.4%	-1.2%	0.004573	4600	4000	5300	0.000672
R-S23592	1	18	0.1%	1.2%	-1.0%	0.011851	4200	3800	4700	0.000701
I1	1	25	0.1%	1.6%	-1.5%	0.001101	4600	25200	29800	0.000708
R-DF27	4	22	0.6%	1.4%	-0.9%	0.09127	4500	3700	5300	0.000724
R-U106	2	27	0.3%	1.8%	-1.5%	0.003722	4600	4300	5300	0.000732
R-Z282	3	32	0.4%	2.1%	-1.7%	0.002708	4800	4300	5300	0.000741
R-Z283	3	37	0.4%	2.4%	-2.0%	0.000756	4800	4400	5400	0.000769
R-Z2125	1	32	0.1%	2.1%	-1.9%	0.000165	4200	3700	5100	0.000833
R-L2	8	59	1.2%	3.8%	-2.7%	0.000408	4300	3900	4700	0.000978
R-U152	8	63	1.2%	4.1%	-3.0%	0.000192	4300	3700	5300	0.000991

Table S 33 High frequency/low TMRCA haplogroups. Haplogroups already present in previous Tables of Supplementary Text S5 are excluded. Times are in years BP. Table includes haplogroups with at least 10 samples and a TMRCA of no more than 6,000 years BP, and is sorted according to the log of the number of samples of each haplogroup divided by the TMRCA.

High prevalence but low time depth haplogroups

We next discuss high frequency but low TMRCA haplogroups (Table S 33). Haplogroup **R-U152** belongs to the common West European **R-P312** which we previously discussed.(462) In our sampling it is found only in Croatia, and in particular in Bezdanjača cave (11 of 13 males were some type of R1b-**P297**, 7 of which could be called down to **R-L2**) during the Bronze Age, with one example from Sv Kriz during the Iron Age (752-417 calBCE). Thus, the dramatic expansion of this lineage which resulted in numerous examples in central-western Europe over the Bronze Age also reached the northwestern periphery of the Southern Arc.

Haplogroup **R-DF27** (also within R-P312) has a complementary distribution to **R-U152** with a probable Iberian origin.(473) Three medieval samples from Lebanon(434) and a Byzantine one from Stratonikeia (I20147; 650-1300 CE) were likely patrilineal descendants of males of Iberian origin. Another Byzantine individual from Balikesir (I14832; 600-1000 CE) had an **I1 / I-DF29** haplogroup, a lineage associated with Scandinavia(474) and found in pre-Christian Icelanders and Swedish Vikings.(429, 446) The genetic profile of this individual does not resemble northern Europeans, so he might be the descendant of a northern European (e.g.,

part of the Varangian guard of Byzantium) who intermarried with the local population, although a more proximal origin is also possible, as this lineage was found also in Langobards from Hungary.(475) The individual was the only one derived for the **I-Y7626** lineage with an estimated TMRCA of 2,500 years BP.

Haplogroup **R-S23592** and its upstream node **R-Z2125** (within **R-Z93**) is represented in our data only by the steppe-related ancient outlier in Samsun (I4531) that we have discussed above. We also discussed the **R-Z283/R-Z282** individuals above, as well as those within **R-U106**.

Haplogroup **E-V13**(476) is an important Southeast European Y-chromosomal lineage, well-represented in present-day people of the Balkans.(467, 477-479) Its estimated TMRCA of 4,800 is most consistent with the inference that this represents a Bronze Age expansion(478) rather than Paleolithic/Neolithic expansions as previously proposed. In the ancient data it is only detected (in the Southern Arc) in the Iron Age with four examples at Kapitan Andreevo in Bulgaria (1100-500 BCE) and one from Sv Kriz in Croatia (I5724; 382-206 calBCE). These samples also belong to downstream clades **E-Z1057** and **E-CTS1273** (with a TRMCA of 4,500 years). Later examples are found in Late Antique and Medieval Spain(449) and Italy(436, 453), while we also find it in Hellenistic and Roman samples from Bulgaria and in a pair of brothers (500-700 CE) from Byzantine Nicaea in Turkey.

Its absence in Bronze Age southeastern Europe (n=107) is in remarkable contrast with its ubiquity in the present day, leading us to hypothesize that either it did exist there prior to our sampling but in a specific region from which we have no samples or it arose elsewhere and migrated to southeastern Europe just prior to the earliest sampled individuals. The parent node of E-V13 is **E-L618** which is called for an earlier sample from the Lengyel culture in Hungary which was ancestral for the V13 SNP (I1900 4797-4619 calBCE; E-L618(xE-BY64249,E-V13)) and which has an estimated TMRCA of 7,800 years BP. Thus, the evidence appears consistent with a scenario in which E-L618 Y-chromosomes entered Europe during the Neolithic and E-V13 representing a remarkably successful lineage within this group that had not yet achieved prominence during the Bronze Age, but had begun to do so by the Iron Age.

We commented above on the specificity of the R-Y13369 lineage to Armenia/Iran and its descent from the general R-M12149 lineage which also encompasses individuals of the Yamnaya cluster from the steppe. A sister lineage of R-Y13369 is **R-Z2106** which is also found in many examples of the Yamnaya cluster.(4, 8, 9, 15, 34) This is found in only two examples from Bronze Age Armenia (I19348 from Karashamb and RISE397.SG from Kaplan(4)), but it also included all 3 individuals of R-M12149 (from North Macedonia and Albania) that we discussed before, which furthermore were all derived for downstream haplogroup **R-Z2108**. Thus, R-Z2106 represents a genetic link between the steppe, the Balkans, and the South Caucasus, with R-Z2108 evident only in the Balkans. The TMRCA of all these lineages (including R-M12149) is ~5,400 years ago, suggesting that the downstream lineages arose in rapid succession.

R-M12149 in Armenia and North Iran and the Great Steppe upheaval of the 3rd millennium BCE

The descendants of the R-M12149 persisted on the Eurasian steppe until the early 2nd millennium BCE when we find I1020, an outlier individual of the Sintashta culture (2016-1773 calBCE) whose genetic makeup did not resemble those of the other Sintashta individuals.(34) We do not detect individuals of this clade in a steppe context until the end of the 1st millennium BCE in a Sarmatian individual from Pokrovka.(430) The demise of this clade on the Eurasian steppe during the 3rd millennium BCE was followed by its rise in the South Caucasus and Iran

during the 2nd millennium BCE. It is possible that the migration of R-Z2106 males that moved from the steppe into both the Balkans and the South Caucasus/Iran thus preserved the patrilineages of Yamnaya-cluster populations in both the western and eastern edges of the Southern Arc, with the more specific R-Y13369 lineage demarcating only the eastern wing of this migration.

When did steppe ancestry arrive in the South Caucasus and was it related to the migration of the R-M12149 Y-chromosome bearers? We propose that this may have occurred in the latter half of the 3rd millennium BCE.

- No steppe ancestry is detected in 18 Early Bronze Age samples from Armenia at a time dominated by the Kura-Araxes culture.
- Steppe ancestry does appear in Bronze/Iron Age samples from the South Caucasus.
- We used DATES to estimate the time of admixture of steppe-admixed samples using the Early Bronze Age (EBA) as one source, members of the Yamnaya cluster from Russia as the other, and 38 radiocarbon dated samples with at least ± 2 standard errors of EHG ancestry greater than zero. We obtain a date of 52.2 ± 8.0 generations ago for the admixture. Given that the 25 samples date to 1119 BCE on average, and assuming a generation length of 28 years,⁽⁵⁴⁾ this points to ~ 2579 BCE (3019-2140 BCE 95% C.I.). It is possible that admixture took place also in the North Caucasus, as the population of the “Maykop cluster”⁽¹⁷⁾ was genetically similar to populations south of the Caucasus. Repeating the analysis, substituting this for the EBA results in an estimate of 64.0 ± 8.9 generations (2911 BCE: 95% C.I.: 3398-2423 BCE).

The earliest carbon dated sample with steppe ancestry from the Bronze Age of Armenia is individual I14813 (2127-1900 calBCE; Tavshut belonging to the Trialeti culture) with $9.7 \pm 3.5\%$ EHG ancestry. This individual belonged to haplogroup I-Y16649 and had EHG ancestry similar to the much later individuals from Armenia. Slightly later was an individual from Nerquin Getashen (RISE413.SG; 1919-1696 calBCE calBCE)⁽⁴⁾ with $18.4 \pm 5.7\%$. It has been proposed that: there were “subsequent movements from the steppes into Transcaucasia probably principally via the Caspian corridor beginning at the end of the first half of the 3rd millennium and continuing into the early 2nd millennium BC.”⁽⁴⁸⁰⁾ Future sampling in Georgia, Armenia, Azerbaijan, and the North Caucasus might flesh out the migratory route and timing of the introduction of steppe ancestry into the South Caucasus.

The genetic data are blind to the causes of the spread of R-M12149 descendants and steppe ancestry to the South Caucasus, but we can add two observations on the basis of Y-chromosome data.

First, the distribution of R-M12149 and R-Z93 descendants on the steppe indicates a replacement of the former by the latter during the 3rd millennium BCE. We have already mentioned above the latest occurrences of the former (I1020 Sintashta outlier) and earliest of the latter (I0432 Potapovka outlier). In Fig. S 77 we plot a histogram of the distribution of the two types of Y-chromosomes from Russia/Ukraine/Kazakhstan over time. R-M12149 appears in Armenia after it disappears from steppe samples, which strongly suggests that its arrival there might be a “survival” of the R-M12149 population north of the Caucasus that evaded the upheaval that took place on the steppe.

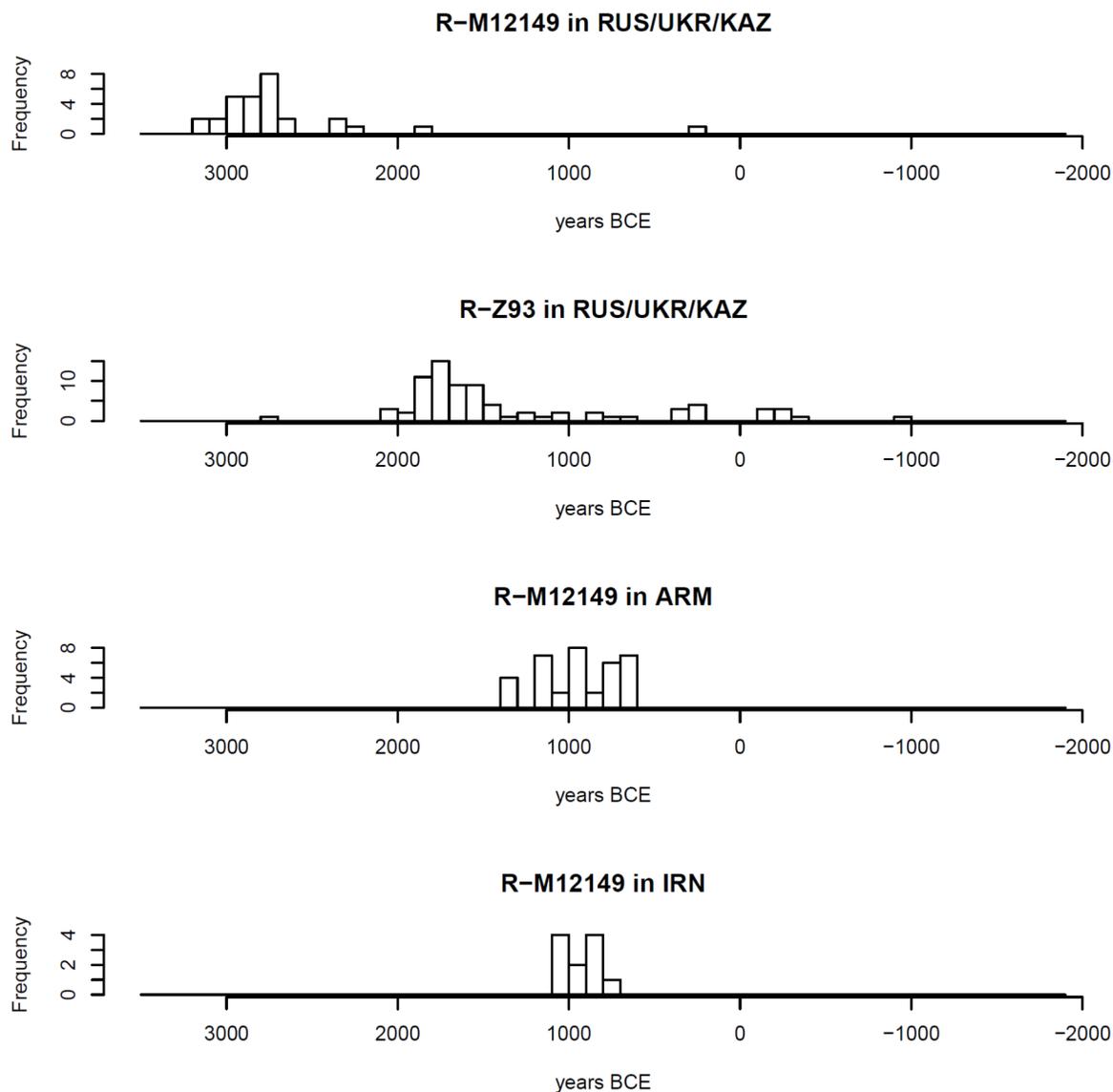


Fig. S 77 The great Steppe upheaval in the mid-3rd millennium BCE

A precise mapping of the route and timing of the disappearance of R-M12149 on the steppe, the arrival of R-Z93 there, and the re-appearance of R-M12149 will determine the temporal sequence of events and clarify whether this involved a “pull” of the population towards opportunities south of the Caucasus or a “push” away from the steppe due to pressure of the (eventually dominant) R-Z93 bearing populations.

The second aspect elucidated by Y-chromosome variation is that by the time we sample individuals with steppe ancestry from the Bronze Age Caucasus any association between them and this ancestry is lost as in the site of Karashamb where we have the largest sample size (Fig. S 78)

Karashamb.Y.bypop: $10.0 \pm 0.9\%$ EHG

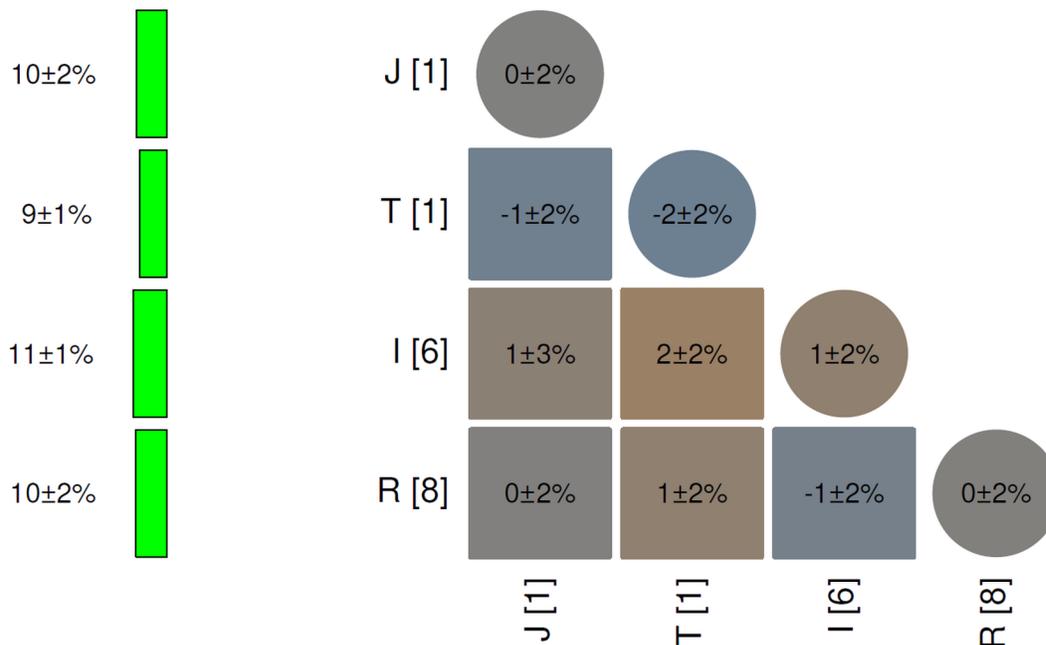


Fig. S 78 No association of Y-chromosome haplogroup and EHG ancestry at Karashamb

We interpret this lack of association as indicating that the migrating population introducing R-haplogroup chromosomes into the South Caucasus did not maintain its separateness from non-R bearing populations (as their ancestors had on the Steppe) but admixed with them to the point that their autosomal ancestral contribution became extremely diluted, with their Y chromosomes potentially preserved in due to social prestige associated with this patriline. The decoupling of genome-wide ancestry from patriline is evident in the fact that the very first individual with steppe ancestry which we mentioned above (I14813) had the typical ~10% seen at Karashamb and belonged to haplogroup I-Y16649.

But we caution that another scenario is also possible: that R-M12149 were not associated with EHG ancestry to begin with. The fact that substantial EHG ancestry is found in Areni1 Chalcolithic samples(10) and also at similar levels of ~10% ~2,000 BCE in the I14813 individual indicates that the lack of association of steppe ancestry with R-M12149 may not necessarily have been the result of a long process of intermarriage between steppe-derived R-M12149 bearers and the local population.

This decoupling probably continued until the formation of the present-day Armenian gene pool which as we have seen in Supplementary Text S3 was already in place ~2,000 years ago. Present-day Armenians continue to have Y-chromosomes of their Bronze Age ancestors, but with further dilution of the steppe ancestry compared to the Bronze and Iron Age.

We also looked at the samples from the site of Hasanlu in Iron Age Iran where we also see no association of R-M12149 bearers with autosomal EHG ancestry (Fig. S 79)

IRN_Hasanlu.Y.bypop: $3.7 \pm 1.0\%$ EHG

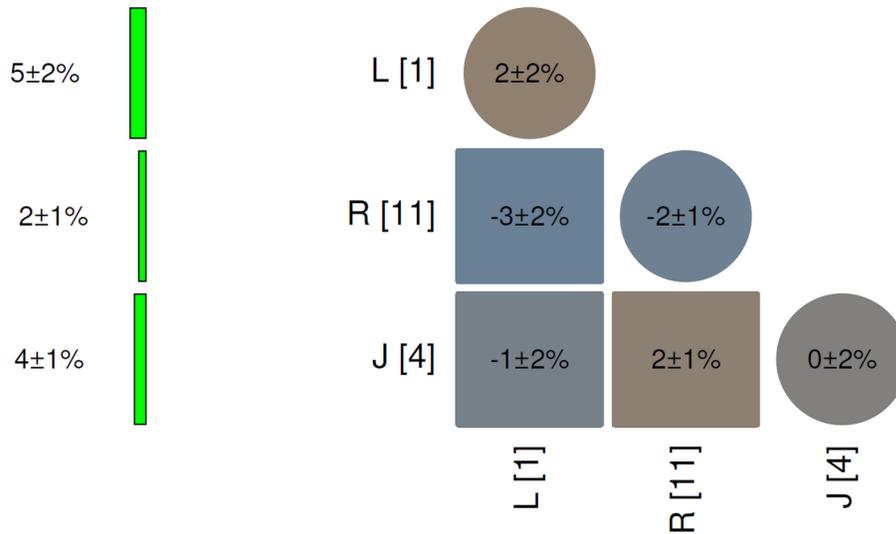


Fig. S 79 No association of Y-chromosome haplogroup and EHG ancestry at Hasanlu

The EHG ancestry of R-haplogroup bearers is nominally (but not significantly) lower than that of the other haplogroups present at the site, and thus provides no evidence for an association of this lineage with this type of ancestry.

Haplogroup	Count	Average distance (km)	Maximum distance (km)	TMRCAs	Low age	High age
I-Y16419	7	73	164	3100	13700	19200
J-Y3441	5	345	345	4100	3700	4500
J-Y3442	7	345	345	4100	3700	4800
J-Z38240	8	301	468	3700	3300	4900
J-Z1297	8	276	664	4200	3600	4800
J-Z638	8	276	664	4200	3800	5000
E-PF6748	7	344	711	5700	5500	7500
E-Y6720	5	380	711	5500	5100	6300
R-Z49	5	382	735	4300	3900	4700
E-BY3880	5	688	1150	4300	3900	5000
R-Z325	5	789	1659	3000	2700	4200
R-Z330	7	606	1659	3400	3700	4800
R-Z331	7	606	1659	4200	4000	5300
I-CTS10228	5	1625	1940	3400	4200	5800
I-CTS4002	6	1625	1940	5000	4600	6500
R-Z9	9	703	2058	4600	4000	5300
J-Z423	6	1029	2218	3600	3000	4600
R-PF7562	6	1247	2526	5400	5700	7100
R-PF7563	6	1247	2526	4600	4800	6100
R-S1161	7	1204	2533	4500	3800	5200
R-Z2116	8	1106	2533	4500	4500	5600
J-Y6094	5	1346	2839	4200	3700	4800
J-L70	7	1268	2999	3800	5900	8000
I-CTS10936	7	1967	3014	5500	5400	7700
I-S19848	7	1967	3014	5500	4600	6500
R-FGC79182	5	1526	3174	3500	3300	4300
R-ZP87	5	1526	3174	3400	3000	4000
I-P78	6	1638	3539	5100	8400	10800
R-Z198	7	1859	3951	4500	3700	5300
R-YP1558	5	1999	4108	4200	3800	4700
R-Z19	6	2110	5266	3800	4000	5300
J-M205	9	2382	6770	5800	13800	17200
J-PF7321	5	3504	6770	5800	5100	6500

Table S 34 Low/high geographical dispersion haplogroups. Haplogroups already present in previous tables in this section or absent from the Southern Arc are excluded. Times are in years BP. Table includes haplogroups with at least 5 samples and a TMRCA of no more than 6,000 years BP, and is sorted according to the maximum geographical distance of any two individuals within each haplogroup.

Very localized or very geographically dispersed haplogroups

We next examined haplogroups that were either very localized or spanned great geographical distances (Table S 34). The great distance between instances of haplogroup J-PF7321 (within J2) is due to its presence in a Roopkund Lake sample from the Himalayas, where a group of individuals only a few centuries old had origins in the eastern Mediterranean, most resembling present-day Greeks and Cretans.(481) But this haplogroup was also found in a “Middle Eastern” outlier from Roman England(448) also a great distance from the Southern Arc. Its oldest examples are from Alalakh(14) in Hatay province of Turkey, an Iron Age sample from Armenia, and an Imperial Roman.(436) The parent node of this haplogroup J-M205 was also found in Bronze Age Jordan,(10) Israel,(432) and a Third Intermediate Period sample from Egypt from the 1st millennium BCE.(468) Overall, this appears then to be a Levantine lineage which had dispersed beyond the Middle East even in ancient times.

The great distance between instances of haplogroup **R-Z19** (within R-U106) is due to its presence in a pre-Christian Icelander(446) and a medieval individual from Lebanon (SI-47.SG) of probable Crusader origin.(434) The remaining instances are a Langobard from Hungary,(475)

medieval individuals from Germany,(423) and a Swedish Viking.(429) All but the Icelander belonged to downstream lineage **R-FGC79182** and **R-ZP87** (TMRCA of 3,400 years ago). It thus appears to have a distribution related to historical Germanic-speaking populations.

The great distance between instances of haplogroup **R-YP1558** (within R1a) is due to its presence in the steppe-like outlier from Samsun previously discussed (I4531) with all the other four instances being steppe individuals from Russia (Sarmatians or Alans,(429, 431) and a Middle-to-Late Bronze Age individual from Krasnoyarsk).(34) A Sarmatian origin of the Samsun outlier is likely given its timeframe.

The great distance between instances of haplogroup **R-Z198** (within R-DF27) is due to its presence in samples from Spain and medieval samples from Lebanon and Stratonikeia, and this lineage most likely represents medieval persons of Iberian origin.

I-P78 (within I2) is found in a Sarmatian from Kazakhstan(431) with all other instances from the Balkans and western Anatolia. It probably reflects a southeastern European lineage that entered steppe populations rather than the opposite.

I-CTS10936/I-S19848 (within I2) was detected in Bronze Age samples from Romania and Croatia in our data, a Byzantine sample from Ilipinar, and a medieval sample from Croatia. It was also found in a 1700-1900 CE individual from Murmansk in Russia (CHV002.A0101)(482) and a medieval sample from Sunghir in Russia (1100-1220 calCE).(483) It is difficult to infer its most ancient origin given the limited samples, other than to note its overall Eastern European distribution.

Haplogroup **J-L70** is not detected prior to the Late Antique/Medieval period in samples from Anatolia (both the SE at Kilis and the Aegean at Muğla), Italy,(436) and Spain.(449) The earliest occurrences of its upstream haplogroup **J-L25** are in Iran (I2337 from Tepe Hissar; 3640-3518 calBCE) and Uzbekistan (I11028; 3332-2937 calBCE), and so it may reflect an “eastern” influence in Anatolia and beyond.

Haplogroup **J-Y6094** is a child lineage of **J-Y2919** whose Levantine associations we have discussed above and is found from Imperial Rome to Dinkha Tepe in Iran. Haplogroup **R-S1161**, its parent **R-Z2116**, and its parent **R-Z2118** occur in the pair of brothers from Stratonikeia (I20140 and I20141) that we have mentioned before with an earliest occurrence in a Bronze Age sample from Spain,(449) and Imperial to Medieval samples from Rome and northern Italy.(436, 475)

An extremely interesting pattern is observed for haplogroup **R-PF7562** represented entirely in our data from its child lineage **R-PF7563**. **R-PF7562** is a child lineage of the prominent West Eurasian **R-M269** lineage whose other child lineage **R-L23** is the parent of the “mainland European” **L-51** and “steppe” **R-Z2103** lineages. The two child lineages of R-M269 are massively disproportionately represented in our data, with the popular R-L23 (from which the dominant lineages of Yamnaya, Bell Beaker, and South Caucasus populations were derived) occurring in 268 samples, while **R-PF7562** only occurs in 5.

The earliest occurrence of **R-PF7562** is in LYG001, a 2866-2580 calBCE sample from Lysogorskaya 6, kurgan 3, grave 4 in the North Caucasus Piedmont of Russia.(17) Given that within the phylogeny of R-M269 (R-PF7562, (R-L51, R-Z2013)) both R-PF7562 and R-Z2013 have their earliest examples in the North Caucasus and steppe to the north, the most likely hypothesis is that the entire R-M269 clade originated there as well, with R-L51 representing a lineage that eventually became highly successful in mainland Europe, R-PF7562 a lineage that did not achieve the prominence of its relatives, and R-Z2013 became highly successful (briefly)

as part of the Yamnaya culture and its offshoots (e.g., in the South Caucasus) that we discussed above.

But, what of the other 4 examples of R-PF7562? The second most ancient example is a Mycenaean individual from the Palace of Nestor in Pylos (I13518; Kokkevis, Tomb V; 1450-1200 BCE) and his 1st degree relative I13506 buried in the same tomb. This establishes a connection between Mycenaean Greece and the North Caucasus on one hand, and more broadly the R-L23 descendants of the steppe and mainland Europe. The remaining samples of R-PF7562 are much later: two Roman/Byzantine individuals from the Aegean region of Anatolia (I20000 and I20266) and a medieval sample from Albania (I13834).

In present-day Armenians and Georgians, haplogroup R-M269(xL23) – which will encompass any R-PF7562 examples if present – was also found at low frequencies. (38) In a very large collection of individuals from the Caucasus (n=1,370) only two examples were found (in a Lezgin and a Tabasaran individual, both from the Northeast Caucasus).(462) The same study found low frequencies of R-M269(xL23) in South/South East Bashkirs from the Circum-Uralic region. But R-M269(xL23) was present in every group sampled from Southeastern Europe (except the Roma and the mainland of Croatia). While the sampling scheme of present-day collections of Y-chromosome data does not allow one to be certain about the prevalence in different regions, the information we could obtain from a public database (<https://www.yfull.com/tree/R-PF7562/>) does suggest that R-PF7562 is present predominantly in Southeastern Europe and the Caucasus, as well as adjacent areas of the Middle East and Eastern Europe. Moreover, it also suggests (https://www.yfull.com/tree/R-M269*/) that all existing R-M269 belong to either R-L23 or R-PF7562 and thus the frequency of R-M269(xL23) can be used as a stand-in for R-PF7562. However, in our ancient data we detect one individual from Armenia (I14057; 776-545 calBCE, Brardzryal monument) that belonged to haplogroup R-M269*(xR-PF7562,R-L23).

Much larger sample sizes (ancient and modern) typed for R-PF7562 are necessary to trace the history of this low frequency lineage. However, the available data are enough to propose that it originated in the North Caucasus or its environs, that it had been present in southeastern Europe by the Late Bronze Age at least, and that it continues to be an important (albeit low frequency) lineage there.

Summary of Key Findings and Discussion

Our examination of the Y-chromosome data is not exhaustive, but underscores the usefulness of examining a broad collection of samples in a joint analysis. Individuals may present themselves as outliers in particular sites, but it is only by examining large collections of samples from diverse regions that may be informative about their origins, uncovering links across space and time that a site-centric analysis would not disclose.

We undertook this process using a set of criteria in order to avoid focusing on Y-chromosome lineages that had risen to our attention in past work. From our observations we summarize a few interesting patterns or individuals:

- Association of J-P58 with Levantine ancestry and possibly with the expansion of Semitic languages
- Association of R-M269 with the Caucasus/steppe area and likely association of its descendants with expansions to southeastern Europe and the South Caucasus

- Detection of outliers within the Southern Arc of possible Iberian, Germanic, or Sarmatian origin, and, conversely, inference of the likely origins of non-Southern Arc individuals from areas such as the West Balkans or the Levant.

Our study has focused on lineages that were *present* in different populations; these establish definite links within a certain timeframe, such as the link of Mycenaean Pylos with Early Bronze Age North Caucasus. Yet, the absence of lineages in particular populations is also informative, provided that large number of individuals have been sampled. We comment on Anatolia (n=163, and n=114 prior to the Roman period). Of these pre-Roman samples, no R-M269 was found.

Together with the paucity of EHG ancestry in Anatolian samples from all periods (except for clear genetic outliers of probably extraneous origin during the later periods), the absence of R-M269 in Anatolian samples suggests strongly that the spread of Anatolian languages was not mediated by this haplogroup which appears to link both southeastern Europe and the south Caucasus with the Eurasian steppe. Anatolian languages are thought to stem from the first split of the Indo-European phylogeny,(43) and thus they may be descended from a part of the Proto-Indo-European community prior to the appearance and wide dispersal of the R-M269 lineage from the Eurasian steppe. (By Anatolian languages we refer to languages such as Hittite, Luwian, Palaic, and Lydian, rather than languages spoken in the territory of Anatolia which also included other, non-Indo-European languages such as Hattic, or Indo-European languages such as Phrygian). Thus, the genetic data appears to be most consistent with the following two scenarios:

- Proto-Indo-European originated in the steppe, in a population of substantial EHG ancestry. Yamnaya and descendant IE languages are derived genetically from this population, and Anatolian language speakers acquired the language without any measurable admixture from the PIE population. It could be argued that our collection of samples may be from both Indo-European and non-Indo-European speakers of Anatolia. It is expected that under this scenario detection of an intrusive population would depend crucially on sampling sites where it was present during its earliest phase, but over time, whatever ancestry was introduced by it would spread geographically. In the case of Anatolia, this is complicated by the influence that neighboring Indo-European peoples may have exerted on the population since the 1st millennium BCE (e.g., Persians, Greeks, Phrygians, Galatians, Romans, to name a few). Yet, despite these influences, steppe-derived Y-chromosomes are rare to non-existent throughout Anatolia.

- Proto-Indo-European originated in the Near East (including the Caucasus region which was genetically an extension of the Near East during the Chalcolithic and Bronze Age(17)) in a population devoid of EHG ancestry. Anatolian language speakers acquired the language from the PIE population, perhaps related with the spread of “eastern” (CHG-related) ancestry across Anatolia since the Chalcolithic. Yamnaya and descendant IE languages acquired the language in conjunction with the “southern” component of their ancestry(8) which had begun to spread into the steppe since at least the Chalcolithic.(9, 17)

We consider the second hypothesis more likely as it postulates that both Anatolian speakers and Yamnaya and Yamnaya-derived speakers of non-Anatolian IE languages have some ancestry from the PIE population which thus served as a medium for the transferal of a new language. Both the spread of “southern” ancestry into the steppe and of “eastern” ancestry across Anatolia are documented for the Chalcolithic period. The first scenario faces the difficulty of explaining why and how a numerically insignificant population had a lasting linguistic effect in Anatolia.

Yet, the second scenario must also explain why the Y-chromosome gene pools of Anatolia and of the steppe were disjoint, for it is not only in Anatolia that steppe-derived Y-chromosomes are rare, but also on the steppe that Near Eastern-derived ones are also rare, with virtually all (27/29) of Yamnaya cluster males from Russia belonging to haplogroup R-M269 and not a single instance of haplogroups prevalent in the Near East such as J.

A possibility that may explain this discrepancy is that Yamnaya cluster males represent a patrilineal elite that was afforded Kurgan burial, and dominated by the R-M269→R-L23→R-Z2103→R-M12149 lineage of its founder. Closely related lineages (such as the above-discussed R-L23→R-L51 in mainland Europe and R-M269→R-PF7562 in the Caucasus/southeastern Europe) participated in the spread of the languages spoken in this population until their ultimate demise on the steppe and replacement by competing patriarchal groups such as the R-M417→R-Z645→R-Z93 descendants.

Where did the R-M269 founder live? The early presence of this lineage in steppe samples and its association with steppe ancestry in many of its descendants may suggest that the R-M269 founder belonged to a population with EHG ancestry. However, the complete lack of association of R-haplogroup descendants and EHG ancestry in either Armenia or Iran is consistent with either a massive dilution of EHG ancestry in these populations resulting in the dissociation of Y-chromosome lineages from autosomal ancestry over time, or with a scenario in which R-M269 was not associated with substantial EHG ancestry to begin with.

At present, we have no archaeogenetic information on where the R-M269 population originated. The TMRCA of R-M269 descendants is 6,400 ybp and of the immediately upstream node R-P297 a much earlier 13,300 ybp. R-P297(xM269) chromosomes are found in hunter-gatherers from the Baltic(3, 458) as well as in a hunter-gatherer from the Samara region of Russia.(8, 9) This would suggest an EHG-associated origin of this lineage, but the “long branch” of R-M269 reduces greatly any confidence in the proximity of the earliest R-M269 bearers to these eastern European relatives. Yet, the data are equally consistent with a scenario in which the R-M269 founder did not have EHG. It is a challenge for future archaeogenetic research to pinpoint the origin of the R-M269 lineage.

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