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Genetic origins of the Minoans and Mycenaeans

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The origins of the Bronze Age Minoan and Mycenaean cultures have puzzled archaeologists for more than a century. We have assembled genome-wide data from 19 ancient individuals, including Minoans from Crete, Mycenaeans from mainland Greece, and their eastern neighbours from southwestern Anatolia. Here we show that Minoans and Mycenaeans were genetically similar, having at least three-quarters of their ancestry from the first Neolithic farmers of western Anatolia and the Aegean[1,2], and most of the remainder from ancient populations related to those of the Caucasus[3] and Iran[4,5]. However, the Mycenaeans differed from Minoans in deriving additional ancestry from an ultimate source related to the hunter–gatherers of eastern Europe and Siberia[6–8], introduced via a proximal source related to the inhabitants of either the Eurasian steppe[1,6,9] or Armenia[4,9]. Modern Greeks resemble the Mycenaeans, but with some additional dilution of the Early Neolithic ancestry. Our results support the idea of continuity but not isolation in the history of populations of the Aegean, before and after the time of its earliest civilizations.

Ancient DNA research has traced the principal ancestors of early European farmers to highly similar Neolithic populations of Greece and western Anatolia, beginning in the seventh millennium BC (refs 1, 2); however, the later history of these regions down to the Bronze Age, a transformational period in the history of Eurasia[4,6,9], is less clear. There is limited genetic evidence suggesting migrations from both the east (the area of Iran and the Caucasus), reaching Anatolia by at least ~3800 BC (ref. 4), and the north (eastern Europe and Siberia) contributing 'Ancient North Eurasian' ancestry[6,10] to all modern Europeans. The timing and impact of these migrations in the Aegean is, however, unknown.

During the Bronze Age, two prominent archaeological cultures emerged in the Aegean. The culture of the island of Crete, sometimes referred to as 'Minoan'[11], was Europe's first literate civilization, and has been described as 'Europe's first major experience of civilization'[12]. However, the Linear A syllabic ideographic and Cretan hieroglyphic scripts used by this culture remain undeciphered, obscuring its origins. Equally important was the civilization of the 'Mycenaean' culture of mainland Greece, whose language, written in the Linear B script, was an early form of Greek[13]. Cretan influence in mainland Greece and the later Mycenaean occupation of Crete link these two archaeological cultures, but the degree of genetic affinity between mainland and Cretan populations is unknown. Greek is related to other Indo-European languages, leading to diverse theories tracing its earliest speakers from the seventh millennium down to ~1600 BC, and proposing varying degrees of population change (Supplementary Information section 1).

Genome-wide ancient DNA data provide a new source of information about the people of the Bronze Age, who were first known through the ancient poetic and historical traditions starting with Homer and Herodotus, later through the disciplines of archaeology and linguistics, and, more recently, by the limited information from ancient mitochondrial DNA[14,15]. Here we answer several questions. First, do the labels 'Minoan' and 'Mycenaean' correspond to genetically coherent populations or do they obscure a more complex structure of the peoples who inhabited Crete and mainland Greece at this time? Second, how were the two groups related to each other, to their neighbours across the Aegean in Anatolia, and to other ancient populations from Europe[1,2,6,8–10] and the Near East[2–5,9,16,17]? Third, can inferences about their ancestral origins inform debates about the origins of their cultures? Fourth, how are the Minoans and Mycenaeans related to Modern Greeks, who inhabit the same area today?

We generated genome-wide data from 19 ancient individuals (Fig. 1a, Extended Data Table 1 and Supplementary Information section 1). These comprised ten Minoans from Crete (approximately 2900–1700 BC; labelled Minoan_Odigitria, from Moni Odigitria near the southern coast of central Crete; and Minoan_Lasithi, from the cave of Hagios Charalambos in the highland plain of Lasithi in east Crete). Four Mycenaeans were included from mainland Greece (approximately 1700–1200 BC; from the western coast of the Peloponnese, from Argolis, and the island of Salamis). An additional individual from Armenoi in western Crete (approximately 1370–1340 BC; labelled Crete_Armenoi) postdated the appearance of Mycenaean culture on the island. Our dataset also included a Neolithic sample from Alepotrypa Cave at Diros Bay in

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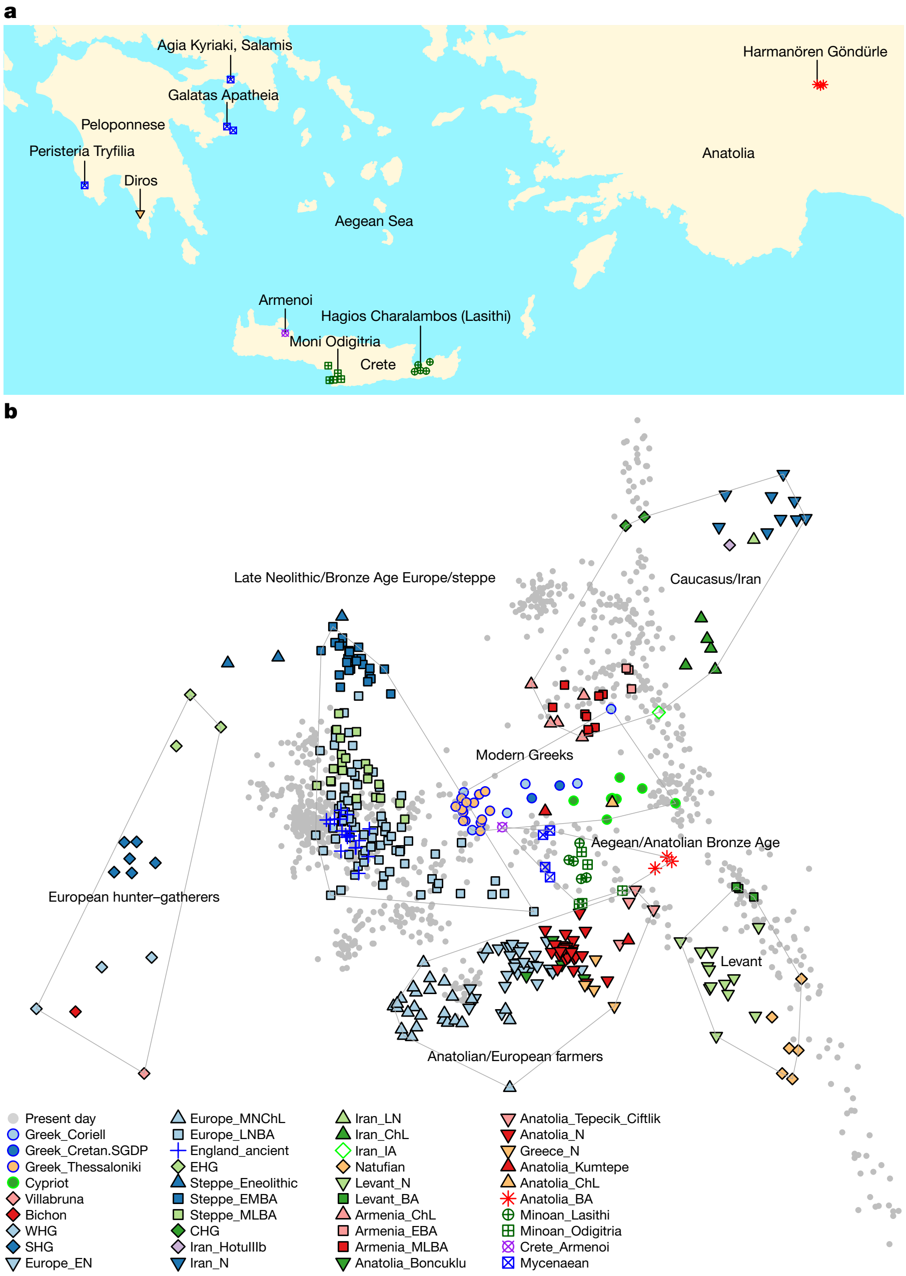

Figure 1 | Samples and PCA. a, Geographical locations of newly reported ancient data. Lines point to sampling locations; jitter is added to show the number of sampled individuals per location. **b**, Three hundred and thirty-four ancient individuals projected onto the first 2 principal components computed on a sample of 1,029 present-day West Eurasians[4,5,10,31], including 30 Modern Greek samples from Greece and Cyprus. For abbreviations of population names, see Methods.

the southern Peloponnese (about 5400 BC), adding to previously published samples from northern Greece[2] (collectively labelled Greece_N). Finally, it included three Bronze Age individuals (approximately 2800–1800 BC; labelled Anatolia_BA) from Harmanören Göndürle in southwestern Anatolia (Turkey), adding knowledge about genetic variation in Anatolia after the Neolithic/Chalcolithic periods[1,2,4,17] (Supplementary Information section 1). We processed the ancient remains, extracted DNA, and prepared Illumina libraries in dedicated clean rooms (Methods and Supplementary Table 1), and, after initial screening for mitochondrial DNA, used in-solution hybridization[18] to capture ∼1.2 million single nucleotide polymorphisms (SNPs)[6,19] on the ancient samples. We assessed contamination by examining the rate at which they matched the mitochondrial consensus sequence (Supplementary Table 2) and the rate at which male samples were heterozygous on the X chromosome (Methods). We combined the dataset of the 19 ancient individuals with 332 other ancient individuals from the literature, 2,614 present-day humans genotyped on the Human Origins array, and 2 present-day Cretans (Methods).

We performed principal component analysis (PCA)[20] (Methods), projecting ancient samples onto the first two principal components inferred from present-day West Eurasian populations[10] that form two south–north parallel clines in Europe and the Near East along principal component 2. Minoans and Mycenaeans were centrally positioned in the PCA (Fig. 1b), framed to the left by ancient populations from mainland Europe and the Eurasian steppe, to the right by ancient populations from the Caucasus and Western Asia, and to the bottom by Early/Middle Neolithic farmers from Europe and Anatolia. The Neolithic samples from Greece clustered with these farmers and were distinct from the Minoans and Mycenaeans. The Bronze Age individuals from southwestern Anatolia were also distinct, intermediate between Anatolian and Levantine populations towards the bottom, and populations from Armenia, Iran, and the Caucasus

Table 1 | Admixture modelling of Bronze Age populations

		Ancestral sources				Mixture proportions				Standard errors			
	Test	A	B	C	D	A	B	C	D	A	B	C	D
Ultimate sources	Anatolia_BA		CHG	Anatolia_N	Levant_N		0.319	0.618	0.063		0.029	0.078	0.063
	Minoan_Odigitria		CHG	Anatolia_N			0.144	0.856			0.031	0.031	
	Minoan_Odigitria		Iran_N	Anatolia_N			0.137	0.863			0.032	0.032	
	Minoan_Lasithi	MA1	CHG	Anatolia_N		0.001	0.152	0.847		0.015	0.021	0.020	
	Minoan_Lasithi	Mota	CHG	Anatolia_N		0.004	0.154	0.842		0.024	0.026	0.020	
	Mycenaean	AfontovaGora3	CHG	Anatolia_N		0.133	0.126	0.741		0.027	0.026	0.024	
	Mycenaean	AfontovaGora3	Iran_N	Anatolia_N		0.161	0.086	0.754		0.026	0.025	0.024	
	Mycenaean	EHG	Iran_N	Anatolia_N		0.065	0.136	0.799		0.016	0.022	0.024	
	Mycenaean	EHG	CHG	Anatolia_N		0.044	0.176	0.780		0.016	0.023	0.024	
	Mycenaean	MA1	CHG	Anatolia_N		0.052	0.159	0.789		0.019	0.026	0.024	
Proximate sources	Anatolia_BA			Anatolia_ChL	Natufian			0.908	0.092			0.039	0.039
	Anatolia_BA			Anatolia_ChL	Levant_BA			0.892	0.108			0.114	0.114
	Anatolia_BA			Anatolia_ChL	Levant_N			0.951	0.049			0.051	0.051
	Anatolia_BA			Anatolia_ChL	Anatolia_N			0.935	0.065			0.062	0.062
	Mycenaean		Armenia_MLBA	Anatolia_N			0.367	0.633			0.020	0.020	
	Mycenaean		Armenia_ChL	Anatolia_N			0.441	0.559			0.025	0.025	
	Anatolia_BA		Anatolia_ChL	Minoan_Lasithi			0.970	0.030			0.108	0.108	
	Mycenaean	Steppe_MLBA		Minoan_Lasithi		0.175		0.825		0.017		0.017	
	Mycenaean	Europe_LNBA		Minoan_Lasithi		0.198		0.802		0.019		0.019	
	Mycenaean	Steppe_EMBA		Minoan_Lasithi		0.132		0.868		0.014		0.014	

For each test population, mixture proportions from four source populations with their standard errors are given. Ancestry is inferred from both 'ultimate' sources representing the earliest populations, and 'proximate' sources representing populations down to the Bronze Age (Supplementary Information section 2). Column A lists 'northern' sources from eastern Europe and Siberia, including the Eurasian steppe; column B lists 'eastern' sources from Iran, the Caucasus, and Anatolia (after the Early Neolithic); column C lists 'local' sources from Anatolia and the Aegean; column D lists sources from the Levant. For abbreviations of population names, see Methods.

towards the top. ADMIXTURE analysis (Methods and Extended Data Fig. 1) showed that Minoans and Mycenaeans both possessed a 'pink' genetic component ($K = 8$ and greater) shared with Bronze Age southwestern Anatolians, Neolithic Central Anatolians from Tepecik-Çiftlik[17], a Chalcolithic northwestern Anatolian[1], and western Anatolians from Kumtepe[16]. This component was maximized in the Mesolithic/Neolithic samples from Iran[4,5] and hunter–gatherers from the Caucasus[3] (Extended Data Fig. 1). It was not found in the Neolithic of northwestern Anatolia, Greece, or the Early/Middle Neolithic populations of the rest of Europe, only appearing in the populations of the Late Neolithic/Bronze Age in mainland Europe[6], introduced there by migration from the Eurasian steppe[1,6].

Beyond the visual impressions of PCA and ADMIXTURE, we formally tested the relationships among populations from our study and the literature, using f_4-statistics of the form $f_4(X, Y; \text{Test}, \text{Chimp})$ that evaluated whether Test shared more alleles with X or Y. We found that Test populations from Iran, the Caucasus, and eastern Europe shared more alleles with Minoans and Mycenaeans than with the Neolithic population of Greece (Extended Data Fig. 2a, b). The Minoans from the Lasithi plateau in the highlands of eastern Crete and from the coast of southern Crete (Extended Data Fig. 2c) were consistent with being a homogeneous population. Mycenaeans differed from these Minoans in sharing significantly fewer alleles with Neolithic people from the Levant, Anatolia, Greece, and mainland Europe (Extended Data Fig. 2d). In comparison, the Bronze Age Anatolians shared fewer alleles with ancient Europeans and more with ancient populations of Iran and the Levant (Extended Data Fig. 3). We used f_3-statistics of the form $f_3(\text{Ref}_1, \text{Ref}_2; \text{Test})$ that, if negative, showed that Test was admixed from sources related to the Ref_1, Ref_2 source populations. We did not find significantly negative (Ref_1, Ref_2) pairs for Minoans or Bronze Age Anatolians ($z > -2.5$), but did for Mycenaeans ($-4.9 < z < -3.0$; Extended Data Fig. 4), involving early farmers from the Levant, Anatolia, Greece, and the rest of Europe as one source, and Iran or the Eurasian steppe or steppe-influenced Europeans as the other.

We modelled Bronze Age populations using the qpAdm/qpWave[6] framework (Methods and Supplementary Information section 2), which relates a set of 'left' populations (admixed population and ancestral source populations) with a set of 'right' populations (diverse outgroups) and allows testing for the number of streams of ancestry from 'right' to 'left' and estimation of admixture proportions. This analysis showed that all Bronze Age populations from the Aegean and Anatolia are consistent with deriving most (approximately 62–86%) of their ancestry from an Anatolian Neolithic-related population (Table 1). However, they also had a component (approximately 9–32%) of 'eastern' (Caucasus/Iran-related) ancestry. It was previously shown that this type of ancestry was introduced into mainland Europe via Bronze Age pastoralists from the Eurasian steppe, who were a mix of both eastern European hunter–gatherers and populations from the Caucasus and Iran[4,6]; our results show that it also arrived on its own, at least in the Minoans, without eastern European hunter–gatherer ancestry. This ancestry need not have arrived from regions east of Anatolia, as it was already present during the Neolithic in central Anatolia at Tepecik-Çiftlik[17] (Supplementary Information section 2). The eastern influence in the Bronze Age populations from Greece and southwestern Anatolia is also supported by an analysis of their Y chromosomes. Four out of five males belonging to Minoans, Mycenaeans, and southwestern Anatolians (Supplementary Information section 3) belonged to haplogroup J, which was rare or non-existent in earlier populations from Greece and western Anatolia who were dominated by Y-chromosome haplogroup G2 (refs 1, 2, 17). Haplogroup J was present in Caucasus hunter–gatherers[3] and a Mesolithic individual from Iran[4], and its spread westwards may have accompanied the 'eastern' genome-wide influence.

The Minoans could be modelled as a mixture of the Anatolia Neolithic-related substratum with additional 'eastern' ancestry, but the other two groups had additional ancestry: the Mycenaeans had approximately 4–16% ancestry from a 'northern' ultimate source related to the hunter–gatherers of eastern Europe and Siberia (Table 1), while the Bronze Age southwestern Anatolians may have had ~6% ancestry related to Neolithic Levantine populations. The elite Mycenaean individual from the 'royal' tomb at Peristeria in the western Peloponnese did not differ genetically from the other three Mycenaean individuals buried in common graves. To identify more proximate sources of the distinctive eastern European/north Eurasian-related ancestry in Mycenaeans, we included later populations as candidate sources (Supplementary Information section 2), and could model Mycenaeans as a mixture of the Anatolian Neolithic and Chalcolithic-to-Bronze Age populations from Armenia (Table 1). Populations from Armenia possessed some ancestry related to eastern European hunter–gatherers[4], so they, or similar unsampled populations of western Asia, could have contributed it to populations of the Aegean. This model makes geographical sense, since a population movement from the vicinity of

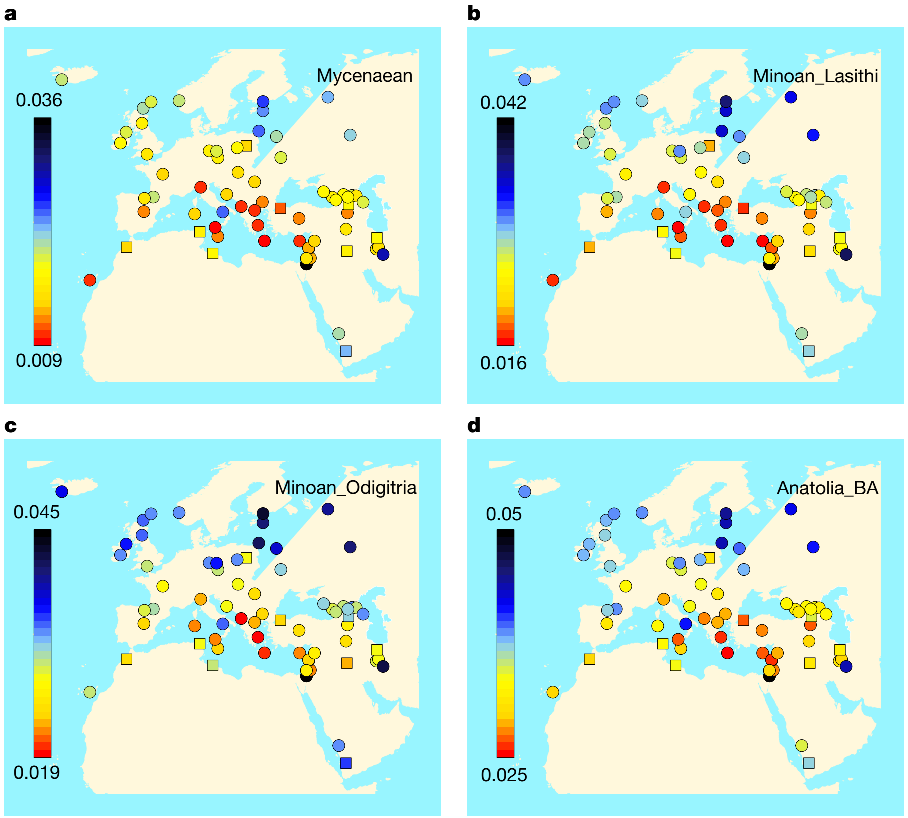

Figure 2 | Genetic differentiation of Bronze Age populations to present-day populations. The F_{ST} inbreeding coefficient (Methods) between newly reported populations and present-day West Eurasian populations. This shows a pattern of genetic affinity between Bronze Age and present-day populations from the corresponding broad geographical regions: **a**, Mycenaeans; **b**, Minoans from Hagios Charalambos (Lasithi regional unit); **c**, Minoans from Moni Odigitria (Herakleion regional unit); **d**, southwestern Bronze Age (BA) Anatolians. The same pattern also applies to Bronze Age populations from other regions of West Eurasia (Extended Data Fig. 5).

Armenia could have admixed with Anatolian Neolithic-related farmers on either side of the Aegean. However, Mycenaeans can also be modelled as a mixture of Minoans and Bronze Age steppe populations (Table 1 and Supplementary Information section 2), suggesting that, alternatively, 'eastern' ancestry arrived in both Crete and mainland Greece, followed by about 13–18% admixture with a 'northern' steppe population in mainland Greece only. Such a scenario is also plausible: first, it provides a genetic correlate for the distribution of shared toponyms in Crete, mainland Greece, and Anatolia discovered in ref. 21; second, it postulates a single migration from the east; third, it proposes some gene flow from geographically contiguous areas to the north where steppe ancestry was present since at least the mid-third millennium BC (refs 6, 9). We validated inferences from qpAdm by treating source populations as 'ghosts' and re-estimating mixture proportions[4], by examining the correspondence between qpAdm estimates and PCA[4] (Extended Data Fig. 5), and by comparing simulated individuals of known ancestry against the Mycenaeans (Extended Data Fig. 6).

Geographical structure may have prevented the spread of the 'northern' ancestry from the mainland to Crete, contributing to genetic differentiation. Such a structure may, in principle, be long-standing, even before the advent of the Neolithic in the seventh millennium BC. Alternatively, both 'northern' and 'eastern' ancestry may have arrived in the Aegean at any time between the Early Neolithic and the Late Bronze Age. Wider geographical and temporal sampling of pre-Bronze Age populations of the Aegean may better trace the advent of 'northern' and 'eastern' ancestry in the region. However, sampled Neolithic samples from Greece, down to the Final Neolithic ~4100 BC (ref. 2), do not possess either type of ancestry, suggesting that the admixture we detect probably occurred during the fourth to second millennium BC time window. Other proposed migrations, such as settlement by Egyptian or Phoenician colonists[22], are not discernible in our data, as there is no measurable Levantine or African influence in the Minoans and Mycenaeans, thus rejecting the hypothesis that the cultures of the Aegean were seeded by migrants from the old civilizations of these regions. On the other hand, migrants from areas east or north of the Aegean, while numerically less influential than the locals, may have contributed to the emergence of the third to second millennium BC Bronze Age cultures as 'creative disruptors' of local traditions, bearers of innovations, or through cultural interaction with the locals, coinciding with the genetic process of admixture[23]. Relative ancestral contributions do not determine the relative roles in the rise of civilization of the different ancestral populations; nonetheless, the strong persistence of the Neolithic substratum does suggest a key role for the locals in this process.

Phenotype prediction from genetic data has enabled the reconstruction of the appearance of ancient Europeans[1,24] who left no visual record of their pigmentation. By contrast, the appearance of the Bronze Age people of the Aegean has been preserved in colourful frescos and pottery, depicting people with mostly dark hair and eyes[25]. We used the HIrisPlex[26] tool (Supplementary Information section 4) to infer that the appearance of our ancient samples matched the visual representations (Extended Data Table 2), suggesting that art of this period reproduced phenotypes naturalistically.

We estimated the fixation index, F_{ST}, of Bronze Age populations with present-day West Eurasians, finding that Mycenaeans were least differentiated from populations from Greece, Cyprus, Albania, and Italy (Fig. 2), part of a general pattern in which Bronze Age populations broadly resembled present-day inhabitants from the same region (Extended Data Fig. 7). Modern Greeks occupy the intermediate space of the PCA along principal component 1 (Fig. 1b) between ancient European and Near Eastern populations, such as those of the Bronze Age. They are not, however, identical to Bronze Age populations, as they are above them along principal component 2 (Fig. 1b). This is because Neolithic farmers shared fewer alleles with Modern Greeks than with Mycenaeans (Extended Data Fig. 8), consistent with additional later admixture[27,28].

The Minoans and Mycenaeans, sampled from different sites in Crete and mainland Greece, were homogeneous, supporting the genetic coherency of these two groups. Differences between them were modest, viewed against their broad overall similarity to each other and to the southwestern Anatolians, sharing in both the 'local' Anatolian Neolithic-like farmer ancestry and the 'eastern' Caucasus-related admixture. Two key questions remain to be addressed by future studies. First, when did the common 'eastern' ancestry of both Minoans and Mycenaeans arrive in the Aegean? Second, is the 'northern' ancestry in Mycenaeans due to sporadic infiltration of Greece, or to a rapid migration as in Central Europe[6]? Such a migration would support the idea that proto-Greek speakers[29] formed the southern wing of a steppe intrusion of Indo-European speakers. Yet, the absence of 'northern' ancestry in the Bronze Age samples from Pisidia, where Indo-European languages were attested in antiquity, casts doubt on this genetic–linguistic association, with further sampling of ancient Anatolian speakers needed. Whatever the answer to these questions, the discovery of at least two migration events into the Aegean in addition to the first farming dispersal before the Bronze Age, and of additional population change since that time, supports the view that the Greeks did not emerge fully formed from the depths of prehistory, but were, indeed, a people 'ever in the process of becoming'[30].

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions G.S. conceived the study. D.R. and J.K. co-supervised the ancient DNA work, sequencing, and data analysis. I.L. performed population genetics analysis and wrote the manuscript with input from other authors. P.J.P.McG., E.K.-Y., G.K., H.M., M.M., M.Ö., N.Ö., A.Pa., M.R., S.A.R., Y.T., A.V., R.A., P.S., R.P., J.K., and G.S. assembled, studied, or described archaeological and osteological material. A.M., S.P., N.R., A.F., C.P., D.M.F., J.R.H., D.M.L., Y.M., J.A.S., K.St., R.P., G.S., D.R., P.A.N., and J.K. performed wet laboratory work. A.M., N.P., S.M., and A.Pe., performed bioinformatics analyses.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations. Correspondence and requests for materials should be addressed to I.L. (lazaridis@genetics.med.harvard.edu), D.R. (reich@genetics.med.harvard.edu), J.K. (krause@shh.mpg.de), or G.S. (gstam@u.washington.edu).

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METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Ancient DNA. An overview of which steps in processing the ancient samples were undertaken in which laboratory is provided in Supplementary Table 1.

Dublin, Ireland. The inner ear area of each petrous bone was identified, isolated, then ground to a fine powder. Cleaning and isolation of the cochlea was performed using aluminium oxide powder in a sandblasting chamber. Once isolated, it was decontaminated by ultraviolet irradiation for 7.5 min on each side, ground on a mixer mill to a weight of about 50 mg, and finally transferred to a sterile Eppendorf tube. All procedures were conducted in clean and dedicated ancient DNA facilities.

Seattle, Washington, USA. Teeth processed in this laboratory were decontaminated and pulverized to powder in clean and dedicated ancient DNA facilities following previously published methods[11].

Leipzig, Germany. As previously described[32], sampling, extraction, and preparation of double-indexed, double-stranded libraries took place in the clean room facilities of the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany (MPI-EVA), followed by enrichment of human mitochondrial DNA[33]. Enriched libraries were sequenced on an Illumina GAIIx platform for $2 \times 76 + 7$ cycles and the resulting data were mapped to the revised Cambridge Reference Sequence using the EAGER pipeline to evaluate DNA preservation (Supplementary Table 2). These libraries were then shipped to Boston, Massachusetts, USA, where nuclear target enrichment was performed (see below).

Tübingen, Germany. Pre-PCR steps took place in the clean room facilities of the Institute for Archaeological Sciences at the University of Tübingen, Germany. After surface irradiation with ultraviolet light, the tooth was sawn apart transversally at the border of crown and root, and dentine powder from the inside the crown was sampled using a sterile dentistry drill. Extraction, library preparation, and enrichment of human mitochondrial DNA used the same protocols as described for MPI-EVA, with the addition of an updated extraction protocol[34]. Sequencing of shotgun and mitochondrial-DNA-enriched libraries took place at the facilities of the Frauenklinik of the University of Tübingen, on an Illumina MiSeq for $2 \times 150 + 8$ cycles or on an Illumina HiSeq 2500 for $2 \times 101 + 8$ cycles (Supplementary Table 2).

Additional libraries were produced including full or partial[35] repair with uracil-DNA glycosylase and endonuclease VIII to remove deaminated bases. In-solution enrichment was performed using previously reported protocols[6,18]. Two SNP sets of 394,577 SNPs ('390k capture'[6]) or 1,237,207 SNPs ('1240k capture'[1]) were targeted. Sequencing took place in the facilities of the Frauenklinik, University of Tübingen, on an Illumina HiSeq 2500 for $2 \times 101 + 8$ cycles and at the facilities of the University of Kiel on a HiSeq 4000 for $2 \times 150 + 8$ cycles. One uracil-DNA glycosylase-treated library (I0071) was sent to Boston, Massachusetts, for nuclear target enrichment (see below).

Boston, Massachusetts, USA. The bone powders, prepared from petrous bones in Dublin, Ireland, were sent to Boston, where DNA extractions and barcoded library preparations without uracil removal were performed in the Harvard Medical School cleanroom following previously described protocols[34–36]. At the screening stage, libraries were (1) shotgun sequenced and (2) sequenced after enriching for the human mitochondrial DNA[37] together with some nuclear loci to approximate the nuclear coverage and mitochondrial contamination.

All four libraries (barcoded) prepared in Boston, three libraries (indexed) prepared in Leipzig, and one library (indexed) prepared in Tübingen, were used to perform 390k (ref. 6) and 840k (ref. 19) or 1240k (=390k + 840k) targeted capture of a total of 1,233,013 SNPs, following the in-solution target enrichment protocol in ref. 18 and sequenced either on an Illumina HiSeq 2500 or an Illumina NextSeq 500 (see Supplementary Table 1 for details).

For each sample, each SNP position was represented by a randomly chosen sequence, restricting to those with a minimum mapping quality ($\text{MAPQ} \geq 10$), sites with a minimum sequence quality (≥ 20), and removing two bases at the ends of reads[4].

Testing for contamination. Modern human contamination of the mitochondrial DNA was assessed using the software schmutzi[38], which took into account that the consensus sequence should be reconstructed from reads showing characteristics of ancient DNA and originating from a single individual (Supplementary Table 2). We assessed contamination by examining heterozygosity on the X chromosome in five males (possessing only one copy of the X chromosome) using ANGSD[39] (Supplementary Information section 3); this was in the range 0.3–4%. Indirect evidence that the females in our dataset (for which X-chromosome-based contamination estimation was impossible) were authentic was furnished by their clustering with male samples and distinctiveness from present-day Greek or central European populations that may have possibly contaminated them (Fig. 1b). We also computed f_4-statistics of the form f_4(Males, Females; Test, Chimp) for populations that had both male and female individuals for all ancient or present-day Test populations in our dataset. If female samples were substantially contaminated from a source related to Test, these statistics would be significantly negative; however, we found that the Z-score of these statistics was $-1.6 < Z < 2.5$. We thus included both male and female samples in our analysis to maximize sample size instead of restricting it to damaged molecules for females[8].

Modern human data. We used a dataset of 2,614 individuals genotyped on the Affymetrix Human Origins array[4,5,10,31], including 28 Modern Greek (from Greece and Cyprus) samples previously described[10]. We also included data from two Modern Greeks from Crete whose whole-genome sequences were published as part of the Simons Genome Diversity Project[40]. We also analysed Modern Greek data from Thessaly and Central Greece[41] and diverse regions[27,42] genotyped on Illumina arrays.

Datasets. We analysed two datasets: HO, which includes the Affymetrix Human Origins genotyping data together with 351 ancient humans (including samples from the literature[1–5,7–10,16,17,43–51] and the newly reported data) on 591,642 autosomal SNPs; and the HOIll dataset, which does not include the Human Origins data, but has a larger number of 1,054,671 autosomal SNPs[4]. We did not use previously performed genotype calls of data from the literature, but re-processed them, beginning with the original data release format (FASTQ or BAM). The main analysis dataset was HOIll, except for analyses that included modern populations, in which case the HO dataset was analysed. For the analysis of Illumina genotype data of Modern Greeks (Extended Data Fig. 6), a total of 489,148 autosomal SNPs were analysed.

Abbreviations used. For brevity, we used the following abbreviations in population names, following the convention of ref. 4: CHG, Caucasus hunter–gatherers; EHG, Eastern European hunter–gatherers; WHG, Western European hunter–gatherers; SHG, Scandinavian hunter–gatherers; N, Neolithic; EN, Early Neolithic; MN, Middle Neolithic; ChL, Chalcolithic; LNBA, Late Neolithic/Bronze Age; BA, Bronze Age; EBA, Early Bronze Age; EMBA, Early/Middle Bronze Age; MLBA, Middle/Late Bronze Age; IA, Iron Age.

PCA. PCA was performed in the smartpca program of EIGENSOFT[20], using default parameters and the lsqproject: YES[10] and numoutlieriter: 0 options. PCA was performed on 1,029 present-day West Eurasians and 334 ancient samples were projected (Fig. 1b); Upper Palaeolithic individuals before the appearance of the Villabruna cluster[8] plot in the middle of present-day West Eurasian variation and are not shown.

ADMIXTURE analysis. ADMIXTURE analysis[52] of the HO dataset was performed after pruning for linkage disequilibrium in PLINK[53,54] with parameters indep-pairwise 200 25 0.4, after which 299,971 SNPs were retained. Twenty replicates of the analysis were performed with different random seeds, and the highest likelihood replicate for each value of K was retained. We show the $K = 2$ to $K = 17$ results for the 351 ancient and 30 Modern Greek samples in Extended Data Fig. 1.

***f*-statistics.** The f_3- and f_4-statistics were computed in ADMIXTOOLS[31] using the programs qp3Pop and qpF4ratio with default parameters, and qpDstat with f4mode: YES. Standard errors were computed with a block jack-knife[55]. When an ancient population was the target for f_3-statistics, we set the inbreed: YES parameter, as our data were represented by pseudo-haploid genotypes, which introduced artificial genetic drift that masked the negative signal of admixture[31].

Testing for the number of streams of ancestry and estimating mixture proportions. We used the qpWave[6,56,57]/qpAdm[6] framework, which relates a set of 'left' populations (the population of interest and candidate ancestral sources) to a set of 'right' populations (diverse outgroups), testing for the number of streams of ancestry from 'right' to 'left' and estimating mixture proportions.

Simulations of admixed individuals. We simulated admixed individuals (Supplementary Information section 2) given a set of sources and mixture proportions by first sampling (at each SNP) one of the sources (according to the mixture proportions), and then one of the individuals from that population (with equal probability). Because of missingness, the data-generating mixture proportions did not correspond precisely to the actual ancestry of simulated individuals and we corrected for this bias (Supplementary Information section 2). We noted the maximum absolute value of the Z-score of the statistic f_4(Mycenaean, Simulated; A, B), where A, B were two outgroup populations to test whether, for a particular choice of ancestry of Simulated, it formed a clade with the sampled Mycenaeans.

Estimation of F_{ST} coefficients. We estimated F_{ST} in smartpca[20] with the default parameters inbreed: YES[57], and fstonly: YES.

Phenotypic inference. The ancient samples had low coverage (median 0.87×) and thus diploid genotypes could not be reliably assessed for them. However, we could use the low coverage data to compute allele frequencies in all individuals and the Bronze Age Aegean using a likelihood approach[1]. We then sampled from the posterior distribution of the genotypes g given the read counts r of the reference allele and t of the total reads covering a site. We took 100 random genotype samples per individuals and submitted them to HIrisPlex[26], obtaining an estimate of the uncertainty of phenotype inference (Supplementary Information section 4 and Extended Data Table 2).

Data availability. The aligned sequences are available through the European Nucleotide Archive under accession number PRJEB20914. Genotype datasets used in analysis are available at https://reich.hms.harvard.edu/datasets. All other data are available from the corresponding authors upon reasonable request.

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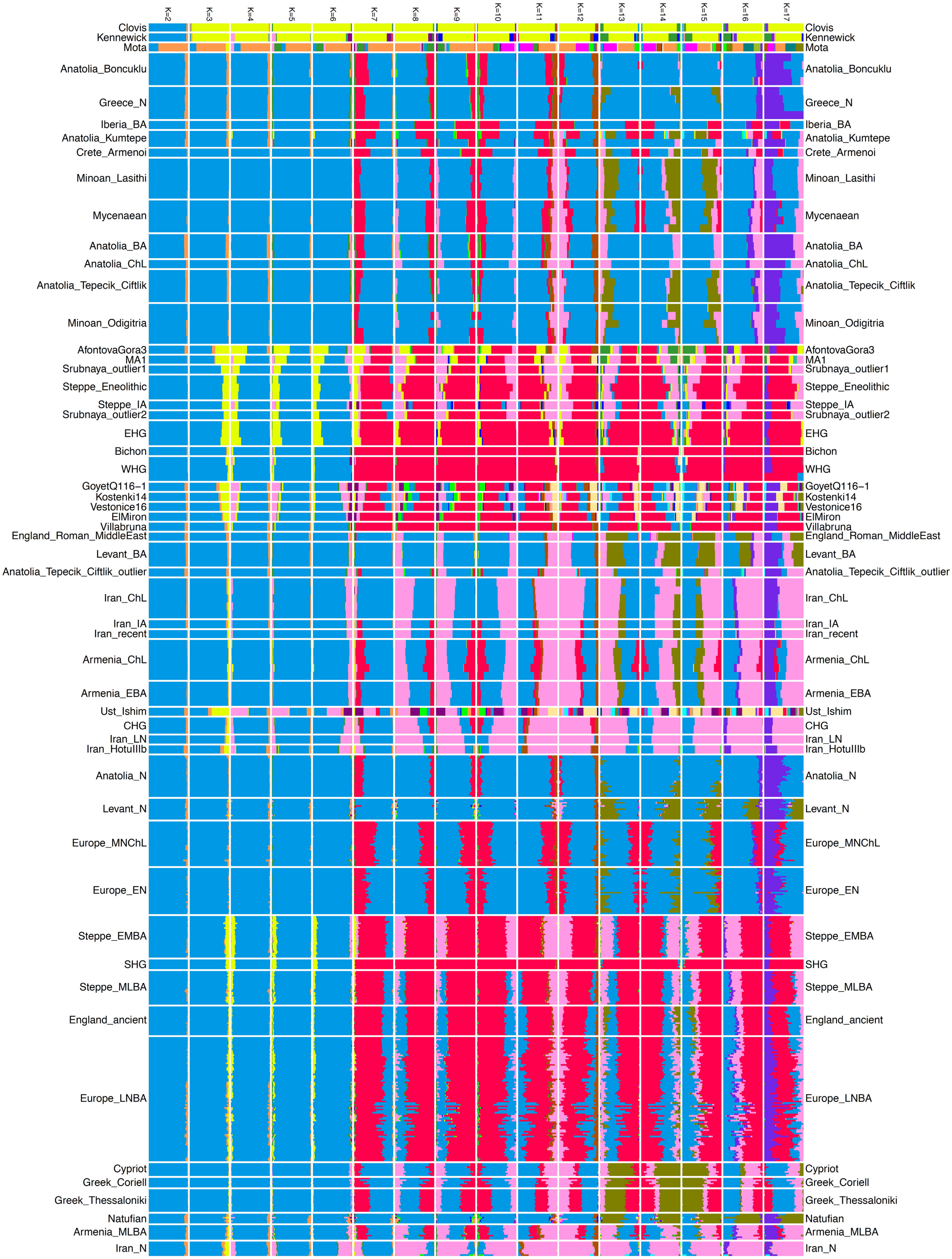
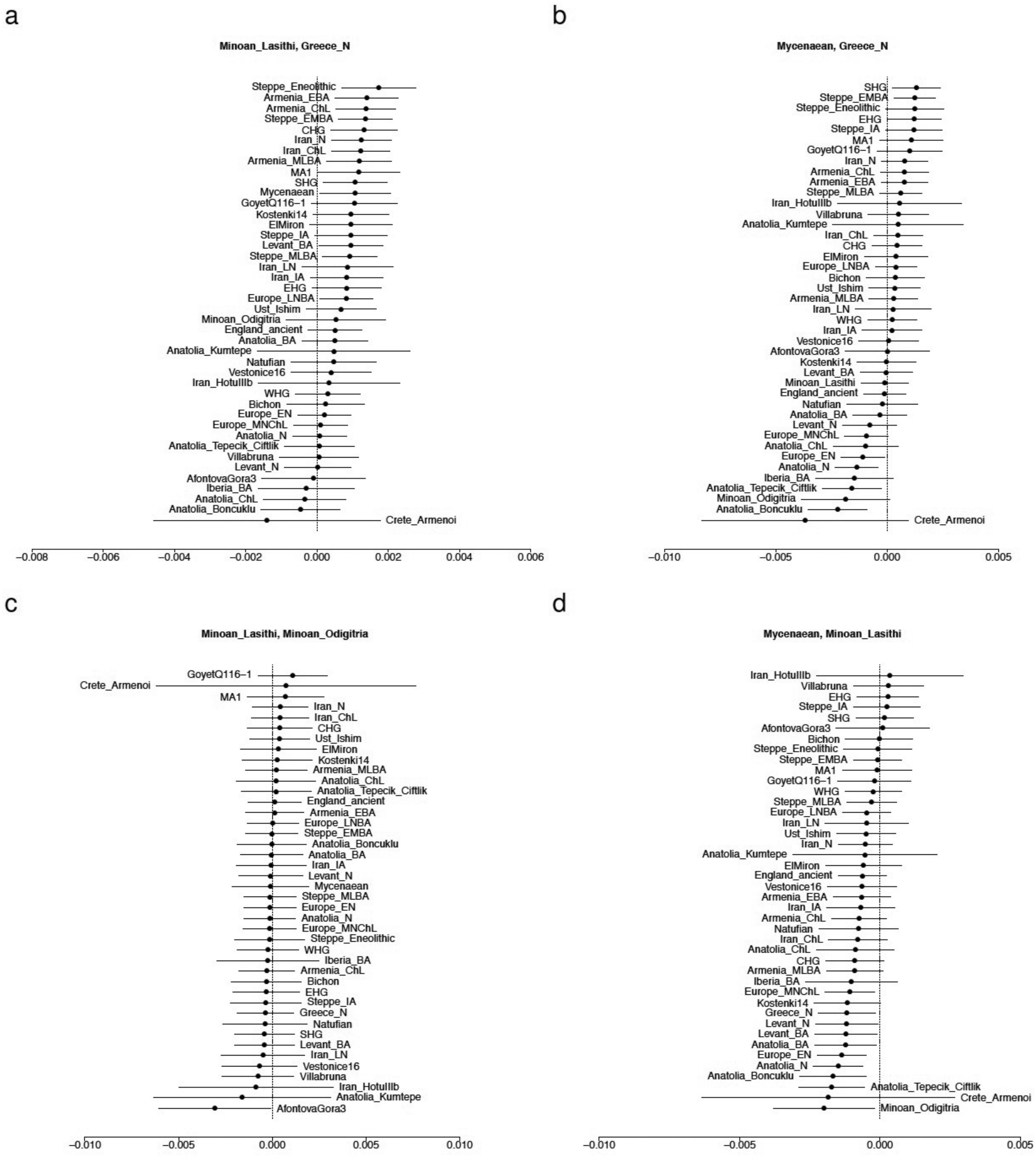
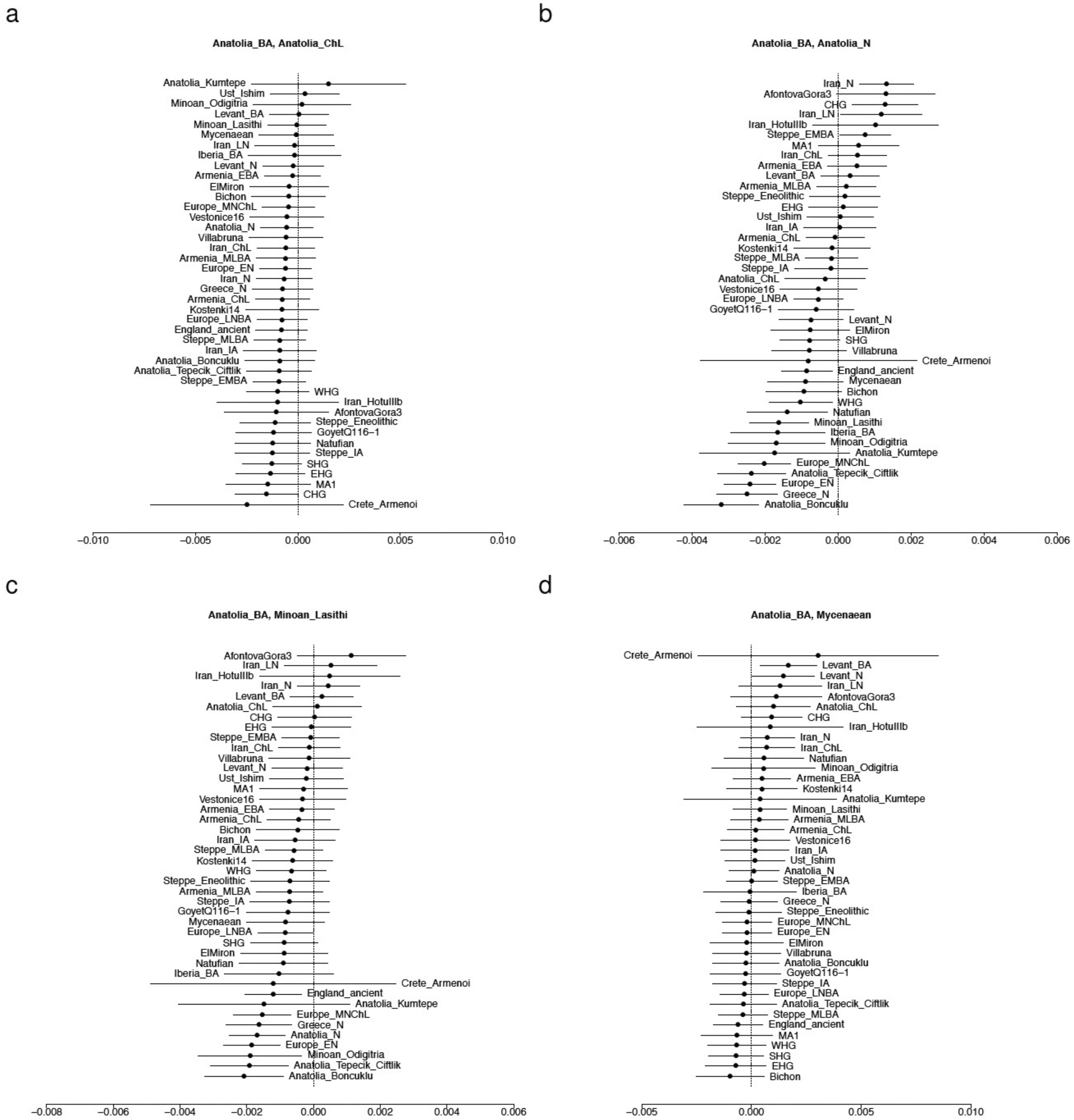


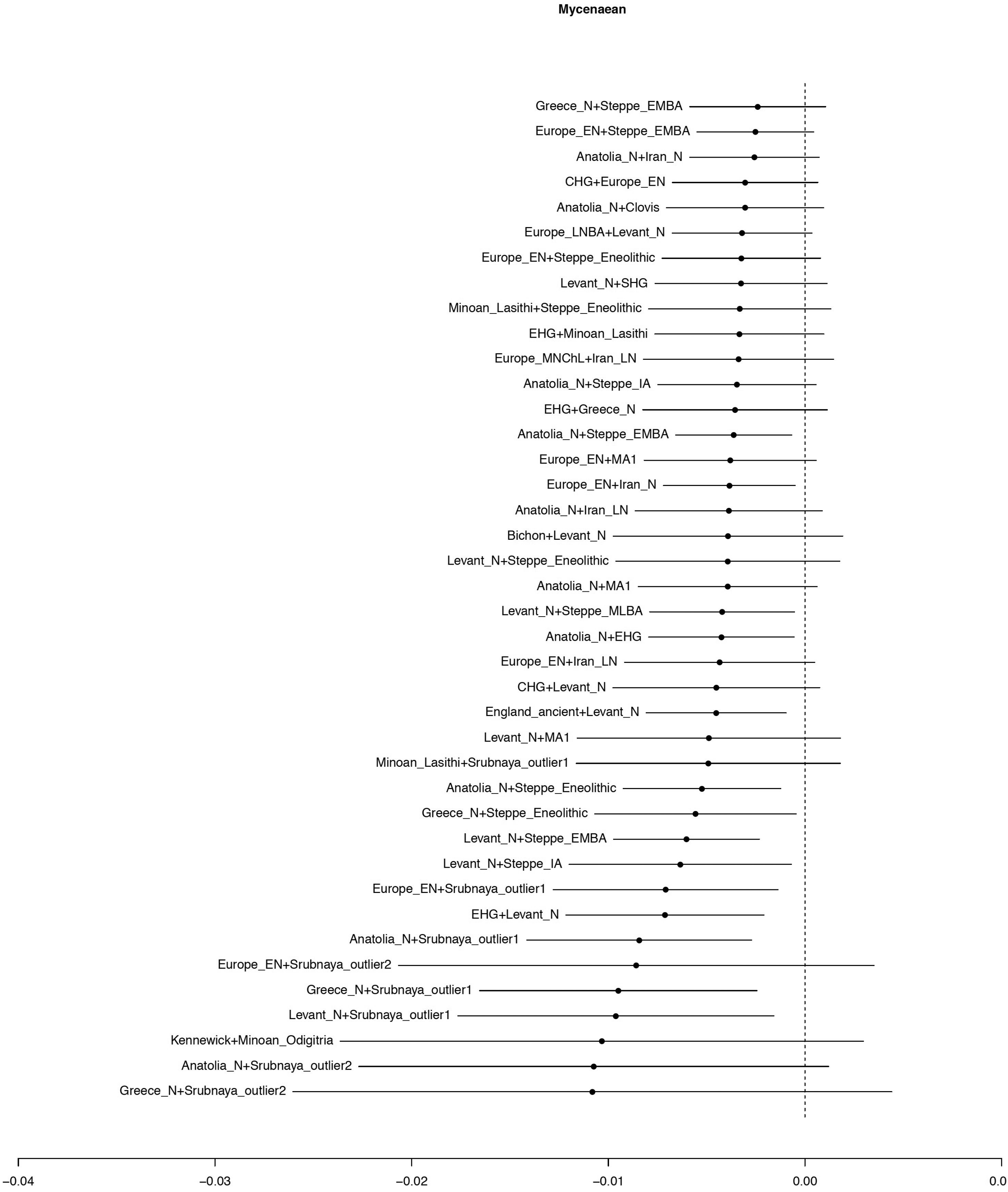
Extended Data Figure 1 | ADMIXTURE analysis. ADMIXTURE analysis (Methods) with $K = 2$ to $K = 17$ is shown. Three hundred and fifty-one ancient and 2,616 present-day individuals were used in this analysis; ancient samples and present-day Greeks are displayed. To avoid visual clutter of labels, individuals in populations with sample size ≤ 5 are shown with thicker lines.



Extended Data Figure 2 | Symmetry testing of Aegean Bronze Age populations. The statistic $f_4(X, Y; \text{Test}, \text{Chimp})$ is shown with ±3 standard errors. Each panel is titled with the pair *X*, *Y*. Populations are ordered according to the value of the statistic. Positive values indicate that Test shares more alleles with *X* than *Y*, and negative values that it shares more with *Y* than *X*. **a**, 'Northern' and 'eastern' populations share more alleles with Minoans than with Neolithic Greece. **b**, 'Northern' and 'eastern' populations share more alleles with Mycenaeans than with Neolithic Greece. **c**, Minoans from Lasithi and Moni Odigitria are symmetrically related to diverse populations. **d**, Neolithic populations from Anatolia, Europe, Greece, and the Levant share fewer alleles with Mycenaeans than with Minoans.

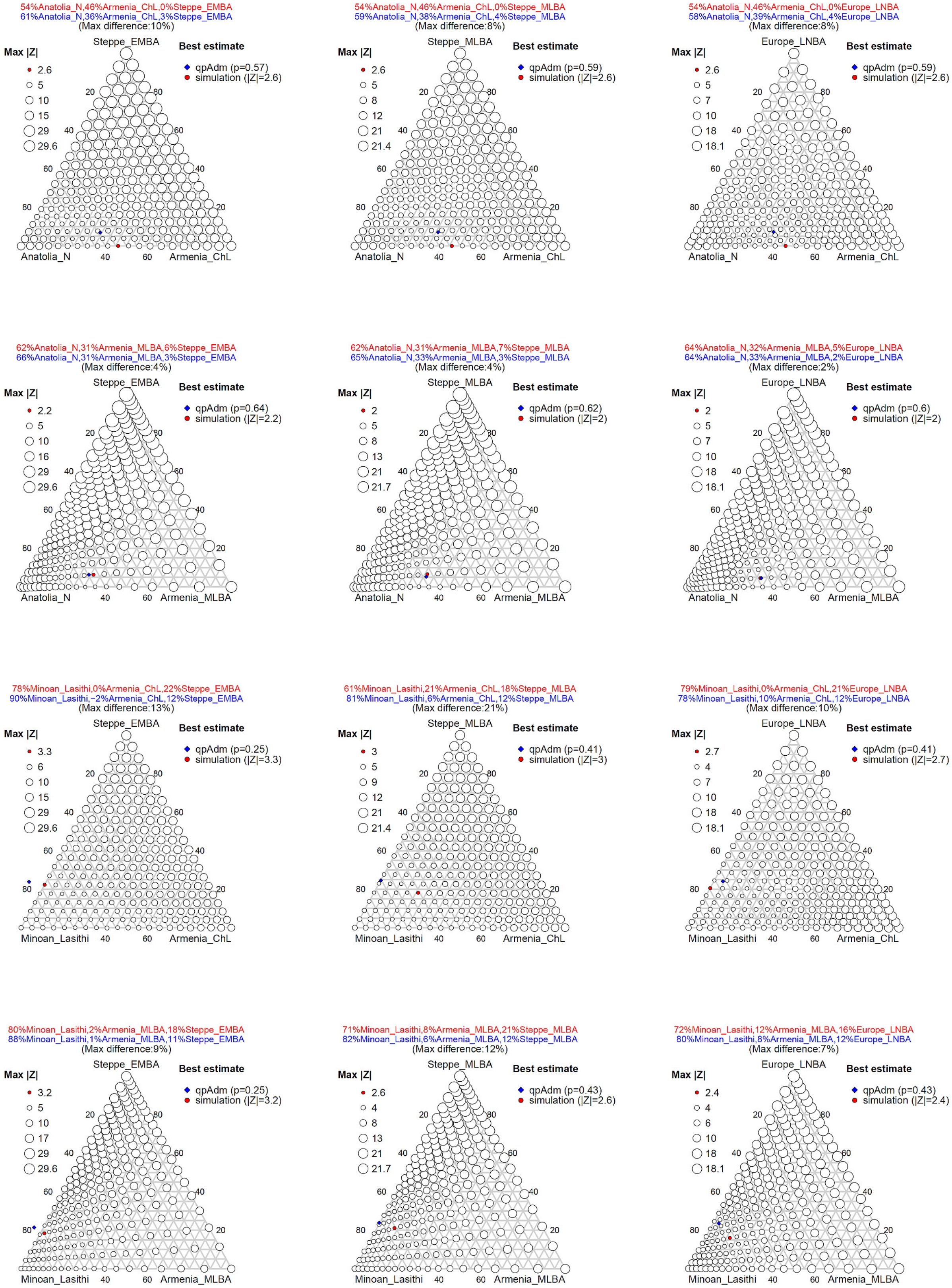


Extended Data Figure 3 | Symmetry testing of Anatolian Bronze Age populations. The statistic $f_4(X, Y; \text{Test}, \text{Chimp})$ is shown with ±3 standard errors. Each panel is titled with the pair *X*, *Y*. Populations are ordered according to the value of the statistic. Positive values indicate that Test shares more alleles with *X* than *Y*, and negative values that it shares more with *Y* than *X*. **a**, European, Siberian, and Caucasus hunter–gatherers share fewer alleles with Bronze Age Anatolians from Harmanören Göndürle than with a Chalcolithic Anatolian from Barcın. **b**, Bronze Age Anatolians differ from Neolithic ones in sharing more alleles with populations of Iran, the Caucasus, and the Steppe than with those of Europe. **c**, Bronze Age Anatolians differ from Minoans in sharing more alleles with populations from Neolithic Iran than Neolithic Anatolia and Europe. **d**, Bronze Age Anatolians differ from Mycenaeans in sharing more alleles with Neolithic and Bronze Age populations of the Levant.

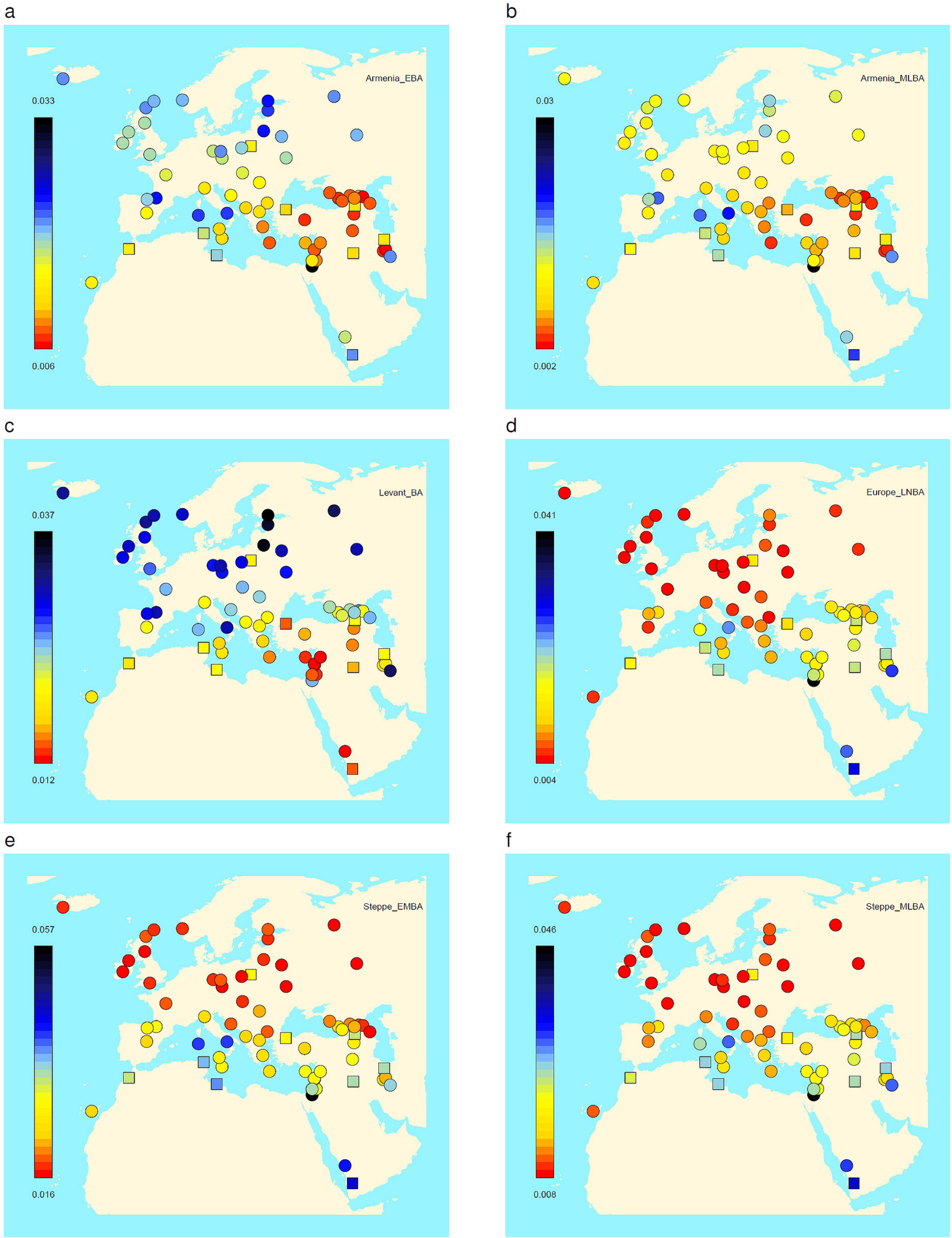


Extended Data Figure 4 | The f_3-statistics of Mycenaeans as a target with different pairs of reference populations. The value of the statistic $f_3(\text{Ref}_1, \text{Ref}_2; \text{Mycenaean})$ with ±3 standard errors; only the population pairs (Ref_1, Ref_2) for which the Z-score of the statistic is less than −2 are shown. Negative values indicate that the Mycenaean population is admixed from sources related to the two reference populations.

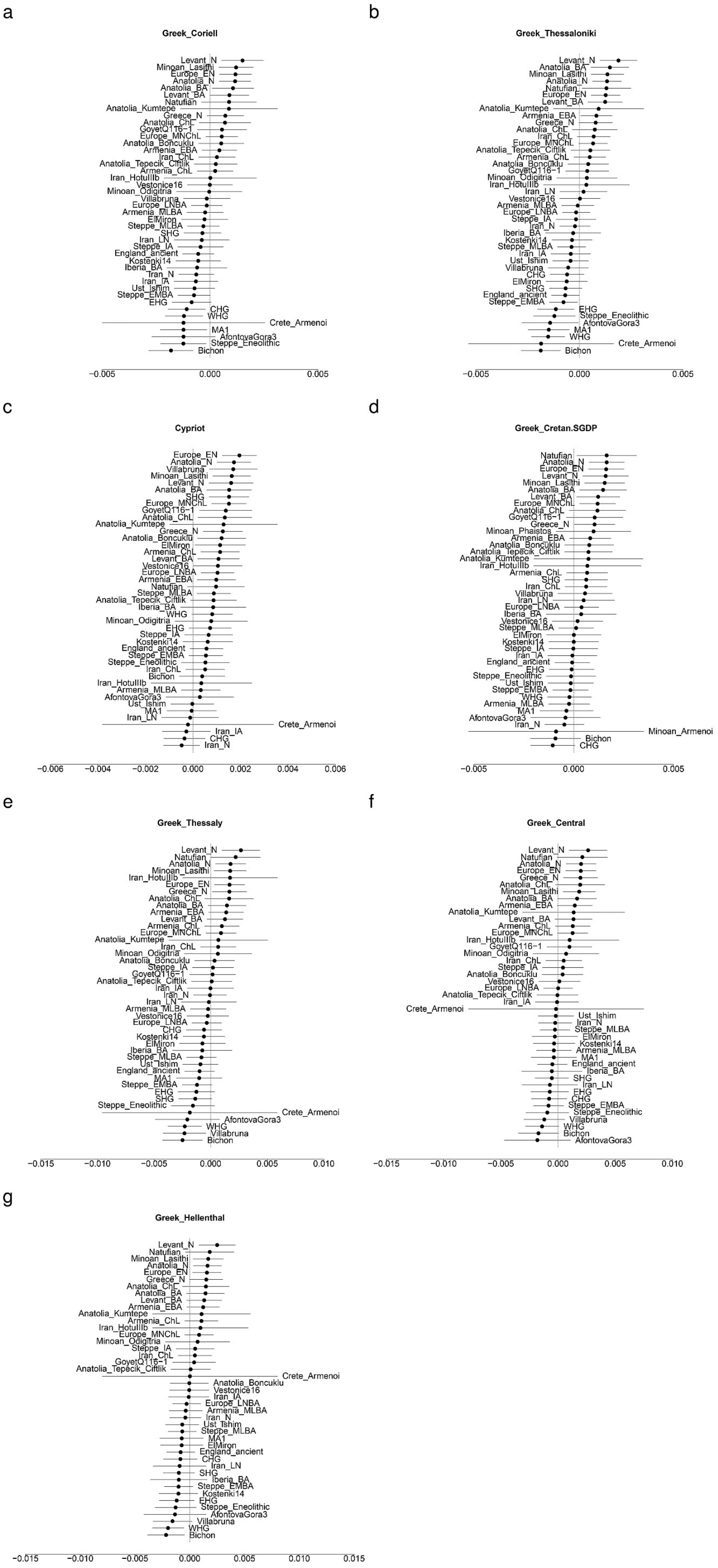
Extended Data Figure 5 | Correspondence of qpAdm estimates with PCA. As a way of validating qpAdm models of admixture for Mycenaeans from three ancestral populations (Anatolia_N or Minoan_Lasithi), (Armenia_ChL or Armenia_MLBA), (Steppe_EMBA, Steppe_MLBA, Europe_LNBA), representing substratum, 'eastern', and 'northern' ancestry, respectively (Supplementary Information section 2), we plot the qpAdm-predicted position in the PCA space of Fig. 1 versus the actual position of the Mycenaean population.



Extended Data Figure 6 | Comparison of Mycenaeans and simulated admixed populations. We simulate admixed individuals with known ancestry from three ancestral populations (Anatolia_N or Minoan_Lasithi), (Armenia_ChL or Armenia_MLBA), (Steppe_EMBA, Steppe_MLBA, Europe_LNBA), representing substratum, 'eastern', and 'northern' ancestry, respectively (Methods and Supplementary Information section 2). The maximum $|Z|$-score of statistics f_4(Mycenaean, Simulated; Outgroup$_1$, Outgroup$_2$) is plotted with circles of varying size (proportional to $\log(|Z|)$) for each assignment of ancestry proportions. The best estimate (red) corresponds to the proportions that minimize $|Z|$, and they are compared against the qpAdm estimate for the same ancestral sources (blue).



Extended Data Figure 7 | F_{ST} between Bronze Age and present-day West Eurasian populations. **a**, The population of Early Bronze Age Armenia[4] shows an affinity to present-day populations from Armenia, Anatolia, the Caucasus, and Iran, as does (**b**) Middle/Late Bronze Age Armenia[4,9]. **c**, The Bronze Age Levant[4] has an affinity to Levantine and Arabian populations. **d**, Late Neolithic/Bronze Age Europeans[1,6,9,43] most resemble present-day northern/central Europeans, as do (**e**) Early/Middle Bronze Age steppe populations[1,6,9], who also resemble populations of the northeast Caucasus, while (**f**) Middle/Late Bronze Age steppe populations resemble central/northern Europeans[1,9]. Jewish populations are plotted with a square to distinguish them from non-Jewish populations from the same geographical area. The plots for the newly reported populations of Mycenaeans, Minoans, and Bronze Age Anatolians are shown in Fig. 2.



Extended Data Figure 8 | Symmetry testing of Mycenaeans with Modern Greek populations. The statistic f_4(Mycenaean, Modern Greek; Test, Chimp) is shown with ±3 standard errors. Modern Greeks share fewer alleles with Levantine/Anatolian/European Neolithic populations and with Minoans than Mycenaeans, suggesting a dilution of Early Neolithic ancestry since the Bronze Age. Human Origins genotype data: **a**, Greeks from the Coriell repository[10]; **b**, Greeks from Thessaloniki[10]; **c**, Cypriots[10]. Whole-genome data: **d**, Cretans[40]. Illumina genotype data: **e**, Greeks from Thessaly[41]; **f**, Greeks from central Greece[41]; **g**, Greeks from the study in ref. 27.

Extended Data Table 1 | Information on ancient samples reported in this study

Individual_ID	Genotype_ID	Other_ID	Source	Date	Population_Label	Location	Country	Latitude	Longitude	Sex	Coverage	Autosomal_SNPs	mtDNA	Y-chromosome
I2937	I2937	A2197	1240K	5419±41 cal BC	Greece_N	Diros, Alepotrypa Cave	Greece	36.64	22.38	F	0.870	481848	K1a26	
I0071	I0071	Lasithi4	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	F	7.312	953157	U5a1	
I0070	I0070	Lasithi2	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	M	1.267	619767	H13a1	J2a1d
I0073	I0073	Lasithi7	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	M	1.481	643360	H	J2a1
I0074	I0074	Lasithi9	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	F	0.874	506434	H5	
I9005	I9005	Lasithi17	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	F	1.351	388859	H	
I9006	I9006	Salamis31	1240K	1411-1262 cal BCE (3067 ± 25 BP, DEM-2905)	Mycenaean	Agia Kyriaki, Salamis	Greece	37.97	23.50	F	1.387	361193	X2d	
I9123	I9123	S-EVA 1263 Armenoi 503	1240K	1370-1340 BCE	Crete_Armenoi	Armenoi, Crete	Greece	35.45	24.17	F	0.041	45158	U5a1	
I9127	I9127	12V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.035	36475	J2b1a1	
I9128	I9128	13V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.016	17081	I5	
I9129	I9129	14V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.063	63986	H+163	
I9130	I9130	16V Tholos	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	M	0.086	92186	U3b3	G2a2b2
I9131	I9131	19V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.095	96946	K1a2	
I9010	I9010	Galatas19	1240K	1700-1200 BCE	Mycenaean	Galatas Apatheia, Peloponnese	Greece	37.50	23.45	F	0.379	242265	X2	
I9033	I9033	Peristeria4	1240K	1416-1280 cal BCE (3084 ± 24 BP, DEM-2903)	Mycenaean	Peristeria Tryfilia, Peloponnese	Greece	36.92	21.70	F	0.439	248912	H	
I9041	I9041	Galatas4	1240K	1700-1200 BCE	Mycenaean	Galatas Apatheia, Peloponnese	Greece	37.50	23.45	M	1.558	417898	X2	J2a1
I2495	I2495	A4-1	1240K	2558-2295 calBCE (3925±35 BP, Poz-81111)	Anatolia_BA	Harmanören-Göndürle Höyük, Isparta	Turkey	37.92	30.71	M	1.981	637146	H	J1a
I2499	I2499	UC1	1240K	2836-2472 calBCE (4040±35 BP, Poz-82213)	Anatolia_BA	Harmanören-Göndürle Höyük, Isparta	Turkey	37.92	30.71	F	0.285	243348	K1a2	
I2683	I2683	G3-95	1240K	2500-1800 BCE	Anatolia_BA	Harmanören-Göndürle Höyük, Isparta	Turkey	37.92	30.71	F	3.695	749308	T2b	

Dates marked simply as BCE (Before Common Era) are based on the associated archaeology of the samples. Dates marked as calBCE are based on radiocarbon dating of the samples (Supplementary Information section 1).

Extended Data Table 2 | Phenotypic inference of ancient individuals

ID	Population	PBlueEye	PIntermediateEye	PBrownEye	PBlondHair	PBrownHair	PRedHair	PBlackHair	PLightHair	PDarkHair	Hair Color	Eye Color
I2495	Anatolia_BA	1.6 (4.4)	3.6 (3.9)	94.9 (8.3)	10.7 (6.1)	51.6 (6.4)	0.1 (0.1)	37.6 (9.3)	18.0 (11.7)	82.0 (11.7)	Brown	Brown
I2499	Anatolia_BA	16.6 (28.3)	7.4 (2.2)	76.0 (28.7)	2.2 (2.2)	64.7 (11.8)	2.0 (5.3)	31.1 (13.8)	12.9 (20.1)	87.1 (20.1)	Brown	Blue or Brown
I2683	Anatolia_BA	0.3 (0.9)	1.3 (1.7)	98.4 (2.6)	3.3 (2.5)	33.0 (4.6)	0.0 (0.0)	63.7 (7.0)	4.9 (4.5)	95.1 (4.5)	Black	Brown
I2937	Greece_N	0.3 (1.3)	2.2 (1.9)	97.5 (3.2)	3.6 (1.9)	33.9 (6.2)	0.1 (0.0)	62.4 (7.4)	6.7 (4.3)	93.3 (4.3)	Black	Brown
I0070	Minoan_Lasithi	0.4 (1.8)	2.2 (1.9)	97.4 (3.7)	30.4 (5.1)	66.4 (5.9)	3.2 (0.9)	0.0 (0.0)	100.0 (0.0)	0.0 (0.0)	Brown	Brown
I0071	Minoan_Lasithi	0.0 (0.0)	0.2 (0.0)	99.8 (0.0)	0.4 (0.0)	20.3 (0.0)	0.0 (0.0)	79.3 (0.0)	0.5 (0.0)	99.5 (0.0)	Black	Brown
I0073	Minoan_Lasithi	0.1 (0.7)	1.7 (1.4)	98.2 (2.2)	12.5 (3.4)	61.1 (1.2)	0.2 (0.1)	26.2 (2.7)	32.4 (8.8)	67.6 (8.8)	Brown	Brown
I0074	Minoan_Lasithi	0.0 (0.0)	1.3 (0.3)	98.7 (0.4)	9.3 (3.2)	54.8 (8.5)	0.1 (0.1)	35.8 (10.5)	18.8 (10.3)	81.2 (10.3)	Brown	Brown
I9005	Minoan_Lasithi	5.2 (0.0)	11.6 (0.0)	83.2 (0.0)	49.6 (1.4)	38.8 (1.2)	4.2 (0.5)	7.4 (0.7)	85.6 (1.7)	14.4 (1.7)	Blond or Brown	Brown
I9006	Mycenaean	0.0 (0.0)	1.1 (0.4)	98.9 (0.4)	8.7 (4.9)	59.9 (6.4)	1.8 (2.9)	29.6 (11.8)	25.7 (16.5)	74.3 (16.5)	Brown	Brown
I9033	Mycenaean	0.4 (1.0)	1.6 (1.9)	98.0 (3.0)	4.6 (3.9)	51.0 (6.3)	0.1 (0.5)	44.2 (9.8)	10.5 (13.2)	89.5 (13.2)	Brown	Brown
I9041	Mycenaean	1.4 (0.5)	5.3 (1.0)	93.3 (1.4)	7.8 (0.7)	63.2 (2.0)	0.2 (0.4)	28.7 (2.3)	21.2 (2.5)	78.8 (2.5)	Brown	Brown

We list the probability assignments for different phenotypes by HIrisPlex[26] and an assessment of the phenotype. We generate 100 random replicates of the genotypes of each individual, listing the standard deviation in parentheses (Supplementary Information section 4).

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Supplementary Information

Genetic origins of the Minoans and Mycenaeans

Table of Contents

Supplementary Information 1

Archaeological and osteological context of ancient samples

In this section we provide some general historical context on the Bronze Age populations from the Aegean and southwestern Anatolia sampled in our paper and more specific information on the 19 ancient samples included in our study.

The Archaeological Context

During the third and second millennia BCE, the first civilisations of Europe, the Minoan and Mycenaean, appeared around the Aegean, on its islands and on the mainland. A distinctive Minoan civilization emerged on Crete after 3100 BCE, but the Mycenaean was a later development, and came into existence on the Greek mainland around 1700-1600 BCE, fusing native elements and cultural influences from Crete. In the fifteenth century BCE, the Mycenaeans replaced the Minoans as the dominant force in the Aegean, but the Minoan civilisation persisted within Crete for another two hundred years.

The Minoans

The Minoans, a name given by Sir Arthur Evans to the population of Crete during the Bronze Age,[1] displayed a very distinctive material culture, which lasted for nearly two thousand years from 3100 BCE to 1050 BCE. [2] From early prehistory, several settlements emerged which eventually culminated in the formation of palatial centers that date from the beginning of the Middle Bronze Age in 1950 BCE, which were to develop later into centralised palace-based economies and complex social structures that dominated most of the island. [2] The Minoans were a maritime society who traded as far as Egypt and the Near East. They established settlements in the Aegean and in Western Anatolia and created a powerful polity, known in later tradition as the thalassocracy. [2][3]

The Minoans were literate and used three different scripts; a Cretan hieroglyphic, that is still undeciphered; a syllabic and ideographic form, called Linear A, also undeciphered; and a similar form, called Linear B, which has proven to be an early form of the Greek language. [4] Tablets have been found at Knossos and on the Greek mainland where it originated, especially at Pylos, Mycenae and Thebes. No scholarly consensus exists about any linguistic affinities between the scripts and there is at present no evidence to point to the origins of the Minoan population that spoke any of these languages.

Archaeologists have deliberated on the origins of the Minoans since the time of the first excavations at Knossos at the very beginning of the twentieth century. It is thought that Crete was first populated by Neolithic settlers from Anatolia during the eighth millennium BCE. [5] Radiocarbon dates from samples from the Neolithic levels at Knossos offer absolute dates of 7030-6780 BCE, as far back as the Aceramic Period and close to the dating of the earliest Neolithic sites on mainland Greece. [5]

There is also evidence for subsequent waves of Chalcolithic settlers from Anatolia, especially during the second half of the fourth millennium BCE. [5] In about 1450 BCE, it is believed that much of a weakened Crete was occupied by Greek-speaking Mycenaeans from the mainland. [2]

A goal of our study is to provide a genetic characterization of the Bronze Age population of Crete to provide information relevant to debates regarding its origins, homogeneity or heterogeneity, and relationships to populations outside Crete.

The Mycenaeans

The Mycenaeans, named after the type-site of that civilization, a term first coined by Christos Tsountas [2] refers to the first advanced civilization in mainland Greece, although there are outstanding debates about whether it reflected a single or multiple cultures, or whether the people who contributed to it were homogeneous. [6][7] The Mycenaean civilization was influenced by the Minoan, but has its own clearly distinct architectural and material culture characteristics and many believe that the two can be differentiated with the Mycenaeans' expressing a more military emphasis in their art and burial customs. [2] The Late Helladic or Mycenaean civilization thrived between 1700 and 1050 BCE, but in the Middle Bronze Age that preceded it, it is possible to witness the origins of many of its features, such as in the contents of the Shaft Graves at Mycenae. [2] Subsequently, the Mycenaeans built a complex palace-dominated society, which is reflected in the contents of the Linear B tablets. [8]

The Mycenaeans settled all of mainland Greece up to Thessaly, and throughout the Aegean islands. There is evidence of extensive Mycenaean acculturation in Western Anatolia, Italy and Cyprus and trading relations with Egypt and the Near East. The Mycenaeans were literate and used for accounting purposes a syllabic script, Linear B, written in an early form of the Greek. They introduced this script into Crete after they occupied the island. [2]

The origin of the Mycenaeans has been intensely debated. Various theories have been proposed to respond to the question of if, when and in what circumstances Greek speakers or their linguistic ancestors, speaking a language that later developed into Greek, entered the Aegean. One theory attributes the origin of Greek speakers to the Balkans, from which waves of Indo-European speakers flowed into the north of Greece during the Bronze Age. These people came from the Eurasian steppe north of the Black and Caspian seas, [9] and they are referred to as the Proto Indo-Europeans. These migrants, together with the local population they encountered, then combined to form the ancestors of the Mycenaeans and later Greek speakers. [10-12] One problem with this theory is that the material culture relationship of Bronze Age populations of the Aegean with populations far to the north is very tenuous. [11-12] Another theory traces the origin of the Proto-Greeks further back in time, to approximately 3000 BCE at the start of the Early Bronze Age. [13] It proposes that as migrants, they filled a largely depopulated landscape.

An additional hypothesis for the origin of the Greeks goes even further back to the seventh millennium BCE and is associated with the view that the Greeks are descended from the first farmers who migrated into Europe from Anatolia. Alternatively, a very late origin of Mycenaean elites, associated with chariot riding warriors from the Caucasus in approximately 1600 BCE and
characterised by those buried in the Shaft Graves at Mycenae, has also been proposed. [14]

These hypotheses differ from each other in many respects. They include: (a) their geographical source; (b) the timing of these migrations and their size; and (c) a difference in demography, whereby some believe that it involved large numbers of migrants, whereas others suggest that Greek was the language of a numerically small elite that politically dominated a much larger native population.

Our paper does not settle this debate, but does provide new information, making it possible to place genetic constraints on the proposed explanations by quantifying both the number of different sources and the extent of admixture in the ancestry of the sampled Mycenaean individuals.

Note on terminology

The terms 'Minoan' and 'Mycenaean' describe the Early-to-Late Bronze Age cultures of Crete and Late Bronze Age cultures of Greece respectively. We are aware that these terms were invented by early archaeologists of the 19th century and we do not wish to essentialize the complex past societies that they have been applied to or to view the world of the Aegean Bronze Age through these labels. We use them as the most common and accessible terms applied to these cultures, and also in order to empirically test their correspondence to genetically coherent clusters of the people of the Aegean Bronze Age. We refer to the Minoan and Mycenaean 'civilizations' in the sense that these were complex archaeological cultures featuring elements of urbanism, hierarchical social organization, and written language, traditionally considered to be some of the characteristics of 'civilization'. We acknowledge that there is no commonly accepted definition of the 'civilization' and our use of the term is not intended as a value judgment on these cultures in comparison to earlier and later cultures that lacked these elements.

Note on Radiocarbon Dating

We give uncalibrated dates in radiocarbon years before 1950 (bp). We give calibrated dates at 95.4% probability in years before the common era (BCE), converting from uncalibrated to calibrated dates using IntCal13 [15] and OxCal4.2. [16]

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Part II: The Archaeological Context: Description of the Archaeological sites and the ancient samples included in this study

The Mycenaean tombs at APATHEIA and SALAMINA

The osteological material from Mainland Greece treated in the present article was retrieved in Mycenaean chamber tombs excavated by Eleni Konsolaki-Yannopoulou on behalf of the Greek

Archaeological Service at the Late Helladic site of Apatheia in Troezenia (NE Peloponnese) and at the known site of a Late Helladic cemetery on the island of Salamina in the Saronic Gulf.

The chamber tombs at APATHEIA

Seven rock-cut chamber toms were excavated between 1985 and 1993 in the area of Apatheia, ca. 2 km west of the modern town of Galatas, in the northern foothills of Mt. Adheres. Those tombs held the burials of ordinary people, judging by the few, common-type furnishings of the deceased. However, some evidence for the practice of funerary libation rites indicated that the lower classes of the Troezenian society were not unfamiliar with the mortuary customs of the ruling elite (1), who performed similar rites when burying their dead in the tholos tombs brought to light on the hill of Megali Magoula, lying ca. 3 km north-east of the site of Apatheia (2).

The human remains sampled for analysis were collected in Tomb A5, which was apparently used as an ossuary at some stage in the Mycenaean period, as it contained an unusually large number of skeletons (more than 31), and nearly all of them were completely or partially disarticulated (**Fig. S1.1**). The only exception was the articulated skeleton of an individual buried in the supine position, with legs extended, within a pit dug out into the chamber floor (**Fig. S1.2**). The sample no. 19 came from the cranium no. 31, which belonged to this skeleton.

Safe evidence for the exact chronology and the status of that primary burial was missing, as all the associated grave goods had been removed, perhaps during the re-use of the tomb. Nevertheless, two dog carcasses deposited next to the pit-grave suggest that the individual buried there may have been a distinguished member of the local community, as the ritual deposition of dogs in Mycenaean tombs was probably connected to the social and ideological role of hunting in Mycenaean society (3).

Above the chamber floor there was a thick deposit of disarticulated skeletal material, possibly representing a single episode of secondary burials coming from the cleaning of other tombs nearby. The sample no. 4 originated in that deposit **(Fig. S1.3)**. The pottery recovered in the layer of secondary burials ranged in date from the 15th to the early 12th cent. BC (LH IIB-LH IIIC Early).

A dental analysis carried out on 245 teeth coming from 61 individuals buried in the Mycenaean chamber tombs at Apatheia gave some clues about their diet and occupation (4). About 7% of all teeth had functional and mechanical attrition on the contact and occlusal surfaces, probably because of hard and gritty substance intake. There was also evidence of non-functional (frictional) abrasion, which may be connected with the occupation of the person. Dentin carries (decay) was three times the enamel carries. These results suggest that the Galatas population may have consumed coarse food; besides, they may have held and cut the string type materials during fishing and sailing.

The chamber tombs at SALAMINA

In 1995 a group of nine Mycenaean tombs were excavated in the modern town of Salamina, near the church of Ayia Kyriaki on Demosthenous street. These tombs formed part of a large chamber tomb cemetery investigated in the same area in 1965 (5). That cemetery most probably belonged to the chief Late Helladic settlement on the island, the predecessor of historic Salamis.

The osteological material sampled for analysis came from Tomb 7, which was partly destroyed by modern activity. The sample no. 31 came from secondary burials, i.e., human skeletons removed from their original position on the tomb floor and deposited, together with some of their grave goods, by the northwestern corner of the rock-cut chamber **(Fig. S1.4)**. In addition to a large number of clay vessels, the furnishings of the deceased included faience jewelry and some objects of bronze, indicating that the individuals buried in that tomb were wealthier than the average people, although they may not be viewed as members of a ruling elite, judging by the absence of any prestige items in the grave offerings. The ceramic finds associated with those burials dated to the 14th - 12th cents BC (LH IIIA-C), thereby demonstrating a continuous use of the tomb from the Palatial into the Post-palatial period of the Mycenaean civilization.

Eleni Konsolaki-Yannopoulou

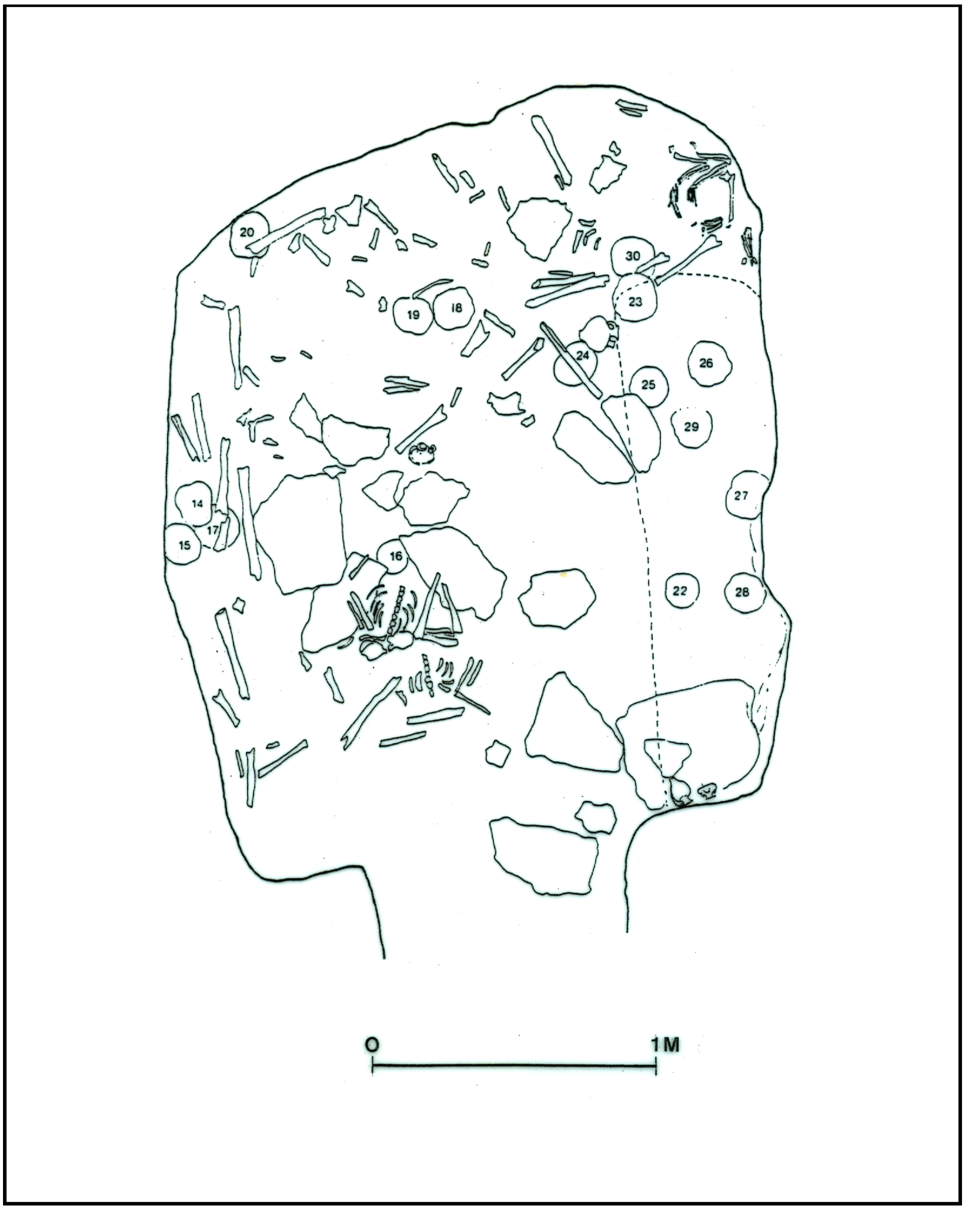

Figure S1.1. Apatheia. Secondary burials in Tomb A5, which was used as an ossuary.

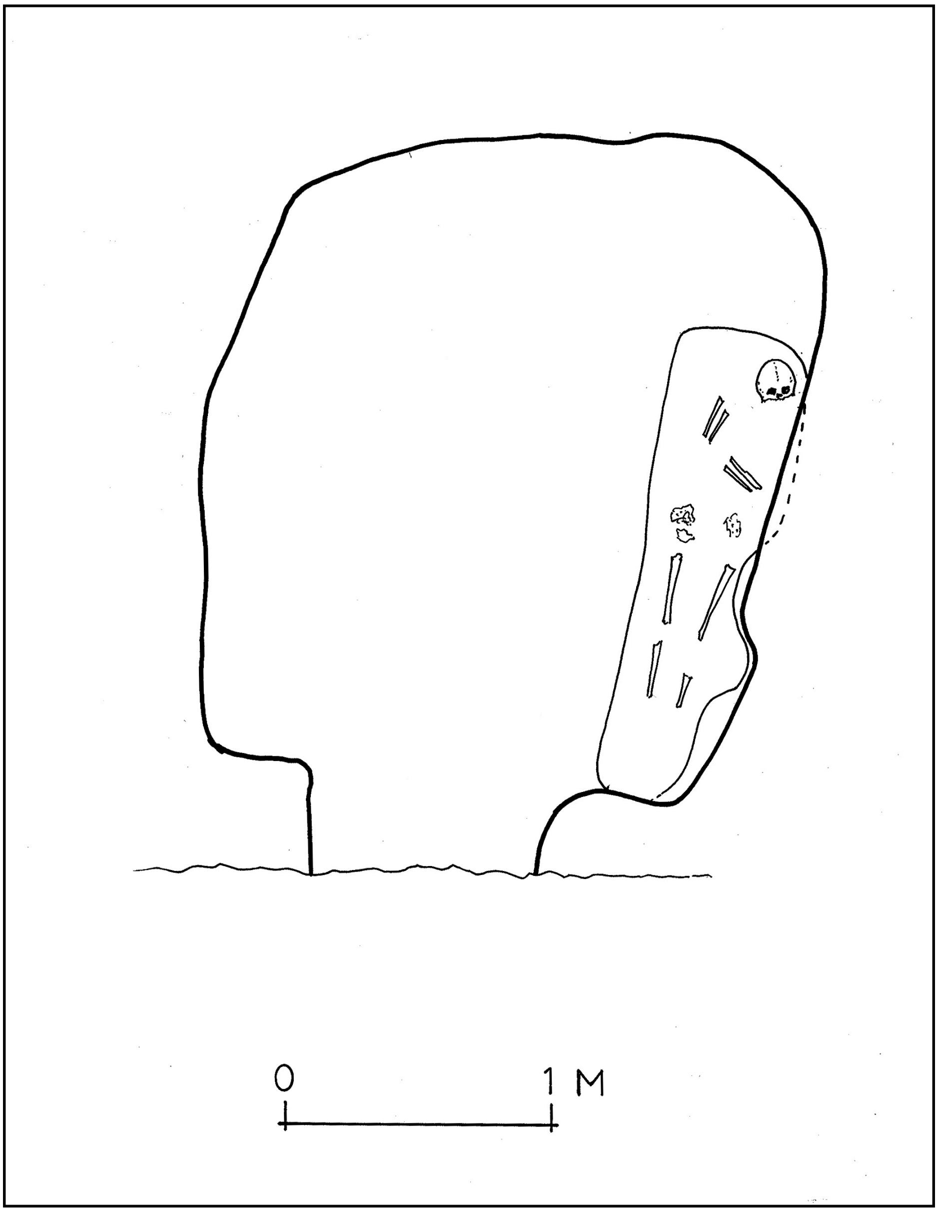

Figure S1.2. Apatheia. Primary burial in the supine position, interred in a pit dug out into the chamber floor of Tomb A5.

Figure S1.3. Apatheia. Deposit of secondary burials above the floor level of Tomb A5.

Figure S1.4. Salamina. Secondary burials deposited by the northwestern corner of Tomb 7.

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Samples that provided working ancient DNA

- Salamis31 (I9006): 1411 – 1262 calBCE (DEM-2905 (MAMS-25209), 3067 ± 25 bp). Child from Tomb 7, North side, group 34.
- Galatas4 (I9041): Male without an osteological age estimate, LH IIB to LH IIIC (15th to early 12th century BCE).
- Galatas19 (I9010): Female without an osteological age estimate, LH IIB to LH IIIC (15th to early 12th century BCE)

Mycenaean cemetery of the Peristeria citadel in Trifylia

Peristeria is a key medium-large archaeological site which, due to the size of its buildings, the burial monuments and the wealth of its rich findings, especially in the tombs, is generally called the "Mycenae of the Western Peloponnese" (37o 16.67΄ North / 21o44.43΄ East), and characterized as the «ήττον πάρισον των Μυκηνών» (the minor equal of Mycenae). It is the site of an important Middle Helladic (Middle Bronze Age) and early Mycenaean (Late Bronze Age) settlement, which may have served as a seat of a local ruler dynasty (flourished from the 17th to the end of 13th century B.C.). The site is located about 8 km northeast of the capital town of Kyparissia in the Triphylia region of north Messenia, on an impressive hill overlooking the plain connecting the interior of Messenia to the Ionian coast. The Kyparissieis river flows by the northern foot of the Peristeria hill.

The site was first excavated by Prof. Spyros N. Marinatos (1960-62, 1964-65) and by Professor George Styl. Korres (1976-77, 1978). Only part of the Peristeria citadel has been excavated; the settlement extends further than the fenced archaeological site. The finds from the Peristeria tombs reveal that the deceased belonged to the ruling class.

Peristeria is considered to have been one of the most important Bronze Age sites in Messenia, as is implied by the wealth of the finds and the large tholos tombs. The hill of Peristeria is very steep, accessible only from the south, where a defensive wall was erected. The earlier houses on the hill date to the end of the Middle Helladic and the beginning of the Mycenaean period (MHIII-LH I). To the west of tholos tomb 1, a square tomb was excavated very near the surface (side measuring 2.50 m), containing very rich grave goods such as diadems made of perishable material decorated with gold bands, gold necklaces in female burials, a deliberately bent ('killed') sword decorated with silver, arrow heads made of obsidian and flint, an elaborately decorated two-handled cup and clay Minyan vases. This small richly furnished grave was succeeded in the acropolis by at least three tholos tombs.

The earliest tholos tomb 3 received two inhumations that were accompanied by many gold ornaments that had originally adorned the funerary dress (shroud) of the deceased. The most important grave goods are the three gold cups, one of which is better preserved and even more exquisite than the equivalent bowl found by Schliemann at Mycenae. Also found in the tomb was a long gold diadem, similar to those known from Mycenae. It is dated to the middle of LH I, probably around the middle of the 16th century BC.

Tholos tomb 2 was erected before the end of Late Helladic I. It consists of a chamber 10.60 m in 10.60 m, a stomion 5.15 m in length and a dromos that was more than 10 m long. The finds from the chamber were very rich. Notable are: the very large number of thin gold strips, the large number of sherds of partially preserved vessels, a silver vessel with inlaid decoration of gold lillies and gold discs, etc.

Tholos tomb 1 is the largest and most impressive tomb in Messenia-Triphylia. Its dromos was 12 m long and 3 m wide, the chamber measured more than 12 m in diameter, while its stomion was 5.10 m high and 6 m long. On the left anta of the entrance there are two incised Knossian masons' marks (a branch and a double axe) which have been interpreted as signs of Minoan influence. Prominent among the finds is the quantity of pottery finds of Mycenaean date; it is the largest pottery assemblage found in family tomb in mainland Greece. We should note the over 100 Keftiu caps, which are dated in LHII. Many finds, such as a gold strip in the shape of a fish with relief decoration of a Minoan ritual procession, originate from Minoan Crete.

Alongside these imposing and richly furnished tombs that belonged to a ruling class, we have located about 100 m south of the above mentioned complex a small tholos tomb, the so-called South tholos tomb 1, which was used for burials of the settlement's population

For DNA preparation we used one or two teeth of 12 crania from the 1976 excavation of South Tholos, of 12 crania from the 1976/1977 excavation of the small surface MH III/LH I grave and of two jaws from the 1965 Marinatos excavation of the main Tholos 1. Enough endogenous DNA for analyses was extracted from one main Tholos 1 sample. 14C measurements by the Laboratory of Democritus Institute (Athens) dated this sample to 1404-1302 BCE. Measurements with accelerator mass spectometry (AMS) at Klaus-Tschira-Labor fuer Physikalische Altersbestimmung, Mannheim Germany, dated the sample to 1416-1280 BCE.

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Sample that provided working ancient DNA

- Peristeria4 (I9033): Female without an osteological age estimate, 1416 – 1280 calBCE (DEM-2903 (MAMS-25207), 3084 ± 24 bp).

Alepotrypa Cave at Diros Bay

Alepotrypa Cave is located at Diros Bay on the western coast of the Tainaron Peninsula, Mani, in Lakonia, Greece. The cave is situated about 20m above sea level, in an arid and rocky limestone environment, and its entrance is about 50m from the present Mediterranean shoreline. It is a massive formation about 300m long and 50m in maximum width, extending along an east-west axis and consisting of several passageways and chambers, the largest of which contains a deep lake and several smaller ones (Papathanassopoulos 2011, Papathanasiou 2005). Alepotrypa revealed stratified anthropogenic deposits up to 5.0 m, which date from approximately 6,000 to 3,200 BC and correspond to the end of Early to the Final Neolithic Periods. Artifacts include a vast variety of pottery, lithic tools, grindstones, copper daggers, bone needles, clay spindle whorls, personal decoration items, as well as figurines. Features include hearths, clay lined pits, and clay floors. Food remains consists of cultivated cereal, legume, and fruit remains, a large number of animal bones from domesticated species, and to a lesser degree of wild plant and animal resources, fish and shells. The diet was attested also by stable isotope analysis suggesting a primarily agricultural diet with emphasis on plant resources. There is also evidence of rich ritualistic expression, including massive concentrations of deliberately broken pots possibly associated with mortuary practices.

In addition to the material culture, the cave has also yielded the largest human skeletal assemblage of Neolithic Greece, including remains of primary single or multiple burials, two formal ossuaries for secondary disposals, and scattered bone. The MNI of the 161 individuals from Alepotrypa Cave showed approximately equal proportions of males (17), females (15), adults (81), and subadults (80) but very few infants (Papathanasiou 2005).

Sample A2197 was found in trench B1, in layer L14, as part of the multiple primary burial complex, which yielded radiocarbon dates of 5406±23 and 5419±41 BC, belonging in the Middle Neolithic (individuals A2201 and A2197). It includes a MNI of 7 individuals, mostly young adults and adolescents. Two individuals were articulated but partially represented, missing one or more limbs, while some other individuals are represented by articulated limps only or even disarticulated elements. A2197 is an adult articulated individual, a female of 30-40 years at death, in extended position face down, with arms along the sides, and the head rotated to the left.

As a sealed, single-component, Neolithic Alepotrypa Cave is one of the richest sites in Greece and Europe in terms of number of artifacts, preservation of biological materials, volume of undisturbed deposits, and horizontal exposure archaeological surfaces of past human activity.

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Sample that provided working ancient DNA

- A2197 (I2937): Female without an osteological age estimate (5419±41 cal BC or 6441±38 BP based on context)

Minoan cemetery near Moni Odigitria

The Minoan Prepalatial cemetery near the Monastery of Odigitria (Moni Odigitria), in the broader area of Phaistos, lies halfway between the Mesara Plain and the south coast in the South-Central Crete. It is a complex of buildings and other minor structures as well as open areas or courtyard. There are two circular tholos tombs, namely Tholos A and Tholos B. A Rectangular Building with three small rooms was attached to the east part of Tholos B, and a Southern Courtyard was in front of the entrance of Tholos A. There is a Southern Courtyard in front of the entrance of Tholos A. To the northeast, there is a Central Zone, which lies between the two tholoi and the Rectangular Building and includes the Ossuary (Fig. S1.5). There was continuous use of Tholos A and the areas to the north and east beginning with its foundation in FN/EM I (second half of the fourth millennium B.C.) through EM II, while Tholos B and its appendices were founded in later EM I and saw continuous use through MM IA and into early MM IB, that is, until the 20th/19th centuries B.C.

The Ossuary is a pit 5.0 x 2.50 m long, dug in the soil south of Tholos B, to a depth 1.35 m. The pit, which is an undisturbed closed deposit, was full of skeletons and skulls carefully deposited with very little soil between them. Pottery and stone vases found among the skeletons were likely deliberately chosen and transferred to the Ossuary pit. The presence of about 2000 sherds in a deposit with little soil in it suggests that these too were deliberately collected and buried with the skeletal material. Twenty-three seals were recovered under the heap of bones in the deeper layers of the Ossuary.

The Ossuary was filled with skeletal and other material, probably in a single episode, in MM IB. In that case the material is likely to have come from Tholos B, as Tholos A barely was used in MM I. The fill of the Ossuary was almost entirely bone material rather than soil mixed with bone. The bones had been selected for re-deposition. Skulls or long bones were put together in groups (Fig. S1.6, Fig. S1.7), suggesting intentional treatment. Multiple thick layers of skeletal material were accumulated at the sides of the pit leaving a depression in the central area. This phenomenon suggests the possibility that every time that the Ossuary was used, care was taken to ensure the efficient management of space to allow for the disposal of further skeletal remains later. The Ossuary appears to have accommodated the remains from some 50 to 55 individuals. Therefore, the overall picture of the use of the Ossuary is consistent with the secondary burial of skeletal materials. There was very little disturbance of the earlier depositions in the Ossuary pit. In other words, the skeletal remains, once placed in the Ossuary, do not seem to have not suffered from additional removal or deliberate disturbance during the re-openings of the pit. Re-openings had taken place in order to clear away earlier burials from the primary disposal area.

Most bones were long bones from the arms and legs, and they seemed to have been deposited in some order. The skulls, for example, were put in groups of five and 10. This physical arrangement was the reason for this burial deposit being named the “Ossuary.” There are 47 almost-complete skulls, which were found in groups either intact or in adjoining fragments. One or two teeth were extracted from forty skulls and used for DNA extraction. Five samples yielded enough endogenous DNA for genomic analyses.

Accelerator Mass Spectrometry (AMS) dates determined by the Vienna Environmental Research
Accelerator in four bone samples from left femora place these four individuals within the brackets of 2210 BCE to 1680 BCE, that is from late EM II through to MM II/III.

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2. Triantaphyllou. Analysis of the Human Bones. In Moni Odigitria, pp 229-248.

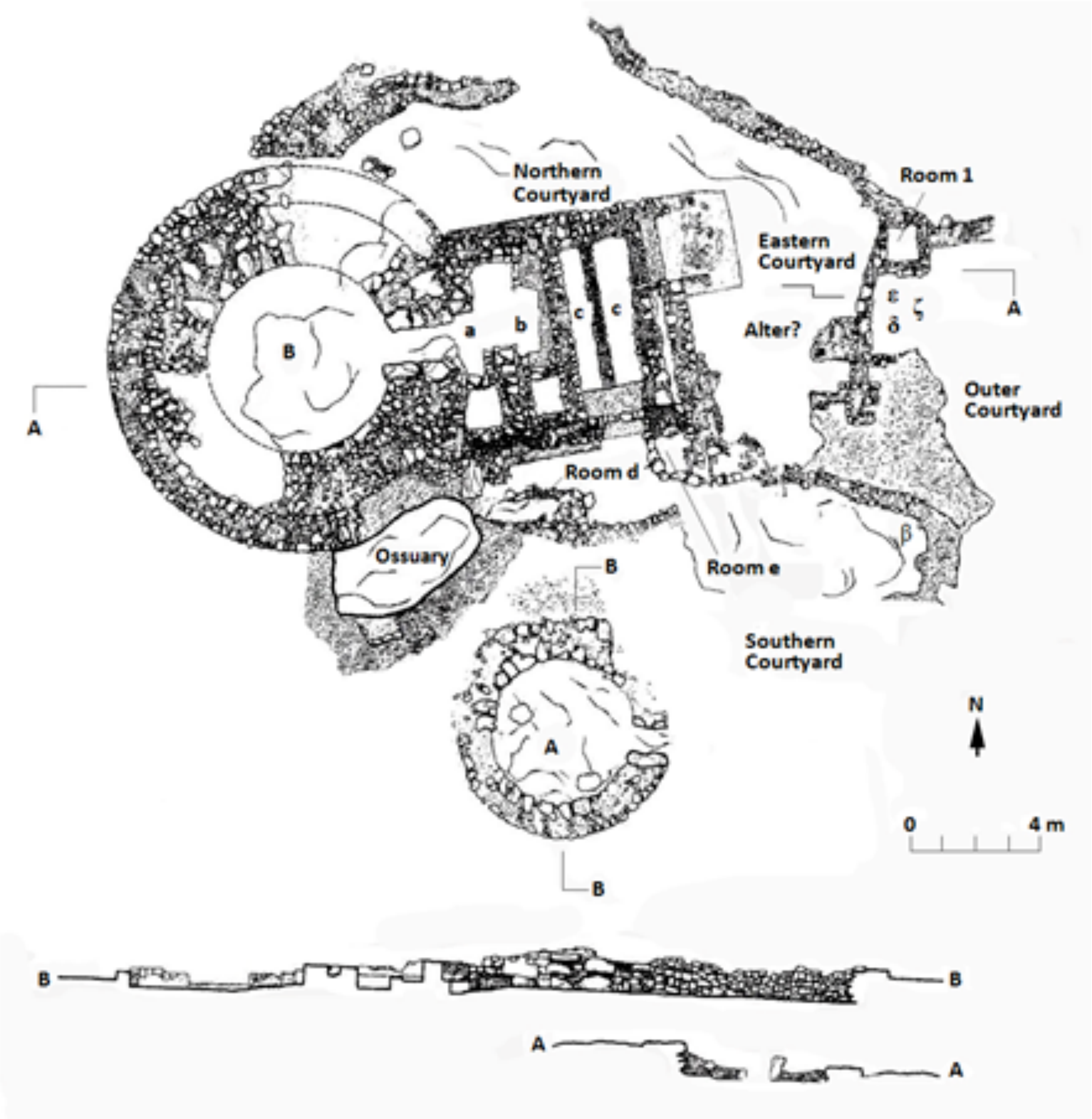

Figure S1.5. Plan and section of the excavated remains at the Moni Odigitria Minoan Cemetery.

Figure S1.6. Ossuary detail: a “nest” of five skulls as found in situ.

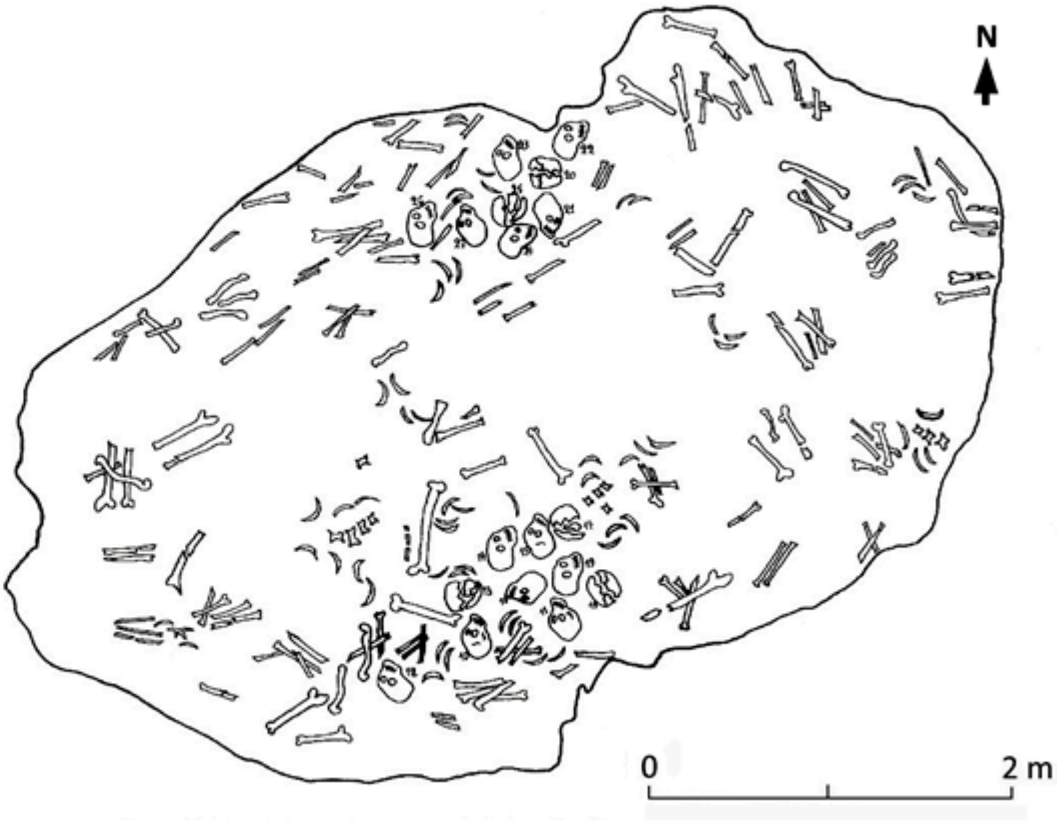

Figure S1.7. Plan of the lower stratum of the Ossuary.

Samples that provided working ancient DNA

- 12V (I9127): Female without an osteological age estimate, 2210-1680 BCE (based on four direct dates of skeletons in the same ossuary).
- 13V (I9128): Female without an osteological age estimate, 2210-1680 BCE (based on four direct dates of skeletons in the same ossuary).
- 14V (I9129): Female without an osteological age estimate, 2210-1680 BCE (based on four direct dates of skeletons in the same ossuary).
- 16V (I9130): Male without an osteological age estimate, 2210-1680 BCE (based on four direct dates of skeletons in the same ossuary).
- 19V (I9131): Female without an osteological age estimate, 2210-1680 BCE (based on four direct dates of skeletons in the same ossuary).

The Hagios Charalambos (Gerontomouri) Cave on the Lasithi Plain

The Hagios Charalambos Cave, also known as Gerontomouri Cave, is a natural cavern on the highland plain of Lasithi. The plain has a microclimate and is often cut off in the winter months. The cave, 835 metres ASL, was discovered in 1976 when dynamiting by road builders destroyed part of the roof of the two outer chambers. It was excavated in 1976, 1982-3 and 2002-3.

Hagios Charalambos was used as an ossuary for secondary burial. Bones and artifacts that had been deposited as primary burials at some other location were transferred to the cave at some point in Middle Minoan IIB. Stones intrusive to the context of the cave suggested a possible origin from built tombs, though neither tombs nor settlement have been found. An elegantly reasoned alternative hypothesis offered by Davaras (2015), proposes that the Psychro Cave, only 1 km distant, could have been the location of the primary burials, which needed to be removed to purify it when Psychro became the focus of cult worship[1] in the Middle Minoan period.

The pottery and other artifacts including figurines, seals, stone tools, metal tools and weapons,

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[1] A cult not necessarily associated with Zeus at this period. Nor is there a consensus of scholarly opinion concerning the identification of Psychro as the Dictaean Cave, mythological birthplace of Zeus (see Davaras 2015 for references).

jewelry and other funerary gifts associated with the burials range in date from the Final Neolithic to the Late Minoan period. However, the bulk of the pottery dates to Early Minoan III-Middle Minoan I, 2200-1950 BCE, whereas there are fewer than five Late Minoan sherds possibly linked to an LM habitation on the hill adjacent to the cave (Betancourt et al 2008, 595).

The excavated material, from all campaigns, represents a minimum number of almost 400 burials. The transfer of the burials took place over a period of time in two phases, both in MM IIB. It was a major labor-intensive undertaking requiring organization and collaborative effort. The bones were meticulously collected since all parts of the human anatomy, including proximal, medial and distal manual and pedal phalanges and tiny sesamoid bones are represented in the corpus of skeletal material.

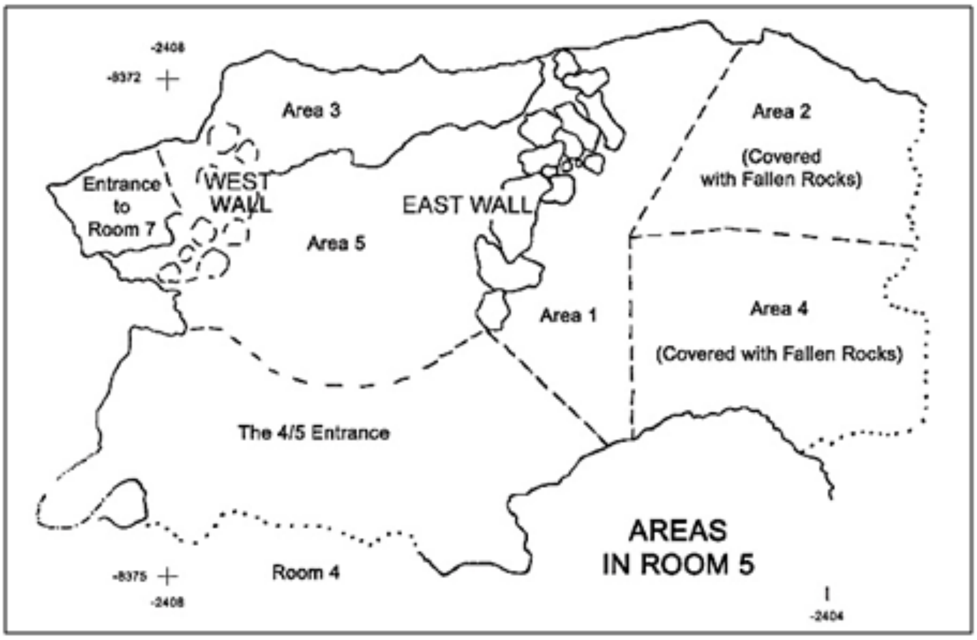

Fig. S1.8 Drawn by T. McDermott. Reproduction of Fig. 4 of Betancourt et al. (2008) courtesy of the Trustees of the American School of Classical Studies at Athens.

Bones were partly sorted for secondary deposition in the cave's various rooms. Two retaining walls had been constructed in Room 5 (Fig. S1.8); near the bottom of the deposit, which was over a meter high, some of the long bones were arranged in a grid to form a 'platform', above which was a mass of human bones mixed with pottery and other artifacts. The top of the deposit in every room consisted of a layer of human skulls and complete vases, proving the deposit had not been disturbed since the Bronze Age.

The human remains constitute the largest and best-preserved corpus of material from periods prior to Middle Minoan. Their study is providing evidence for diseases and medical history, such as trephinations that are the earliest surgical interventions so far attested in Greece. The bones are generally very well preserved because of low temperatures in the cave even at the height of summer. With only minor temperature fluctuations, the cave acted as a natural freezer and contributed to unprecedented standards of preservation for human bones of this early date making them ideal specimens for DNA analysis (McGeorge, 1988).

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Samples

- Lasithi4 (I0071): Female without an osteological age estimate, 2400-1700 BCE.
- Lasithi2 (I0070): Male without an osteological age estimate, 2400-1700 BCE.
- Lasithi7 (I0073): Male without an osteological age estimate, 2400-1700 BCE.
- Lasithi9 (I0074): Female without an osteological age estimate, 2400-1700 BCE.
- Lasithi17 (I9005): Female without an osteological age estimate, 2400-1700 BCE.

Late Minoan III Necropolis of Armenoi

The Necropolis of Armenoi (1390-1190 BCE), situated on the NW coast of Crete, 10 km. south and above the town of Rethymnon, is the only intact necropolis that dates to this period and the preservation of the finds and the human skeletal remains is outstanding. Work at the Necropolis commenced in 1969 and continues under the direction of Dr. Yannis Tzedakis. To date two hundred and thirty-two chamber tombs of varying sizes have been revealed. The abundance and artistic excellence of the artefacts found in the tombs is extraordinary. They include in excess of eight hundred decorated vases, seven hundred undecorated and coarse vessels, and three hundred and fifty bronzes. They include thirty-four decorated larnakes (sarcophagi), two of which are polychrome. Unique finds are a stirrup jar with a Linear B inscription, a boar's tooth helmet, and a reed basket decorated with bronze nails. The tombs contained the human remains of approximately one thousand individuals.

A range of biomolecular analyses (organic residue analysis and stable isotope analysis) was conducted on material from the Necropolis of Armenoi as part of a project directed by Tzedakis and Martlew which covered sixteen Bronze Age Greek sites. The results of the scientific work, in which the Necropolis of Armenoi featured prominently, were incorporated in an exhibition that was mounted in seven international museums.

We undertook biochemical analysis (collagen extraction and isotope analysis) of the sample used for DNA analysis (ARM 503) to assess its state of preservation. The bone was well preserved, with a collagen yield of 6%, and carbon and nitrogen isotope values of $d^{13}C=-19.8$ ‰ and $d^{15}N= 7.4$ ‰.

Sample

- Armenoi 503 (I9123, 89 I): Female adult from Tomb 160 (LM III A2, ca. 1370-1340 BCE).

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Göndürle Höyük (Harmanören)

The Bronze Age cemetery near Göndürle Höyük (Harmanören village, Isparta, southwest Anatolia) was excavated between 1993 and 2005 by the archaeologists Mehmet Özsait and Nesrin Özsait from the Istanbul University (1-2). After Demircihöyük and Semahöyük , the cemetery of Göndürle Höyük is the largest of Anatolia. This cemetery was in use for many centuries judging by the burial jars and pottery vessels found inside, which are typical of the Early Bronze Age phases 2 and 3, and also of the first part of the Middle Bronze Age. These large burial jars often contained the remains of more than one deceased. The jars had their opening to the east, which was closed by a stone slab.

The results of the anthropological analysis concern human remains from 77 jar burials and 2 pit burials from the cemetery. The collection comprises a total of 115 individuals including 74 adults and 41 children (3). The number of females and males buried in the graveyard was coincidentally equal. Half of the children are estimated to have died between 2 to 7 years old. At the age of death females were relatively young and males middle-aged or older.

Osteoarthritis was a common pathological condition. Anemia and hypoplasia were found in a few individuals, which may mean that some individuals among the village population were underfed. We observed dental problems such as caries, periodontitis and abscess in some middle-aged and older adults. Also traumas were recorded, but had not been fatal in any case. As a result of the poor bone conservation it was impossible to report all anthropological data.

Figure S1.9. Göndürle Höyük (Harmanören) in southwest Anatolia: Burial jar U1c containing three individuals with grave goods.

Samples

- **A4-1** (I2495): 2558 – 2295 calBCE (Poz-81111, 3925 ± 35 bp). Male. Estimated age at death is 7 years (± 2 years). Macroscopic observation of the mandibular incisors indicate a moderate level of enamel hypoplasia.
- **U1c** (I2499): 2836 – 2472 calBCE (Poz-82213, 4040 ± 35 bp). Female. Estimated age at death is ca. 13-14 years. The bones of this adolescent female were found in a large jar together with the skeletal remains of two adults. The latter were identified as a middle-aged female and an adult male. As the adolescent was lying on top of the other two, she

had probably been the last individual buried in the jar. She lay in a flexed position on her right side. Three jugs accompanied the small group of deceased (see Fig. S1.9).

- **G3-95** (I2683): Female, 2500-1800 BCE. Estimated age at death is 5 years (+-16 months). Fragmentary remains of the child were found in a badly disturbed jar (1).

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2. Özsait, M. – « Les fouilles du cimetière de Göndürle Höyük à Harmanören », *Anatolica*, XXIX, 2003, 87-102.
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Supplementary Information 2

Admixture modeling of ancient populations

While the analysis with *f*-statistics shows that Bronze Age populations of the Aegean and southwestern Anatolia differ from previous (Chalcolithic and Neolithic) populations of the area, they do not show which are the likely sources of their ancestry or how much ancestry they can trace to each of them. In this section, we model these populations using the *qpWave*/*qpAdm* framework[1] which allows us to model a Left set consisting of a *Test* population (whose history of admixture we are investigating) and *Reference* populations (potential sources of ancestry) in relation to a Right set of outgroups. This methodology allows one to model the *Test* population as an *N*-way mixture of the *Reference* populations by exploiting the fact that the *Reference* populations differ in their relationship to the outgroups, without requiring the formulation of the (likely complex) web of relationships between Left and Right populations.

Modeling ancient populations as mixtures of hunter-gatherers and earliest Neolithic populations

We first model ancient populations as having ancestry from *N*=1, 2, 3 other populations. We define the following set of 16 populations, which includes ancient Eurasian hunter-gatherers and the earliest Neolithic populations from Iran, the Levant, Anatolia and Europe.

All: Mota[2], Ust_Ishim[3], Kostenki14[4], GoyetQ116-1[4], Vestonice16[4], MA1[5], AfontovaGora3[4], ElMiron[4], Villabruna[4], WHG[1,6-9], EHG[1,10], CHG[11], Iran_N[12,13], Natufian[13], Levant_N[13], Anatolia_N[8,14]

This set includes an African outgroup (Mota), an Upper Paleolithic Eurasian (Ust_Ishim) that is symmetrically related to European hunter-gatherers and eastern non-Africans[3], representatives of diverse Ice Age Europeans[4] (we choose the best representative of the different clusters identified by the analysis of Upper Paleolithic Europeans[4]; we use the capture version of Kostenki14[4] rather than the shotgun version[15]), the ~24,000 year old “Ancient North Eurasian” Mal’ta 1 (MA1) sample which represents a population that contributed ancestry to both the Americans and West Eurasia[5,7], as well as the later (~15,000 year old) Afontova Gora 3 sample[4] from the same region, the Caucasus hunter-gatherers (CHG), the Natufian hunter-gatherers, the four Neolithic and hunter-gatherer sources of West Eurasians[16] (Neolithic Iran and Levant, Western and Eastern European hunter-gatherers), and finally Neolithic Anatolians who represent a source of early Neolithic Europeans[8,16] and are related to Neolithic individuals from Greece[14] (Fig. 1b). Note that in earlier uses of this methodology[1,7,8,16] we included diverse world outgroup populations genotyped on the Human Origins array[7,17] in the set of outgroups. However, with the availability of diverse old European and Near Eastern populations, this is no longer necessary and we can use these more relevant outgroups that maximize our ability to differentiate between West Eurasian populations and, also use the maximal set of SNPs (in the *HOIll*) dataset, rather than only the Human Origins ones. An added benefit of including no modern populations as outgroups is that these are not affected by ancient DNA damage, a potential source of bias in the computation of f_4-statistics as there might be spurious shared alleles at sites affected by damage between ancient samples that are not shared by modern ones.

We include the *Test* population (which we are modelling) and *N* populations from the All set into the Left set, and set Right to be All \ Left. This approach differs from that of ref.[16] in which the Left set was first modelled against a conservative minimal set of Right outgroups, with additional outgroups added to test any successful models until only a single "best" one survived. Here, we test against the maximal (All \ Left) set of Right outgroups, wishing to determine whether the *Test* population and a subset of the All set can be modelled with respect to the remainder of the All set.

We test for rank=*N*-1 using *qpWave* and estimate mixture proportions using *qpAdm*[1]. We report only feasible mixture proportions (in interval [0, 1]). We use a significance level of p=0.05 for rejecting models and mark p-values greater than 0.05 (that represent feasible models) in red.

Table S2.1: *N*=2 modeling of Mycenaeans. Left=(Mycenaean, Ref_1, Ref_2). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥1e-10 are shown.

		P-value for rank=1	Mixture Proportions		Standard Errors	
***Ref*₁**	***Ref*₂**		***Ref*₁**	***Ref*₂**	***Ref*₁**	***Ref*₂**
CHG	Anatolia_N	5.14E-03	0.201	0.799	0.024	0.024
AfontovaGora3	Anatolia_N	8.05E-05	0.202	0.798	0.022	0.022
Iran_N	Anatolia_N	5.35E-05	0.166	0.834	0.023	0.023
MA1	Anatolia_N	1.66E-08	0.101	0.899	0.018	0.018
EHG	Anatolia_N	1.80E-10	0.072	0.928	0.016	0.016

Table S2.2: *N*=3 modeling of Mycenaeans. Left=(Mycenaean, Ref_1, Ref_2, Ref_3). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥1e-3 are shown.

				Mixture Proportions			Standard Errors		
***Ref*₁**	***Ref*₂**	***Ref*₃**	**P-value for rank=2**	***Ref*₁**	***Ref*₂**	***Ref*₃**	***Ref*₁**	***Ref*₂**	***Ref*₃**
AfontovaGora3	CHG	Anatolia_N	5.69E-01	0.133	0.126	0.741	0.027	0.026	0.024
AfontovaGora3	Iran_N	Anatolia_N	4.75E-01	0.161	0.086	0.754	0.026	0.025	0.024
EHG	Iran_N	Anatolia_N	3.92E-01	0.065	0.136	0.799	0.016	0.022	0.024
EHG	CHG	Anatolia_N	2.86E-01	0.044	0.176	0.780	0.016	0.023	0.024
MA1	CHG	Anatolia_N	9.55E-02	0.052	0.159	0.789	0.019	0.026	0.024
WHG	CHG	Anatolia_N	1.80E-02	0.029	0.202	0.769	0.012	0.024	0.027
MA1	Iran_N	Anatolia_N	1.61E-02	0.074	0.106	0.820	0.020	0.027	0.023
Vestonice16	CHG	Anatolia_N	9.43E-03	0.032	0.196	0.772	0.019	0.023	0.028
GoyetQ116-1	CHG	Anatolia_N	5.90E-03	0.018	0.201	0.781	0.018	0.024	0.028
Ust_Ishim	CHG	Anatolia_N	5.02E-03	0.026	0.187	0.788	0.022	0.028	0.025
Villabruna	CHG	Anatolia_N	4.19E-03	0.012	0.209	0.778	0.011	0.024	0.028
Kostenki14	CHG	Anatolia_N	4.18E-03	0.027	0.193	0.780	0.020	0.024	0.027
ElMiron	CHG	Anatolia_N	4.11E-03	0.023	0.206	0.772	0.015	0.023	0.029
WHG	Iran_N	Anatolia_N	1.61E-03	0.042	0.175	0.782	0.012	0.025	0.028

Mycenaeans

Mycenaeans do not form a clade with any single (N=1) population of the All set (p-value for rank=0 < 1e-15). We can reject any 2-way mixtures (N=2) of populations of the All set (p-value for rank=1 < .05) (Table S2.1). The top 2-way mixture involves a mixture of Neolithic Anatolians and Caucasus hunter-gatherers (CHG) (p=5.14E-03 for rank=1).

We can model Mycenaeans as a 3-way mixture of Anatolian Neolithic, Iran Neolithic or Caucasus hunter-gatherers, and Eastern European hunter-gatherers (EHG) or Upper Paleolithic Siberians (MA1 or AfontovaGora3). This is not surprising as CHG can be modelled as a mixture of primarily Iran Neolithic and European hunter-gatherers and EHG as a mixture of primarily "Ancient North Eurasians" from Upper Paleolithic Siberia (like MA1) and western European hunter-gatherers[16]. Eastern European hunter-gatherers and Neolithic people from Iran represent two ends of a "northeastern interaction sphere"[16] whose deep history is unclear but which is formed by increased affinity to Upper Paleolithic Siberians in eastern Europe and Basal Eurasian[7] admixture in the Caucasus and Iran[13].

The successful models agree that Mycenaeans have most of their ancestry from the Neolithic substratum (~74-79%), with the remainder from both the Eastern European/Siberian set of populations (~5-16%), and the Iran/Caucasus populations (~9-18%). These results do not, of course determine whether the non-Anatolian Neolithic-related admixture in Mycenaeans was introduced by a single population that was itself a mix of the Eastern European/Siberian and Iran/Caucasus sources, or by separate admixtures that reached the Aegean presumably from the north and east. They do, however, show that admixture from only a single of those sources is insufficient to properly model the ancestry of Mycenaeans (as the failure of any 2-source model in Table S2.1 indicates).

We were concerned that the admixture from these three sources could be driven by heterogeneity within the Mycenaean population itself. Mycenaeans do appear to form a tight cluster in PCA (Fig. 1b) and to have similar admixture proportions in ADMIXTURE analysis (Extended Data Fig. 1). More formally, we tested all $\binom{4}{2} = 6$ pairs of Mycenaean individuals in our dataset as a Left list, using the All as the Right list. All 6 pairs were consistent with forming a clade with respect to the All set to the limits of our resolution (p-value for rank=0 ≥0.08). We also estimated mixture proportions per-individual (Table S2.3) using the five successful models of the population as a whole (Table S2.2). Predictably, when estimating mixture proportions per-individual there is a doubling of standard errors. Virtually all mixture proportions have positive values, again consistent with the different individuals all being made up of the same ancestral sources. We cannot exclude variation in the proportions of these sources, however the study of any such variation could only be accomplished with a more extensive dataset. Given the lack of evidence for population structure in this population with the available data, we will treat it as a unit in the remainder of this section.

Table S2.3: Mixture proportions for Mycenaean individuals from the sources of the successful models applicable to the Mycenaean population as a whole (Table S2.2).

					Mixture Proportions			Standard Errors		
ID	*Ref_1*	*Ref_2*	*Ref_3*	P-value for rank=2	*Ref_1*	*Ref_2*	*Ref_3*	*Ref_1*	*Ref_2*	*Ref_3*
I9010	AfontovaGora3	CHG	Anatolia_N	3.81E-01	0.134	0.016	0.850	0.044	0.039	0.043
I9006	AfontovaGora3	CHG	Anatolia_N	7.21E-02	0.127	0.148	0.725	0.046	0.044	0.040
I9033	AfontovaGora3	CHG	Anatolia_N	1.71E-01	0.030	0.114	0.856	0.050	0.045	0.045
I9041	AfontovaGora3	CHG	Anatolia_N	5.84E-01	0.145	0.186	0.668	0.043	0.040	0.037
I9010	AfontovaGora3	Iran_N	Anatolia_N	3.65E-01	0.145	-0.005	0.860	0.045	0.044	0.044
I9006	AfontovaGora3	Iran_N	Anatolia_N	8.76E-02	0.163	0.093	0.744	0.043	0.042	0.040
I9033	AfontovaGora3	Iran_N	Anatolia_N	1.25E-01	0.067	0.067	0.866	0.046	0.043	0.045
I9041	AfontovaGora3	Iran_N	Anatolia_N	2.39E-01	0.165	0.149	0.686	0.043	0.042	0.038
I9010	EHG	CHG	Anatolia_N	6.79E-01	0.025	0.051	0.924	0.027	0.039	0.041
I9006	EHG	CHG	Anatolia_N	2.89E-02	0.046	0.196	0.758	0.028	0.040	0.041
I9033	EHG	CHG	Anatolia_N	1.17E-01	0.021	0.119	0.860	0.028	0.040	0.042
I9041	EHG	CHG	Anatolia_N	4.16E-01	0.041	0.238	0.721	0.026	0.036	0.038
I9010	EHG	Iran_N	Anatolia_N	6.32E-01	0.026	0.047	0.927	0.028	0.043	0.043
I9006	EHG	Iran_N	Anatolia_N	4.22E-02	0.072	0.146	0.782	0.028	0.040	0.042
I9033	EHG	Iran_N	Anatolia_N	1.11E-01	0.038	0.085	0.877	0.028	0.041	0.042
I9041	EHG	Iran_N	Anatolia_N	2.62E-01	0.060	0.196	0.744	0.026	0.038	0.040
I9010	MA1	CHG	Anatolia_N	1.27E-01	0.078	0.030	0.892	0.037	0.041	0.041
I9006	MA1	CHG	Anatolia_N	7.08E-02	0.021	0.193	0.786	0.034	0.044	0.040
I9033	MA1	CHG	Anatolia_N	2.67E-01	0.064	0.098	0.838	0.033	0.042	0.041
I9041	MA1	CHG	Anatolia_N	1.87E-01	0.043	0.234	0.723	0.031	0.040	0.037

Table S2.4: *N*=2 modeling of Minoans from Moni Odigitria. Left=(Minoan_Odigitria, *Ref_1*, *Ref_2*). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥1e-10 are shown.

			Mixture Proportions		Standard Errors	
Ref_1	*Ref_2*	P-value for rank=1	*Ref_1*	*Ref_2*	*Ref_1*	*Ref_2*
CHG	Anatolia_N	2.33E-01	0.144	0.856	0.031	0.031
Iran_N	Anatolia_N	2.25E-01	0.137	0.863	0.032	0.032
Levant_N	Anatolia_N	5.73E-03	0.004	0.996	0.114	0.114
Ust_Ishim	Anatolia_N	5.73E-04	0.063	0.937	0.026	0.026
AfontovaGora3	Anatolia_N	4.84E-04	0.072	0.928	0.038	0.038
MA1	Anatolia_N	2.21E-04	0.059	0.941	0.026	0.026
Mota	Anatolia_N	7.27E-05	0.053	0.947	0.030	0.030
GoyetQ116-1	Anatolia_N	6.03E-05	0.002	0.998	0.023	0.023
EHG	Anatolia_N	5.28E-05	0.030	0.970	0.022	0.022
Kostenki14	Anatolia_N	2.88E-05	0.014	0.986	0.024	0.024

Minoans from Moni Odigitria

Minoans from Moni Odigitria in the Heraklion regional unit (south-central Crete) do not form a clade with any single (*N*=1) population of the All set. The best single population is Neolithic Anatolians, for which rank=0 can be rejected with p=9.13e-05, with all others being rejected much more strongly (p<1e-16). We can model Minoans from Moni Odigitria as a 2-way mixture of Anatolian Neolithic and Caucasus hunter-gatherers or Neolithic Iran (Table S2.4), with most ancestry (~86%) derived from a Neolithic Anatolian-related population. Contrast the fact that the Anatolia_N+(Iran_N or CHG) models work for Minoans from Moni Odigitria (p>0.22), but are rejected for Mycenaeans (p<.006; Table S2.1). Thus, it appears that Minoans from Moni Odigitria could be modelled as a mixture of the local Neolithic substratum and a population from the east, and do not require also some ancestry from northern Eurasia/eastern Europe as do Mycenaeans.

Table S2. 5: *N*=2 modeling of Minoans from Agios Charalambos cave in Lasithi. Left=(Minoan_Lasithi, *Ref*$_1$, *Ref*$_2$). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥1e-10 are shown.

			Mixture Proportions		Standard Errors	
***Ref*$_1$**	***Ref*$_2$**	**P-value for rank=1**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_1$**	***Ref*$_2$**
CHG	Anatolia_N	2.33E-02	0.159	0.841	0.019	0.019
Iran_N	Anatolia_N	1.06E-03	0.156	0.844	0.018	0.018

Table S2.6: *N*=3 modeling of Minoans from Lasithi. Left=(Minoan_Lasithi, *Ref*$_1$, *Ref*$_2$, *Ref*$_3$). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥1e-10 are shown.

				Mixture Proportions			Standard Errors		
***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	**P-value for rank=2**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**
MA1	CHG	Anatolia_N	1.33E-01	0.001	0.152	0.847	0.015	0.021	0.020
Mota	CHG	Anatolia_N	8.33E-02	0.004	0.154	0.842	0.024	0.026	0.020
AfontovaGora3	CHG	Anatolia_N	2.46E-02	0.042	0.136	0.821	0.023	0.022	0.021
CHG	Natufian	Anatolia_N	1.95E-02	0.159	0.052	0.790	0.021	0.072	0.084
GoyetQ116-1	CHG	Anatolia_N	1.66E-02	0.010	0.156	0.834	0.013	0.019	0.021
Vestonice16	CHG	Anatolia_N	1.33E-02	0.009	0.156	0.836	0.016	0.019	0.022
Ust_Ishim	CHG	Anatolia_N	1.13E-02	0.004	0.159	0.837	0.017	0.022	0.020
MA1	Iran_N	Anatolia_N	1.04E-02	0.009	0.139	0.852	0.015	0.021	0.019
EHG	CHG	Anatolia_N	9.22E-03	0.004	0.158	0.838	0.013	0.020	0.020
AfontovaGora3	Iran_N	Anatolia_N	2.56E-03	0.058	0.125	0.817	0.024	0.021	0.021
ElMiron	Iran_N	Anatolia_N	2.05E-03	0.000	0.156	0.843	0.012	0.019	0.024
GoyetQ116-1	Iran_N	Anatolia_N	9.88E-04	0.012	0.153	0.835	0.013	0.019	0.021
Villabruna	Iran_N	Anatolia_N	9.06E-04	0.002	0.154	0.844	0.008	0.019	0.023
EHG	Iran_N	Anatolia_N	6.94E-04	0.019	0.149	0.832	0.013	0.019	0.020
Vestonice16	Iran_N	Anatolia_N	5.61E-04	0.014	0.151	0.835	0.016	0.019	0.023
Kostenki14	Iran_N	Anatolia_N	3.22E-04	0.001	0.155	0.844	0.016	0.019	0.021
WHG	Iran_N	Anatolia_N	3.07E-04	0.001	0.155	0.844	0.009	0.020	0.023

Minoans from Lasithi

Minoans from the Agios Charalambos Cave in Lasithi regional unit (which we refer to as Minoan_Lasithi for brevity) do not form a clade with any single (*N*=1) population of the All set (p-value for rank=0 is < 1e-17). We cannot model them as a 2-way mixture of any populations (Table S2.5), with rank=1 excluded strongly (p < 1e-10) for all pairs except a mixture of ~84% of Anatolian Neolithic and either Iran Neolithic or Caucasus hunter-gatherers (CHG) (0.02 > p >.001). This type of mixture fits Minoans from Moni Odigitria (Table S2.4). We can model them as a 3-way mixture (Table S2.5) of ~84-85% Neolithic Anatolians, ~15% CHG, and <1% MA1 or Mota (the third type minor ancestry is within 1 standard error of zero). The mixture proportions for Lasithi Minoans are thus practically the same as with the Moni Odigitria Minoans (Table S2.4). The lack of differentiation between these two Bronze Age Cretan populations can also be shown by their clustering in PCA (Fig.

1b), ADMIXTURE analysis (Extended Data Fig. 1) and the lack of significant asymmetries between them when tested with f_4-statistics (Extended Data Fig. 2). In the *qpWave* framework, we test Left=(Minoan_Lasithi, Minoan_Odigitria) against Right=All, finding that we cannot reject rank=0 (p=0.07) to the limits of our resolution.

Table S2.7: *N*=2 modeling of Cretan from Armenoi. Left=(Crete_Armenoi, Ref_1, Ref_2). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥1e-3 are shown.

			Mixture Proportions		Standard Errors	
Ref_1	***Ref_2***	**P-value for rank=1**	***Ref_1***	***Ref_2***	***Ref_1***	***Ref_2***
EHG	Anatolia_N	4.94E-01	0.224	0.776	0.050	0.050
AfontovaGora3	Anatolia_N	3.99E-01	0.336	0.664	0.060	0.060
MA1	Anatolia_N	1.08E-01	0.237	0.763	0.054	0.054
Vestonice16	Anatolia_N	3.54E-02	0.191	0.809	0.057	0.057
CHG	Anatolia_N	1.47E-02	0.213	0.787	0.070	0.070
Natufian	Levant_N	7.36E-03	0.491	0.509	1.933	1.933
EHG	Levant_N	6.45E-03	0.211	0.789	0.043	0.043
WHG	Anatolia_N	4.96E-03	0.114	0.886	0.038	0.038
ElMiron	Anatolia_N	3.12E-03	0.127	0.873	0.044	0.044
Villabruna	Anatolia_N	2.47E-03	0.089	0.911	0.032	0.032
Mota	Anatolia_N	2.08E-03	0.096	0.904	0.077	0.077
Ust_Ishim	Anatolia_N	1.50E-03	0.145	0.855	0.060	0.060
GoyetQ116-1	Anatolia_N	1.18E-03	0.125	0.875	0.057	0.057

Cretan from Armenoi

This individual has only 42,052 SNPs covered in the HOIll dataset and it belongs to a later period (Late Minoan III A-B ~ 1400-1200 BC) than the samples from Moni Odigitria and Lasithi. It does not form a clade with any single (*N*=1) population of the All set (p-value for rank=0 < 0.001). There are several models that fit (p-value for rank=1 > 0.05) for *N*=2 that agree on this individual having most of its ancestry from Anatolian Neolithic-related population with additional ancestry from eastern European/North Eurasian hunter-gatherers (Table S2.7), as also suggested by the shift of this individual in PCA relative to other Minoans and indeed even the Mycenaeans (Fig. 1b). We acknowledge the possibility that there was geographical structure in the Bronze Age Cretan population (the Armenoi sample comes from northwestern Crete; Fig. 1a), or that population change had occurred between the time of the samples from Moni Odigitria and Lasithi and the time of this individual, however, the lack of high quality data does not allow us to test these hypotheses further.

Table S2.8: *N*=2 modeling of Bronze Age Anatolia. Left=(Anatolia_BA, Ref_1, Ref_2). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥ 1e-10 are shown.

			Mixture Proportions		Standard Errors	
Ref_1	**Ref_2**	**P-value for rank=1**	**Ref_1**	**Ref_2**	**Ref_1**	**Ref_2**
Iran_N	Anatolia_N	1.31E-03	0.196	0.804	0.022	0.022
CHG	Anatolia_N	1.28E-03	0.224	0.776	0.021	0.021

Table S2.9: *N*=3 modeling of Bronze Age Anatolia. Left=(Anatolia_BA, Ref_1, Ref_2, Ref_3). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥1 e-10 are shown.

				Mixture Proportions			Standard Errors		
Ref₁	***Ref₂***	***Ref₃***	**P-value for rank=2**	***Ref₁***	***Ref₂***	***Ref₃***	***Ref₁***	***Ref₂***	***Ref₃***
CHG	Levant_N	Anatolia_N	9.52E-01	0.32	0.06	0.62	0.03	0.06	0.08
CHG	Iran_N	Anatolia_N	1.22E-02	0.01	0.15	0.84	0.12	0.11	0.03
CHG	Natufian	Anatolia_N	1.75E-03	0.23	0.09	0.68	0.02	0.09	0.10
AfontovaGora3	Iran_N	Anatolia_N	7.67E-04	0.01	0.19	0.80	0.03	0.03	0.03

Bronze Age Anatolia

The population from Bronze Age southwestern Anatolia does not form a clade with any single (*N*=1) population of the All set (p-value for rank=0 < 1e-25). It cannot be modelled as any 2-way mixture (Table S2.8), with the best ones involving a mixture of Anatolian Neolithic and either Iran Neolithic or Caucasus hunter-gatherers. This population can be modelled as a 3-way mixture (Table S2.9) of ~62% Neolithic Anatolian, ~32% Caucasus hunter-gatherer (CHG), and ~6% Levantine Neolithic ancestry. This extra Levantine Neolithic ancestry parallels the PCA (Fig. 1b) that shows that the Bronze Age Anatolian sample is to the "east" (towards the Levant) relative to the Minoans and Mycenaeans.

Summarizing our results, we see that all Bronze Age populations considered have most of their ancestry from an Anatolian Neolithic-related population, a conclusion that was arrived at in an unsupervised manner, without taking into account that it is precisely this type of population that is attested to in southeastern Europe and western Anatolia during the Neolithic period prior to the Bronze Age[8,14,18]. However, all the Bronze Age populations also have ancestry related to the Caucasus or Iran, consistent with their shift in PCA (Fig. 1b). This shift began in Anatolia no later than the Chalcolithic (3943-3708 calBCE)[16] and was not evident in Greece by the time of the Final Neolithic (4,230–3,995 calBCE) individual from Kleitos[14] that resembled (like all other Greek Neolithic individuals) Anatolian farmers (Fig. 1b). The newly reported Neolithic individual from Diros Cave in the Peloponnese (where most of the Mycenaean samples are from) did not have this ancestry as late as 5479-5338 calBCE (Extended Data Table 1). (Future studies may show when the transformation occurred in Greece, but by the time of the Minoan and Mycenaean samples, both populations traced some ancestry to this eastern source, as did the southwestern Anatolians from Harmanören Göndürle. In addition to the common Neolithic Anatolian and eastern (Caucasus/Iran-related) ancestry, the Mycenaeans also had extra ancestry related to eastern European hunter-gatherers and Upper Paleolithic Siberians, while the Bronze Age southwestern Anatolians had extra ancestry related to Levantine Neolithic populations.

Population structure of Anatolian farmers

We were intrigued by the fact that the central Anatolian Neolithic population from Tepecik-Çiftlik[19] appears at the edge of the cluster of ancient Anatolian/European farmers in the PCA (Fig. 1b), and also appears to possess some of the "pink" component maximized in Neolithic Iran and hunter-gatherers from the Caucasus and Iran (Extended Data Fig. 1) that is shared with Bronze Age populations from the Aegean and southwestern Anatolia. This suggests that the excess of CHG-related ancestry in the Bronze Age populations (relative to the Anatolia_N northwestern Anatolian baseline) we have just described could in fact be mediated by a population such as the Tepecik-Çiftlik population.

We first tested whether the Tepecik-Çiftlik population did in fact have CHG-related ancestry relative to the Anatolia_N population, by modeling as having ancestry from N=1, 2, 3 sources in the same manner as the Bronze Age populations; no feasible models were discovered for N=1, 2, and the population could be modelled as a having ~19-24% CHG-related ancestry in the feasible N=3 models (Table S2.10).

Table S2.10: N=3 modeling of Anatolia_Tepecik_Ciftlik. Left=(Anatolia_Tepecik_Ciftlik, Ref_1, Ref_2, Ref_3). Right= All \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥1 e-5 are shown.

				Mixture Proportions			Standard Errors		
Ref_1	Ref_2	Ref_3	P-value for rank=2	Ref_1	Ref_2	Ref_3	Ref_1	Ref_2	Ref_3
CHG	Levant_N	Anatolia_N	2.37E-01	0.238	0.094	0.668	0.028	0.069	0.082
CHG	Natufian	Anatolia_N	6.40E-02	0.191	0.246	0.563	0.025	0.099	0.115
Iran_N	Natufian	Anatolia_N	1.84E-02	0.153	0.022	0.826	0.024	0.093	0.101

We also formed the set All^A = All ∪ (Anatolia_Tepecik_Ciftlik, Anatolia_Boncuklu), which includes both the Tepecik-Çiftlik population and the earlier Aceramic Neolithic population from Boncuklu and tried to model the Bronze Age populations as derived from N=1, 2, 3 sources of this set, thus not assuming that the Anatolia_N population from northwestern Anatolia is the source. We could find feasible models with 2 sources for the Minoans from Moni Odigitria (Table S2.11), and with 3 sources for the Minoans from Lasithi, Mycenaeans, and Bronze Age Anatolians (Table S2.12). All Neolithic Anatolian populations are feasible sources for the Bronze Age populations, but we note that the feasible models agree on the main conclusions of our analysis using the Anatolia_N population: (i) CHG/Iran_N-related ancestry in all populations, either directly, or mediated by Tepecik-Çiftlik, and additional eastern European/Siberian input into Mycenaeans, and Levantine input into the southwestern Anatolian Bronze Age population. Table S2.12 also shows that the three models that fit the Minoans of Lasithi do not fit the Mycenaeans, suggesting that the ancestry of the latter cannot be ascribed to the same set of sources (in different proportions) as that of the Minoans. We also show in Table S2.12 the two models that fit Mycenaeans but do not fit Minoans; in these models the ancestry of the Minoans from the eastern European/Siberian-related source is ~0%. In the remaining analysis we use Anatolia_N as a source, bearing in mind that mixtures involving it and CHG-related populations may have taken place during the Neolithic in Anatolia itself (or indeed Greece), and future sampling may better identify them.

Table S2.11: *N*=2 modeling of Minoans from Moni Odigitria. Left=(Minoan_Odigitria, Ref_1, Ref_2). Right= All^A \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥ 0.05 are shown.

			Mixture Proportions		**Standard Errors**	
Ref_1	**Ref_2**	**P-value for rank=1**	**Ref_1**	**Ref_2**	**Ref_1**	**Ref_2**
CHG	Anatolia_N	3.54E-01	0.146	0.854	0.028	0.028
Iran_N	Anatolia_N	3.15E-01	0.131	0.869	0.028	0.028
Anatolia_N	Anatolia_Tepecik_Ciftlik	2.93E-01	0.234	0.766	0.195	0.195
WHG	Anatolia_Boncuklu	9.27E-02	0.008	0.992	0.019	0.019

Table S2.12: *N*=3 modeling of Minoans from Lasithi, Mycenaeans, and Bronze Age Anatolians. Left=(*Test*, Ref_1, Ref_2, Ref_3). Right= All^A \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥ 0.05 are shown; we also show (in italics) the three models that fit Minoans from Lasithi but do not fit Mycenaeans, and also the two models that fit Mycenaeans but do not fit Minoans from Lasithi.

					Mixture Proportions			**Standard Errors**		
Test	**Ref_1**	**Ref_2**	**Ref_3**	**P-value for rank=2**	**Ref_1**	**Ref_2**	**Ref_3**	**Ref_1**	**Ref_2**	**Ref_3**
Minoan_Lasithi	MA1	CHG	Anatolia_N	1.02E-01	0.004	0.158	0.838	0.014	0.021	0.017
Minoan_Lasithi	Mota	CHG	Anatolia_N	7.35E-02	0.013	0.154	0.832	0.021	0.026	0.017
Minoan_Lasithi	Iran_N	Anatolia_N	Anatolia_Tepecik_Ciftlik	5.41E-02	0.028	0.004	0.967	0.341	2.010	2.348
Minoan_Lasithi	*AfontovaGora3*	*Anatolia_Boncuklu*	*Anatolia_Tepecik_Ciftlik*	*1.98E-03*	*0.016*	*0.185*	*0.800*	*0.020*	*0.178*	*0.187*
Minoan_Lasithi	*EHG*	*Anatolia_Boncuklu*	*Anatolia_Tepecik_Ciftlik*	*1.56E-03*	*-0.003*	*0.157*	*0.846*	*0.011*	*0.183*	*0.183*
Mycenaean	AfontovaGora3	Anatolia_Boncuklu	Anatolia_Tepecik_Ciftlik	1.17E-01	0.170	0.181	0.650	0.020	0.127	0.133
Mycenaean	EHG	Anatolia_Boncuklu	Anatolia_Tepecik_Ciftlik	8.82E-02	0.089	0.007	0.904	0.014	0.152	0.150
Mycenaean	*MA1*	*CHG*	*Anatolia_N*	*4.41E-05*	*0.085*	*0.180*	*0.735*	*0.018*	*0.026*	*0.020*
Mycenaean	*Mota*	*CHG*	*Anatolia_N*	*4.02E-09*	*-0.002*	*0.265*	*0.737*	*0.030*	*0.036*	*0.023*
Mycenaean	*Iran_N*	*Anatolia_N*	*Anatolia_Tepecik_Ciftlik*	*6.94E-02*	*0.475*	*2.148*	*-1.623*	*0.332*	*1.728*	*2.050*
Anatolia_BA	CHG	Levant_N	Anatolia_N	5.97E-01	0.369	0.161	0.470	0.022	0.049	0.052
Anatolia_BA	Iran_N	Anatolia_N	Anatolia_Tepecik_Ciftlik	7.13E-02	0.158	0.357	0.485	0.693	3.742	4.428

Modeling ancient populations as mixtures of populations down to the Bronze Age

In the preceding analysis we modelled ancient populations as mixtures of the earliest Neolithic populations of West Eurasia and the pre-Neolithic hunter-gatherers. After the early Neolithic and by the Bronze Age, the highly differentiated source populations of West Eurasia admixed with each to drastically reduce differentiation[16]. In order to identify more proximate sources of the Bronze Age populations of the Aegean and southwestern Anatolia, we added additional later populations, forming the following augmented set.

All$^+$: Mota, Ust_Ishim, Kostenki14, GoyetQ116-1, Vestonice16, MA1, AfontovaGora3, ElMiron, Villabruna, WHG, EHG, CHG, Iran_N, Natufian, Levant_N, Anatolia_N, Anatolia_ChL, Armenia_ChL, Armenia_EBA, Armenia_MLBA, Europe_LNBA, Europe_MNChL, Iberia_BA, Iran_ChL, Levant_BA, Steppe_EMBA, Steppe_MLBA

Adding these later populations has one disadvantage: if populations A and B are both included in the larger set and are composed of the same ancestral elements in similar proportions then A may be modeled as deriving most of its ancestry from B and vice versa. This does not clarify the ancestral origins of either population. However, this approach also has the advantage of identifying mixture when the admixing populations are themselves complex. For example, if a population A is a mix of B and C, and B and C are themselves 2- or 3-way mixtures, then this approach might identify a simpler mix in the origin of A than would be possible if B and C were not considered as source populations.

Table S2.13: N=2 modeling of Mycenaeans. Left=(Mycenaean, Ref_1, Ref_2). Right= All$^+$ \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 $\geq$ 1e-10 are shown.

			Mixture Proportions		Standard Errors	
***Ref*$_1$**	***Ref*$_2$**	**P-value for rank=1**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_1$**	***Ref*$_2$**
Anatolia_N	Armenia_MLBA	2.68E-01	0.633	0.367	0.020	0.020
Anatolia_N	Armenia_ChL	6.96E-02	0.559	0.441	0.025	0.025
Anatolia_ChL	Europe_MNChL	1.56E-03	0.822	0.178	0.036	0.036
Anatolia_N	Steppe_EMBA	5.25E-04	0.798	0.202	0.012	0.012
CHG	Anatolia_N	1.91E-04	0.239	0.761	0.014	0.014
Anatolia_N	Anatolia_ChL	9.60E-05	0.272	0.728	0.058	0.058
Anatolia_N	Armenia_EBA	5.78E-05	0.621	0.379	0.022	0.022
WHG	Anatolia_ChL	1.86E-05	0.047	0.953	0.013	0.013
Anatolia_ChL	Europe_LNBA	6.56E-06	0.956	0.044	0.029	0.029
Villabruna	Anatolia_ChL	4.48E-06	0.033	0.967	0.011	0.011
ElMiron	Anatolia_ChL	8.70E-07	0.032	0.968	0.016	0.016
Anatolia_ChL	Steppe_EMBA	4.34E-07	0.998	0.002	0.020	0.020
Anatolia_ChL	Steppe_MLBA	3.24E-07	0.979	0.021	0.025	0.025
EHG	Anatolia_ChL	3.17E-07	0.016	0.984	0.014	0.014
GoyetQ116-1	Anatolia_ChL	2.78E-07	0.021	0.979	0.019	0.019
Vestonice16	Anatolia_ChL	2.26E-07	0.016	0.984	0.019	0.019
Kostenki14	Anatolia_ChL	2.03E-07	0.006	0.994	0.019	0.019
AfontovaGora3	Anatolia_N	1.27E-07	0.268	0.732	0.013	0.013
Anatolia_N	Steppe_MLBA	2.03E-10	0.744	0.256	0.015	0.015

Mycenaeans

Mycenaeans do not form a clade (N=1) with any population of the All$^+$ set (p-value for rank=0 < 1e-6). They can only be modelled as a 2-way mixture of Neolithic Anatolia and Chalcolithic or Middle/Late Bronze Armenia (Table S2.13). This suggests that Mycenaeans could be a mixture of early Neolithic people (represented by the Neolithic Anatolian population) and further input from the east related to populations of Armenia. This seemingly contradicts the results of our earlier modeling as a 3-way mixture of Anatolian Neolithic, Iran Neolithic or Caucasus hunter-gatherers, and Eastern European hunter-gatherers or Upper Paleolithic Siberians (Table S2.2), which suggests input from both the east (related to Iran) and north. However, populations of Armenia themselves have some EHG-related ancestry[16], so it is possible that Mycenaeans received both the Iran-related and EHG-related ancestry together from a population similar to that which inhabited Armenia. Thus, it is possible that Mycenaeans received ancestry from these sources separately (from the north and the east; Table S2.2), or in a population that had ancestry from both, as in the populations of Armenia. Note that a combination of EHG-related and Iran-related ancestry also existed on the Eurasian steppe[16] in roughly equal proportions. However, we cannot model Mycenaeans as a mixture of Anatolian Neolithic and steppe populations (Table S2.13). This is due to the fact that Mycenaeans have more Iran-related than EHG-related ancestry (Table S2.2). It is possible that there were other populations along the Iran/EHG "northeastern interaction sphere[13]" than the ones sampled here.

Note that when modeling Mycenaeans as a mixture of Anatolian Neolithic- and Armenia-related populations (Table S2.13) we infer that they have ~56-63% Anatolian Neolithic-related ancestry, which is smaller than the ~74-80% of such ancestry when modeling them without the later populations as a source (Table S2.2). This is due to the fact that populations from Armenia themselves have Anatolian Neolithic-related ancestry[16]. Since such ancestry existed in both Anatolia and Neolithic Europe, it is likely that any migrations from either east or north would introduce some of it into the Aegean; thus some Anatolian Neolithic-related ancestry may correspond to the pre-Mycenaean inhabitants of Greece, while some of it may have arrived together with later migrations from the north or east from populations that already possessed some of it.

Nonetheless, if it arrived with populations like those of Armenia, it is still inferred that the majority (~56-63%) of the ancestry of Mycenaeans was Anatolian Neolithic-related, and so while non-trivial genetic turnover occurred in Greece, it was not as significant as in central Europe where ~3/4 of the ancestry of the Corded Ware people was of steppe origin[1]. The evidence of a more dramatic transformation in Central Europe is also seen in PCA (Fig. 1b) which shows that while population change occurred in both mainland Europe (Europe_LNBA) and the Aegean, it was more extreme in the former. Note, however, that there is a bigger temporal gap between the Neolithic populations of Greece (which were quite similar to the Anatolian Neolithic) and the Mycenaeans; it is possible that populations from the Aegean prior to Mycenaeans but after the Final Neolithic may have had more ancestry from the migrants. This would then parallel the situation in central Europe where the earlier groups (Corded Ware) had more exogenous ancestry than the later Bronze Age groups[1].

Table S2.14: *N*=2 modeling of Minoans from Moni Odigitria. Left=(Minoan_Odigitria, *Ref*$_1$, *Ref*$_2$). Right= All$^+$ \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥ 1e-5 are shown.

			Mixture Proportions		Standard Errors	
***Ref*$_1$**	***Ref*$_2$**	**P-value for rank=1**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_1$**	***Ref*$_2$**
Anatolia_N	Armenia_EBA	4.61E-02	0.807	0.193	0.030	0.030
Anatolia_N	Anatolia_ChL	1.58E-02	0.574	0.426	0.090	0.090
Anatolia_N	Armenia_MLBA	1.29E-02	0.838	0.162	0.027	0.027
CHG	Anatolia_N	1.11E-02	0.110	0.890	0.018	0.018
Anatolia_N	Armenia_ChL	9.57E-03	0.803	0.197	0.034	0.034
Anatolia_N	Iran_ChL	2.78E-03	0.858	0.142	0.025	0.025
Iran_N	Anatolia_N	2.46E-03	0.103	0.897	0.018	0.018
Anatolia_N	Steppe_EMBA	1.68E-04	0.939	0.061	0.017	0.017
Levant_N	Anatolia_N	5.43E-05	0.157	0.843	0.074	0.074
Anatolia_N	Levant_BA	1.50E-05	0.829	0.171	0.053	0.053
AfontovaGora3	Anatolia_N	1.45E-05	0.088	0.912	0.023	0.023
Anatolia_N	Steppe_MLBA	1.31E-05	0.920	0.080	0.020	0.020

Table S2.15: *N*=3 modeling of Minoans from Moni Odigitria. Left=(Minoan_Odigitria, *Ref*$_1$, *Ref*$_2$, *Ref*$_3$). Right= All$^+$ \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥ 1e-3 are shown.

				Mixture Proportions			Standard Errors		
***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	**P-value for rank=2**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**
Levant_N	Anatolia_N	Armenia_EBA	1.18E-01	0.026	0.802	0.172	0.073	0.066	0.034
Levant_N	Anatolia_N	Anatolia_ChL	1.05E-01	0.022	0.604	0.374	0.069	0.086	0.084
Levant_N	Anatolia_N	Armenia_MLBA	4.92E-02	0.056	0.806	0.138	0.074	0.068	0.030
Levant_N	Anatolia_N	Armenia_ChL	3.94E-02	0.063	0.769	0.168	0.070	0.067	0.036
CHG	Levant_N	Anatolia_N	3.82E-02	0.093	0.061	0.846	0.020	0.072	0.067
Levant_N	Anatolia_N	Iran_ChL	1.83E-02	0.017	0.855	0.127	0.080	0.070	0.029
Iran_N	Levant_N	Anatolia_N	1.29E-02	0.090	0.026	0.884	0.021	0.079	0.071
Anatolia_N	Armenia_MLBA	Iran_ChL	8.87E-03	0.836	0.109	0.054	0.027	0.061	0.055
Anatolia_N	Armenia_ChL	Iran_ChL	8.12E-03	0.815	0.116	0.069	0.036	0.072	0.053
Iran_N	Anatolia_N	Armenia_MLBA	7.15E-03	0.029	0.849	0.122	0.050	0.035	0.076
Anatolia_N	Iran_ChL	Steppe_EMBA	6.28E-03	0.868	0.118	0.014	0.025	0.032	0.021
Iran_N	Anatolia_N	Armenia_ChL	5.88E-03	0.042	0.833	0.124	0.052	0.053	0.099
Levant_N	Anatolia_N	Steppe_EMBA	5.21E-03	0.129	0.825	0.045	0.067	0.069	0.017
AfontovaGora3	Anatolia_N	Iran_ChL	3.16E-03	0.016	0.853	0.131	0.031	0.027	0.033
Iran_N	Anatolia_N	Steppe_EMBA	2.66E-03	0.083	0.906	0.011	0.026	0.020	0.023
EHG	Anatolia_N	Iran_ChL	2.12E-03	0.016	0.855	0.129	0.014	0.025	0.028
Anatolia_N	Iran_ChL	Steppe_MLBA	2.07E-03	0.850	0.124	0.027	0.026	0.030	0.024
Anatolia_N	Europe_LNBA	Iran_ChL	2.02E-03	0.846	0.031	0.123	0.028	0.027	0.029
MA1	Anatolia_N	Iran_ChL	1.76E-03	0.010	0.858	0.133	0.018	0.025	0.031
EHG	Iran_N	Anatolia_N	1.41E-03	0.005	0.099	0.895	0.016	0.022	0.018
Iran_N	Anatolia_N	Steppe_MLBA	1.37E-03	0.095	0.892	0.013	0.024	0.021	0.026
Iran_N	Anatolia_N	Europe_LNBA	1.28E-03	0.094	0.890	0.016	0.023	0.024	0.029
Anatolia_N	Levant_BA	Steppe_EMBA	1.21E-03	0.866	0.080	0.054	0.051	0.056	0.018

Minoans from Moni Odigitria

Minoans from Moni Odigitria do not form a clade (*N*=1) with any population of the All$^+$ set (p-value for rank=0 < 1e-6). The best 2-way mixture models (*N*=2) involve a pairing of Anatolian Neolithic with an eastern population from Armenia, Iran, or the Caucasus (Table S2.14). We can successfully model them as 3-way mixtures composed primarily of these two components with a minor (~2-3% and not significantly different from zero) contribution from the Levantine Neolithic (Table S2.15).

Table S2.16: *N*=2 modeling of Minoans from Lasithi. Left=(Minoan_Lasithi, *Ref*$_1$, *Ref*$_2$). Right= All$^+$ \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥ 1e-10 are shown.

			Mixture Proportions		Standard Errors	
***Ref*$_1$**	***Ref*$_2$**	**P-value for rank=1**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_1$**	***Ref*$_2$**
Anatolia_N	Armenia_EBA	2.76E-04	0.757	0.243	0.018	0.018
Anatolia_N	Anatolia_ChL	2.57E-05	0.501	0.499	0.052	0.052
Anatolia_N	Armenia_MLBA	4.81E-07	0.792	0.208	0.017	0.017
CHG	Anatolia_N	8.57E-08	0.146	0.854	0.012	0.012
Anatolia_N	Armenia_ChL	1.88E-09	0.737	0.263	0.022	0.022

Table S2.17: *N*=3 modeling of Minoans from Lasithi. Left=(Minoan_Lasithi, *Ref*$_1$, *Ref*$_2$, *Ref*$_3$). Right= All$^+$ \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥ 1e-10 are shown.

				Mixture Proportions			Standard Errors		
***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	**P-value for rank=2**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**
CHG	Anatolia_N	Armenia_MLBA	1.25E-06	0.126	0.850	0.024	0.115	0.055	0.169
Anatolia_N	Armenia_MLBA	Iran_ChL	3.08E-07	0.790	0.177	0.034	0.017	0.037	0.035
Iran_N	Anatolia_N	Armenia_MLBA	2.59E-07	0.018	0.796	0.186	0.031	0.021	0.046
CHG	Anatolia_N	Steppe_EMBA	3.38E-08	0.150	0.848	0.002	0.020	0.013	0.016
AfontovaGora3	CHG	Anatolia_N	2.41E-08	0.001	0.145	0.854	0.024	0.021	0.014
CHG	Anatolia_N	Armenia_ChL	2.31E-08	0.137	0.846	0.016	0.068	0.059	0.124
Anatolia_N	Armenia_ChL	Iran_ChL	1.23E-09	0.744	0.206	0.049	0.023	0.048	0.036
Iran_N	Anatolia_N	Armenia_ChL	9.37E-10	0.036	0.761	0.203	0.035	0.035	0.066

Minoans from Lasithi

Minoans from Lasithi do not form a clade (*N*=1) with any population of the All$^+$ set (p-value for rank=0 < 1e-16). The best 2-way mixture models (*N*=2) involve a pairing of Anatolian Neolithic with populations from Anatolia or Armenia (Table S2.16), while the best 3-way mixture models (*N*=3; Table S2.17) involve a pairing of Anatolian Neolithic with two populations from Anatolia, Armenia, the Caucasus, or Iran. None of the 2- or 3-way mixture models fit (p<1e-3). Recall that Minoans from Lasithi can be modelled as a mixture of mainly Anatolian Neolithic and Caucasus hunter-gatherers (CHG) (Table S2.6), but, unlike Mycenaeans, do not appear to be reducible to admixture between any of the sampled later populations. This might suggest an earlier formation of the Minoans by a relatively simple admixture of the Anatolia-related substratum with an eastern (CHG-like) population, or back-flow from a Minoan-related populations into the ancestors of populations in the All$^+$ set. Sampling of earlier populations from Crete and eastern populations may find a better surrogate for the eastern ancestry in this population than the CHG.

Table S2.18: N=2 modeling of Bronze Age Anatolians. Left=(Anatolia_BA, Ref_1, Ref_2). Right= All$^+$ \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥ 1e-5 are shown.

			Mixture Proportions		Standard Errors	
***Ref*$_1$**	***Ref*$_2$**	**P-value for rank=1**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_1$**	***Ref*$_2$**
Natufian	Anatolia_ChL	2.61E-01	0.092	0.908	0.039	0.039
Anatolia_ChL	Levant_BA	9.55E-02	0.892	0.108	0.114	0.114
Levant_N	Anatolia_ChL	8.16E-02	0.049	0.951	0.051	0.051
Anatolia_N	Anatolia_ChL	5.79E-02	0.065	0.935	0.062	0.062
Mota	Anatolia_ChL	1.80E-02	0.008	0.992	0.022	0.022

Table S2.19: N=3 modeling of Bronze Age Anatolians. Left=(Anatolia_BA, Ref_1, Ref_2, Ref_3). Right= All$^+$ \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥ 1e-5 are shown.

				Mixture Proportions			Standard Errors		
***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	**P-value for rank=2**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**
Natufian	Anatolia_N	Anatolia_ChL	2.27E-01	0.083	0.059	0.858	0.038	0.058	0.063
Mota	Natufian	Anatolia_ChL	1.47E-01	0.005	0.105	0.889	0.022	0.044	0.043
Anatolia_N	Anatolia_ChL	Levant_BA	8.96E-02	0.085	0.805	0.110	0.057	0.130	0.112
Levant_N	Anatolia_ChL	Levant_BA	8.93E-02	0.029	0.954	0.017	0.095	0.160	0.229
Anatolia_ChL	Europe_MNChL	Levant_BA	6.43E-02	0.886	0.002	0.112	0.134	0.036	0.118
Levant_N	Anatolia_N	Anatolia_ChL	5.56E-02	0.033	0.048	0.920	0.061	0.074	0.064
Levant_N	Anatolia_ChL	Iran_ChL	4.67E-02	0.051	0.946	0.003	0.060	0.097	0.051
Anatolia_N	Anatolia_ChL	Iran_ChL	3.16E-02	0.076	0.912	0.012	0.115	0.190	0.083
Anatolia_N	Armenia_EBA	Levant_BA	2.86E-02	0.426	0.362	0.212	0.044	0.043	0.074
Mota	Levant_N	Anatolia_ChL	1.37E-02	0.005	0.027	0.968	0.022	0.056	0.059
Mota	Anatolia_N	Anatolia_ChL	1.22E-02	0.013	0.068	0.919	0.024	0.066	0.078
Natufian	Anatolia_N	Armenia_EBA	1.74E-03	0.150	0.431	0.418	0.032	0.033	0.023
CHG	Anatolia_N	Levant_BA	9.21E-04	0.209	0.519	0.272	0.026	0.052	0.072
Levant_N	Anatolia_N	Armenia_EBA	8.04E-04	0.107	0.431	0.463	0.045	0.046	0.024
Anatolia_N	Armenia_MLBA	Levant_BA	5.10E-05	0.369	0.257	0.375	0.042	0.034	0.064
Anatolia_N	Armenia_ChL	Levant_BA	5.05E-05	0.316	0.326	0.358	0.040	0.043	0.067

Bronze Age Anatolia

Bronze Age Anatolians do not form a clade (N=1) with any population of the All$^+$ set (p-value for rank=0 < 1e-17), except with a Chalcolithic northwestern Anatolian[13] (p=0.072). The rather low p-value together with the fact that the Chalcolithic Anatolian (Anatolia_ChL) does not cluster with the Bronze Age southwestern Anatolians led us to also test statistics of the form f_4(Anatolia_BA, Anatolia_ChL; *Ancient*, Chimp) for all other *Ancient* populations (Extended Data Fig. 3). These do not reach significance at the |Z|=3 level, but statistics involving *Ancient* as CHG, EHG, SHG, or MA1 approach this level, which appears to be consistent with the more "northern" position of the Chalcolithic Anatolian in the PCA (Fig. 1b). Overall, we believe that it is reasonable to think that these differences are real, although it is unclear whether they reflect spatial structure (as the two populations were sampled ~260 km apart) or a temporal change (as the two populations lived >1,000 years apart). A more thorough sampling of ancient Anatolian variation may clarify this. When we model Bronze Age Anatolians as 2-way mixtures (N=2), the best models (Table S2.18) involve Chalcolithic Anatolians and populations from the Levant (Natufians, Neolithic and Bronze Age

Levantines), as do the best N=3 models (Table S2.19). Recall that we could model this population as a mixture of Neolithic Anatolians, Caucasus hunter-gatherers, and Levantine Neolithic (Table S2.9)

Modeling Mycenaeans, Minoans, and Bronze Age Anatolians as mixtures of each other

In the preceding section we modelled Bronze Age populations from the Aegean and Anatolia as mixtures of earlier populations. We now add them as potential sources, forming:

All^{++}: All^{+} $\cup$ (Mycenaean, Minoan_Lasithi, Anatolia_BA)

We study mixture models in which at least one of the reference populations belongs to the set (Mycenaean, Minoan_Lasithi, Anatolia_BA). We do not include Minoan_Odigitria in the set, since we have seen that they form a clade with Minoan_Lasithi, and thus doing so results in them being modelled as simply each other which does not help elucidate the origins of either population. We verify again that Minoan_Odigitria forms a clade with Minoan_Lasithi to the limits of our resolution, by testing Left=(Minoan_Odigitria, Minoan_Lasithi) and Right= All^{+} $\cup$ (Mycenaean, Anatolia_BA) with p-value for rank=0 equal to 0.116.

Table S2.20: N=2 modeling of Mycenaeans. Left=(Mycenaean, Ref_1, Ref_2). Right= All^{++} $\setminus$ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 $\geq$ 1e-5 are shown.

			Mixture Proportions		**Standard Errors**	
***Ref*$_1$**	***Ref*$_2$**	**P-value for rank=1**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_1$**	***Ref*$_2$**
Steppe_MLBA	Minoan_Lasithi	3.34E-01	0.175	0.825	0.017	0.017
Europe_LNBA	Minoan_Lasithi	1.76E-01	0.198	0.802	0.019	0.019
Steppe_EMBA	Minoan_Lasithi	1.74E-01	0.132	0.868	0.014	0.014
EHG	Minoan_Lasithi	4.05E-02	0.099	0.901	0.011	0.011
Armenia_MLBA	Minoan_Lasithi	9.21E-03	0.237	0.763	0.026	0.026
MA1	Minoan_Lasithi	3.77E-03	0.110	0.890	0.012	0.012
AfontovaGora3	Minoan_Lasithi	3.34E-03	0.175	0.825	0.017	0.017
Armenia_ChL	Minoan_Lasithi	6.52E-04	0.296	0.704	0.034	0.034
CHG	Minoan_Lasithi	1.49E-05	0.132	0.868	0.017	0.017

Mycenaeans

Mycenaeans do not form a clade (N=1) with any populations of the All^{++} set (p-value for rank=0 < 1e-6). We can model it as a 2-way mixture (N=2) of Minoans from Lasithi (Table S2.20) and Bronze Age steppe populations or steppe-influenced populations of the Late Neolithic/Bronze Age[1,20] from mainland Europe.

Recall that in our previous analysis using hunter-gatherer and Neolithic source populations we showed that Eastern European hunter-gatherer/Upper Paleolithic Siberian admixture was present in Mycenaeans but not in Minoans (Table S2.2, S2.4, S2.6). Steppe populations of the Bronze Age have substantial such ancestry, as do Late Neolithic/Bronze Age populations that were influenced by them[1,8,20]. Thus, the discovery that Mycenaeans can be modelled as a mixture of Minoans and Bronze

Age steppe populations can explain the presence of this type of ancestry in them. The amount of steppe ancestry is about ~13% when the Early/Middle Bronze Age group ("Yamnya/Afnasievo/Poltavka-related") is used as a source (Steppe_EMBA), which is in harmony with our finding of ~7% EHG ancestry in Mycenaeans, as this group has about half of its ancestry from the EHG[1,8,16]. The proportion is slightly higher when the Middle/Late Bronze Age (Steppe_MLBA) group ("Srubnaya/Andronovo/Sintashta-related") is used as a source, and higher still when the Late Neolithic/Bronze Age populations from mainland Europe (Europe_LNBA) are used as a source, reflecting the fact that these have substantial European/Anatolian Neolithic-related ancestry[1,8,20] which dilutes their EHG-related ancestry further. We cannot distinguish which of these populations was a source for Mycenaeans (whether there was a migration directly from the steppe, from populations related to the Early, Middle/Late Bronze Age steppe, or an indirect migration from central Europe from steppe-influenced populations that were formed there during the Late/Neolithic Bronze Age).

Table S2.21: *N*=2 modeling of Minoans from Lasithi. Left=(Minoan_Lasithi, Ref_1, Ref_2). Right= All^{++} \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥ 1e-10 are shown.

			Mixture Proportions		Standard Errors	
***Ref*₁**	***Ref*₂**	**P-value for rank=1**	***Ref*₁**	***Ref*₂**	***Ref*₁**	***Ref*₂**
Anatolia_N	Mycenaean	3.41E-06	0.227	0.773	0.056	0.056

Table S2.22: *N*=3 modeling of Minoans from Lasithi. Left=(Minoan_Lasithi, Ref_1, Ref_2, Ref_3). Right= All^{++} \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥ 1e-10 are shown.

				Mixture Proportions			Standard Errors		
***Ref*₁**	***Ref*₂**	***Ref*₃**	**P-value for rank=2**	***Ref*₁**	***Ref*₂**	***Ref*₃**	***Ref*₁**	***Ref*₂**	***Ref*₃**
Anatolia_N	Iran_ChL	Mycenaean	1.83E-06	0.293	0.030	0.677	0.120	0.039	0.156
Anatolia_N	Europe_LNBA	Anatolia_BA	2.52E-10	0.496	0.013	0.491	0.052	0.019	0.062
Anatolia_N	Europe_MNChL	Anatolia_BA	1.54E-10	0.357	0.024	0.619	0.124	0.035	0.101
WHG	Anatolia_N	Anatolia_BA	1.13E-10	0.003	0.508	0.489	0.008	0.051	0.050

Minoans from Lasithi

Minoans do not form a clade (*N*=1) with any populations of the All^{++} set (p-value for rank=0 < 1e-16). No convincing *N*=2 (Table S2.21) or *N*=3 (Table S2.22) model of this population could be found. When one of the sources is Mycenaean, additional Anatolian Neolithic ancestry is inferred for the Minoan population, consistent with the analysis of *f*-statistics (Extended Data Fig. 2d), which shows that Neolithic Anatolians share fewer alleles with Mycenaeans than with Minoans. By adding Anatolian Neolithic to Mycenaean ancestry, the best models attempt to compensate for this difference.

However, the models fail because Mycenaeans have EHG-related ancestry that the Minoans lack, so any model which uses them as a source is inherently deficient.

Table S2.23: *N*=2 modeling of Bronze Age Anatolia. Left=(Anatolia_BA, *Ref*$_1$, *Ref*$_2$, *Ref*$_3$). Right= All^{++} \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=1 ≥ 1e-10 are shown.

			Mixture Proportions		Standard Errors	
***Ref*$_1$**	***Ref*$_2$**	**P-value for rank=1**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_1$**	***Ref*$_2$**
Anatolia_ChL	Minoan_Lasithi	7.46E-02	0.970	0.030	0.108	0.108
Levant_BA	Mycenaean	2.83E-06	0.380	0.620	0.100	0.100
Levant_BA	Minoan_Lasithi	5.40E-07	0.561	0.439	0.053	0.053

Table S2.24: *N*=3 modeling of Bronze Age Anatolia. Left=(Anatolia_BA, *Ref*$_1$, *Ref*$_2$, *Ref*$_3$). Right= All^{++} \ Left. Models with mixture proportions in [0, 1] interval and P-value for rank=2 ≥ 1e-5 are shown.

				Mixture Proportions			Standard Errors		
***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	**P-value for rank=2**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**	***Ref*$_1$**	***Ref*$_2$**	***Ref*$_3$**
Natufian	Anatolia_ChL	Minoan_Lasithi	2.85E-01	0.095	0.835	0.070	0.038	0.108	0.095
Anatolia_ChL	Levant_BA	Minoan_Lasithi	1.68E-01	0.659	0.173	0.168	0.182	0.109	0.102
Levant_N	Anatolia_ChL	Minoan_Lasithi	8.70E-02	0.040	0.904	0.056	0.053	0.105	0.109
Mota	Anatolia_ChL	Minoan_Lasithi	1.49E-02	0.015	0.912	0.073	0.026	0.150	0.133
Armenia_MLBA	Levant_BA	Minoan_Lasithi	4.38E-03	0.147	0.381	0.472	0.028	0.060	0.048
Armenia_EBA	Levant_BA	Minoan_Lasithi	4.34E-03	0.188	0.347	0.465	0.038	0.067	0.049
CHG	Levant_BA	Minoan_Lasithi	2.88E-03	0.103	0.367	0.530	0.020	0.066	0.054
Levant_BA	Steppe_EMBA	Minoan_Lasithi	1.73E-03	0.485	0.051	0.465	0.051	0.013	0.048
Armenia_ChL	Levant_BA	Minoan_Lasithi	1.61E-03	0.195	0.373	0.432	0.039	0.064	0.049
Levant_BA	Steppe_MLBA	Minoan_Lasithi	1.27E-04	0.505	0.070	0.425	0.052	0.016	0.050
Natufian	Armenia_EBA	Minoan_Lasithi	9.96E-05	0.209	0.285	0.507	0.030	0.027	0.037
Levant_N	Armenia_EBA	Minoan_Lasithi	6.37E-05	0.188	0.344	0.468	0.041	0.028	0.054
Europe_LNBA	Levant_BA	Minoan_Lasithi	5.43E-05	0.074	0.510	0.416	0.018	0.053	0.052
Iran_N	Levant_BA	Minoan_Lasithi	4.77E-05	0.085	0.371	0.543	0.024	0.087	0.070
Iran_ChL	Levant_BA	Minoan_Lasithi	4.04E-05	0.137	0.340	0.523	0.041	0.093	0.063
AfontovaGora3	Levant_BA	Minoan_Lasithi	4.03E-05	0.066	0.462	0.472	0.017	0.057	0.051
EHG	Levant_BA	Minoan_Lasithi	3.86E-05	0.038	0.509	0.453	0.010	0.053	0.051
CHG	Levant_N	Minoan_Lasithi	1.85E-05	0.196	0.200	0.604	0.016	0.044	0.050
MA1	Levant_BA	Minoan_Lasithi	1.63E-05	0.042	0.464	0.494	0.012	0.060	0.055
CHG	Natufian	Minoan_Lasithi	1.58E-05	0.158	0.230	0.613	0.015	0.030	0.033
Levant_BA	Mycenaean	Minoan_Lasithi	1.40E-05	0.419	0.433	0.148	0.102	0.245	0.163

Bronze Age Anatolia

Bronze Age southwestern Anatolians do not form a clade (*N*=1) with any populations of the All^{++} set (p-value for rank=0 < 1e-13), with the most plausible single source being Chalcolithic northwestern Anatolians (p=0.036); the relationship between the two populations has been discussed above. When we model them as 2-way mixtures (*N*=2) (Table S2.23) they derive virtually all (~97%) their ancestry from the Chalcolithic Anatolians in the only feasible (p=0.0746) model (Anatolia_ChL+Minoan_Lasithi). When we model them as 3-way mixtures (*N*=3) (Table S2.24) they can be modelled with ancestry from both Minoans and the Levant in addition to Chalcolithic Anatolians. The three feasible models (Table S2.24) all involve some Levantine ancestry (from Natufians, Neolithic or Bronze Age Levant), confirming our previous modeling of this population that suggested they could be a mixture of Anatolian, Levantine Neolithic and Caucasus hunter-gatherers

(CHG) (Table S2.9) and that the Levantine affinity differentiates them from the populations of the Aegean.

Modeling admixture from ghost populations

We have previously introduced a method of testing the robustness of an admixture model via modeling "ghost populations."[13] Briefly, a ghost population contributes ancestry to the *Test* population of interest but is not actually present in the dataset. This method can be used to test the robustness of an admixture model by removing an actual ancestral population (treating it as a "ghost"), re-estimating mixture proportions, and seeing how closely they correspond to the estimates when the population is included as a source.

We apply this method to model Mycenaeans as a 2-way mixture of Minoans from Lasithi and a steppe-related/admixed population (Table S2.20). We treat each of the three "real" steppe-related populations as a ghost population. The composition of the "ghost" corresponds to the "real" one (taken from ref.[13]) within ~5-20%, but the mixture proportions of steppe-related ancestry into Mycenaeans are inferred within ~1-4%. Thus, while we cannot distinguish between the different source populations of 'northern' ancestry, our results do not depend strongly on the sampled populations, as quantitatively similar estimates of their impact on Mycenaeans are inferred when we either use any of them, or use none of them, but simply infer ancestry from an unsampled "ghost" population from either the eastern European-Iran continuum that formed the early populations of the steppe[1,10,13], or the steppe-European farmer continuum of the Middle/Late Bronze Age[8,20].

Table S2.25: Modeling Mycenaeans via cline intersection. Mycenaeans are modeled as a mixture of Ref_1 and a ghost population residing on the $Ref_2 \rightarrow Ref_3$ cline. The set of outgroups is taken to be All^{++} except (Mycenaean, Ref_1, Ref_2, Ref_3, Real).

						Composition of "Ghost"		**Composition of "Real"[13]**	
Ref_1	**Real**	**Ref_2**	**Ref_3**	α_{Ghost}	α_{Real}	**Ref_2**	**Ref_3**	**Ref_2**	**Ref_3**
Minoan_Lasithi	Steppe_EMBA	EHG	Iran_ChL	0.094	0.132	0.668	0.332	0.568	0.432
Minoan_Lasithi	Steppe_MLBA	Steppe_EMBA	Europe_MNChL	0.185	0.175	0.484	0.516	0.685	0.315
Minoan_Lasithi	Europe_LNBA	Steppe_EMBA	Europe_MNChL	0.185	0.198	0.487	0.514	0.531	0.469

Mycenaean origins

European Early Neolithic farmers from central and western Europe resembled each other genetically[1], suggesting a common source in southeastern Europe, prior to the migration along inland (Danubian) and coastal (Mediterranean) routes into mainland Europe. The Neolithic Anatolians from northwestern Anatolia also resembled early Neolithic Europeans[8], providing a plausible source for the early farmers of Europe near its southeastern periphery from whence the Neolithic spread into the continent's north and west. Aegean Neolithic populations also resembled Neolithic northwestern

Anatolians[14]. Thus, the totality of the evidence suggests a fairly homogeneous set of populations from western Anatolia, Greece, and much of Europe. It is likely that the Bronze Age populations of our study succeeded these earlier Neolithic inhabitants, a conclusion supported by the fact that Anatolian Neolithic populations feature as primary sources for them when considering a large set of West Eurasian Neolithic and hunter-gatherer populations as outgroups for comparison.

Our study shows that the Bronze Age populations were not descended only from a population related to the Neolithic Anatolians. We have successfully modelled Mycenaeans as a mix of (i) Neolithic populations of Anatolia, Neolithic Iran or Caucasus hunter-gatherers, and eastern European hunter-gatherers or Upper Paleolithic Siberians, (ii) Neolithic Anatolians and Chalcolithic-to-Bronze Age people from Armenia, or (iii) Minoans and Bronze Age people from the Eurasian steppe (or from mainland Europe after the arrival of steppe ancestry there); the Minoans themselves could be modelled as a mixture of Neolithic Anatolians and Caucasus hunter-gatherers, but they could not be successfully modelled as mixtures of later populations. We do not know whether a “Minoan-like” population extended into mainland Greece prior to the emergence of Mycenaean civilization, or whether the transformation of the Anatolian Neolithic population substratum in both mainland Greece and Crete into the Mycenaean and Minoan populations occurred in parallel. Samples from the Early Bronze Age may clarify this question. Whatever the history, it is clear that Mycenaeans and Minoans shared most of their ancestry, as we can model Mycenaeans as having most of their ancestry from a population like the Minoans (Table S2.20), confirming the clustering of the two Aegean Bronze Age populations in PCA in the context of West Eurasian genetic variation (Fig. 1b).

Against an Anatolian Neolithic baseline, Mycenaeans could not be modelled as having additional ancestry only from the Near East or continental Europe (Table S2.1), but could be modelled as having additional ancestry from both the Near East and eastern Europe/Siberia (Table S2.2). This suggests that at some time between the dispersal of early farmers into Europe and the mid-2nd millennium BCE, there was migration from both sources into continental Greece. While there might have been independent migrations from the north and east, the dynamics of this process are unclear and will be elucidated by further sampling.

One possibility, suggested by our ability to model Mycenaeans as a mix of Minoans and steppe (and steppe-influenced) populations is that the eastern influence came first, creating a “Minoan-like” population in Crete and mainland Greece, while the northern influence came afterwards, adding extra ancestry on top of the Minoan-like substratum (Table S2.20). An alternative possibility is that the pre-Mycenaean inhabitants of mainland Greece resembled the early Neolithic farmers and ~37-44% ancestry on top of the Anatolian Neolithic-like substratum was added from the east, from a population like those of Armenia (Table S2.15).

The two alternative scenarios differ in their derivation of the northern (steppe)/eastern (Near East) non-Anatolian Neolithic ancestry in Mycenaeans. In the first one, Anatolian Neolithic first admixed with an eastern population in the Aegean, with subsequent admixture from a northern population. In the second one, the eastern/northern populations admixed east of Greece (in a population related to Middle/Late Bronze Age Armenia), and then the aggregate population admixed into the Aegean.

While both ‘eastern’ and ‘northern’ 2-way mixture models fit the data statistically, we were curious whether a more complicated model could provide additional insight, so we tested 3-way mixture models with Anatolia_N or Minoan_Lasithi as the substratum population and both steppe-related ‘northern’ ancestry (Steppe_EMBA, Steppe_MLBA, or Europe_LNBA) and Armenia-related ‘eastern’ ancestry (Armenia_MLBA or Armenia_ChL). The results are presented in Table S2.26. Anatolian Neolithic/Minoans make up the majority of the ancestry (~59-90%) in all these models. Most of the coefficients for the ‘northern’ and ‘eastern’ ancestry are positive, suggesting that there is migration from both sources, but many of these positive coefficients do not significantly differ from zero (explaining why the simpler 2-way mixture models fit the data adequately without taking into account a 3rd ancestral source). Interestingly, the proportion of ‘eastern’ and ‘northern’ ancestry in Table S2.26 are anti-correlated (r=-0.95) suggesting again that they both capture the same underlying phenomenon.

Table S2.26: 3-way mixture models. Left = (Mycenaean, A, B, C). The Right set is All++ except Mycenaeans and all populations in columns A, B, C of the Table.

				Mixture Proportions			Standard Errors		
A	**B**	**C**	**P-value for rank=2**	**A**	**B**	**C**	**A**	**B**	**C**
Anatolia_N	Armenia_MLBA	Steppe_EMBA	6.36E-01	0.662	0.307	0.031	0.028	0.054	0.033
Minoan_Lasithi	Armenia_MLBA	Steppe_EMBA	2.46E-01	0.885	0.008	0.107	0.045	0.078	0.041
Anatolia_N	Armenia_MLBA	Steppe_MLBA	6.17E-01	0.647	0.326	0.026	0.022	0.039	0.032
Minoan_Lasithi	Armenia_MLBA	Steppe_MLBA	4.32E-01	0.825	0.056	0.119	0.033	0.052	0.036
Anatolia_N	Armenia_MLBA	Europe_LNBA	6.04E-01	0.643	0.334	0.023	0.023	0.035	0.033
Minoan_Lasithi	Armenia_MLBA	Europe_LNBA	4.31E-01	0.798	0.085	0.118	0.032	0.045	0.034
Anatolia_N	Armenia_ChL	Steppe_EMBA	5.75E-01	0.606	0.359	0.035	0.038	0.066	0.034
Minoan_Lasithi	Armenia_ChL	Steppe_EMBA	2.50E-01	0.903	-0.022	0.119	0.070	0.107	0.044
Anatolia_N	Armenia_ChL	Steppe_MLBA	5.87E-01	0.586	0.378	0.036	0.028	0.047	0.032
Minoan_Lasithi	Armenia_ChL	Steppe_MLBA	4.13E-01	0.815	0.062	0.123	0.045	0.066	0.035
Anatolia_N	Armenia_ChL	Europe_LNBA	5.87E-01	0.578	0.386	0.036	0.027	0.041	0.032
Minoan_Lasithi	Armenia_ChL	Europe_LNBA	4.12E-01	0.776	0.103	0.121	0.041	0.056	0.034

Correspondence with PCA

We test the robustness of the *qpAdm* estimates by plotting populations with the inferred mixture proportions (Table S2.26) in the weighted average position of their source populations in PCA space[13]. The results (Extended Data Fig. 5) indicate a close correspondence between the two in all models considered.

Admixture simulations

We performed simulations to infer the ancestry of the Mycenaeans using an alternative method that uses simulated individuals with known mixture proportions and tries to match the admixed *Test* population to the simulated ones. The procedure generated 4 individuals (to match the sample size of the Mycenaeans) for each simulated population. The alleles for these individuals at each locus were sampled as follows. First, we sample one of the N ancestral sources with probability q_i which we refer to as the *data-generating proportion*. Then, we sample (without replacement) an allele from one of the n_i different individuals of the source population with equal probability. We may sample either observed alleles (ACGTs) or missing alleles, depending on what the state of the randomly chosen individual is at the particular locus. (If we only sampled observed alleles, the simulated individuals would not have missing data, making them unrealistic for ancient DNA samples).

Because the different sources have varying amounts of missing data, the *actual ancestry proportion* α_i of a population thus generated will not match the data-generating proportion. Suppose, for example, that two populations have genotyping rates g_1=0.99 and g_2=0.01; if we were to sample with equal data-generating probabilities q_1=0.25, and q_2=0.75, we would obtain a population which possessed 0.99*0.25/(0.99*0.25+0.01*0.75) ≈ 0.97 of its alleles from the first population. We thus note the actual ancestry proportion as:

$$\alpha_i = \frac{g_i q_i}{\sum_{k=1}^{N} g_k q_k}$$

To summarize, we begin with the data-generating proportions (q_i), generate simulated individuals, and then record their actual ancestry proportions (α_i) using the above formula. The goal is then to find which set of actual ancestry proportions best match the population of interest (Mycenaeans).

We consider the models of Table S2.26, and generate simulated populations with data-generating proportions from the three sources in 5% increments from 0-100%. (This allows us to also consider simpler models with two or one source, when one or two populations are given 0% ancestry). The genotyping rates in the source populations are given in Table S2.27

Table S2.27: Genotyping rates of source populations.

Population	Genotyping rate
Anatolia_N	66.1%
Minoan_Lasithi	54.6%
Armenia_ChL	56.6%
Armenia_MLBA	19.3%
Europe_LNBA	33.0%
Steppe_EMBA	47.1%
Steppe_MLBA	48.8%

We use the simulated individuals by studying statistics of the form f_4(Mycenaean, *Simulated*; *A*, *B*), where (*A*, *B*) is a pair from the All^{++} set, excluding Mycenaeans, and the source populations (Table S2.27). By observing the maximum Z-score (in absolute value) of these statistics we can see whether the pair (Mycenaean, *Simulated*) is symmetrically related to the (*A*, *B*) pairs, and see which actual mixture proportions produce *Simulated* populations that best approximate the Mycenaeans. In Extended Data Fig. 6 we plot these Z-scores, together with the *qpAdm* estimates; the two estimates are within 2-21% of each other and are qualitatively similar in supporting the idea that the substratum population (Anatolia_N or Minoan_Lasithi) is the major component in the ancestry of Mycenaeans, on top of which was added ancestry from either a steppe-related ‘northern’ or Armenia-related ‘eastern’ population.

The simulation framework also allows us to compare different models directly. Suppose that there are two models ($Simulated_1$, $Simulated_2$) and we wish to examine whether either of them is a better description of a population of interest (in this case, Mycenaeans). We test f_4($Simulated_1$, $Simulated_2$; Mycenaean, Chimp), which directly determines whether the observed Mycenaeans shares more alleles with one or the other of the two models. When we apply this intuition to the best models for the Mycenaeans (Extended Data Fig. 6), we observe that none of them clearly outperforms the others as there are no statistics with $|Z|>3$ (Table S2.28). However, we do notice that the model 79%Minoan_Lasithi+21%Europe_LNBA tends to share more drift with Mycenaeans (at the $|Z|>2$ level). Europe_LNBA is a diverse group of steppe-admixed Late Neolithic/Bronze Age individuals from mainland Europe, and we think that the further study of areas to the north of Greece might identify a surrogate for this admixture event – if, indeed, the Minoan_Lasithi+Europe_LNBA model represents the true history.

Table S2.28: Z-score of the statistic *f4(Simulated$_1$, Simulated$_2$;* Mycenaean, Chimp). *Simulated*$_1$ is the population of each row, and *Simulated*$_2$ of each column. The 12 models listed in each row and column correspond to the best simulation-based estimates of mixture proportions from three source populations ("red" estimates of Extended Data Fig. 6).

	54Anatolia_N_46Armenia_ChL_0Europe_LNBA	54Anatolia_N_46Armenia_ChL_0Steppe_EMBA	54Anatolia_N_46Armenia_ChL_0Steppe_MLBA	61Minoan_Lasithi_21Armenia_ChL_18Steppe_MLBA	62Anatolia_N_31Armenia_MLBA_6Steppe_EMBA	62Anatolia_N_31Armenia_MLBA_7Steppe_MLBA	64Anatolia_N_32Armenia_MLBA_5Europe_LNBA	71Minoan_Lasithi_8Armenia_MLBA_21Steppe_MLBA	72Minoan_Lasithi_12Armenia_MLBA_16Europe_LNBA	78Minoan_Lasithi_0Armenia_ChL_22Steppe_EMBA	79Minoan_Lasithi_0Armenia_ChL_21Europe_LNBA	80Minoan_Lasithi_2Armenia_MLBA_18Steppe_EMBA
54Anatolia_N_46Armenia_ChL_0Europe_LNBA		0.0	0.0	-1.3	0.7	0.7	0.6	-0.9	-1.4	-0.5	-2.1	-0.6
54Anatolia_N_46Armenia_ChL_0Steppe_EMBA	0.0		0.0	-1.3	0.7	0.7	0.6	-0.9	-1.4	-0.5	-2.1	-0.6
54Anatolia_N_46Armenia_ChL_0Steppe_MLBA	0.0	0.0		-1.3	0.7	0.7	0.6	-0.9	-1.4	-0.5	-2.1	-0.6
61Minoan_Lasithi_21Armenia_ChL_18Steppe_MLBA	1.3	1.3	1.3		1.9	1.8	1.7	0.7	0.3	1.2	-1.5	0.8
62Anatolia_N_31Armenia_MLBA_6Steppe_EMBA	-0.7	-0.7	-0.7	-1.9		0.3	0.5	-1.6	-2.1	-1.5	-2.9	-1.7
62Anatolia_N_31Armenia_MLBA_7Steppe_MLBA	-0.7	-0.7	-0.7	-1.8	-0.3		-0.1	-1.6	-2.1	-1.6	-2.9	-1.9
64Anatolia_N_32Armenia_MLBA_5Europe_LNBA	-0.6	-0.6	-0.6	-1.7	-0.5	0.1		-1.3	-2.0	-1.4	-2.8	-1.6
71Minoan_Lasithi_8Armenia_MLBA_21Steppe_MLBA	0.9	0.9	0.9	-0.7	1.6	1.6	1.3		-0.2	0.6	-2.2	0.2
72Minoan_Lasithi_12Armenia_MLBA_16Europe_LNBA	1.4	1.4	1.4	-0.3	2.1	2.1	2.0	0.2		0.8	-1.8	0.7
78Minoan_Lasithi_0Armenia_ChL_22Steppe_EMBA	0.5	0.5	0.5	-1.2	1.5	1.6	1.4	-0.6	-0.8		-3.0	-1.2
79Minoan_Lasithi_0Armenia_ChL_21Europe_LNBA	2.1	2.1	2.1	1.5	2.9	2.9	2.8	2.2	1.8	3.0		2.8
80Minoan_Lasithi_2Armenia_MLBA_18Steppe_EMBA	0.6	0.6	0.6	-0.8	1.7	1.9	1.6	-0.2	-0.7	1.2	-2.8	

Implications for language dispersals

The decipherment of Linear B tablets from the Aegean Bronze Age[21] has proven that an early form of Greek was spoken during the Mycenaean period. The language(s) spoken by the Minoans are unknown pending a successful decipherment of the Cretan hieroglyphic and Linear A scripts from Crete. Greek belongs to the Indo-European language family, the origins of which have been contentious. According to the Anatolian farming dispersal hypothesis[22], the linguistic ancestor of Greek was spoken by early farmers migrating to the Aegean from Anatolia. As discussed above, there is strong evidence for such a migration. However, the fact that Mycenaean Greeks can be modelled as having two types of ancestry added to the Anatolian Neolithic substratum suggests one or more additional opportunities for the dispersal of a language family into the Aegean. If the additional ancestry was the vector for the dispersal of the linguistic ancestors of Greeks, then this would be consistent with alternative hypotheses deriving early Indo-Europeans from the Eurasian steppe[23] or the highlands of the Armenian plateau[24].

A population transect of Aegean populations will clarify the trajectory of ancestry proportions in the area. A key question, apart from that of directionality (from the north, east, or both), is whether migration into the Aegean occurred by gradual intrusion or by massive migration. Gradual intrusion predicts a monotonic increase of non-local ancestry, while migration predicts a sudden increase of non-local ancestry coinciding with the migration, perhaps followed by a resurgence of local ancestry as occurred in central Europe where ~3/4 of the ancestry of the people associated with the Corded Ware culture ~4,500 years ago could be derived from populations related to the Yamnaya Early Bronze Age population of the Eurasian steppe, but this proportion diminished in later populations of the Bronze Age reaching up to ~1/2 in present-day northern Europeans[1].

The existence of Eurasian steppe ancestry in Mycenaeans (either directly from the north, or indirectly from the east) suggests the possibility that the Indo-European linguistic ancestors of the Greeks also came from the Eurasian steppe as was likely for central/northern Europe[1]. The finding that up to ~1/2 of the ancestry of some populations of south Asia could also be derived from steppe populations[13] provides a unifying factor for the dispersal of a substantial subset of Indo-European languages. However, the low amount of steppe-like ancestry in Mycenaeans might also be consistent with the gradual intrusion of this type of ancestry from central Europe where it had existed since the 3rd millennium BCE[1,20]. If steppe migration did effect linguistic change in the Aegean, this would require different process of linguistic change than in central Europe to account for the fact that the language of a population that contributed only a small part of the ancestry of the Mycenaean population could replace the language of the previous population.

Indo-European languages were also spoken in Anatolia, but there is no firm association of our samples from Chalcolithic/Bronze Age Anatolia with historical speakers of the Anatolian branch of the Indo-European family. The Bronze Age Anatolians had no discernible ancestry from eastern Europe (Table S2.9). Under a steppe hypothesis of Indo-European origins, if the Bronze Age Anatolians were Indo-European speakers this would imply transmission of Indo-European languages without any major genetic contribution. According to one version of the steppe hypothesis[25], Anatolian languages split off from the rest of the Indo-European speakers ~4,000BCE. If this version of the steppe hypothesis is true, then massive dilution of their steppe ancestry in the ensuing two millennia would be needed to account for its disappearance in the Bronze Age Anatolian sample. It is critical to obtain data from additional (and later) Anatolians in order to determine whether migrations from the Eurasian steppe could have been vectors for the introduction of a new language family into Anatolia, or (alternatively) whether steppe populations were responsible for the spread of only a subset of Indo-European languages and not for Anatolian, considered to be the earliest diverging branch of this family after the breakup of Proto-Indo-European[26].

In summary: populations of the Bronze Age Aegean and southwestern Anatolia were not simply descended from Neolithic Anatolian-related populations but also from the east (Iran/Caucasus/Armenia); Mycenaeans also had some Eastern European/Siberian-related ancestry, and Bronze Age southwestern Anatolians also had some Levantine-related ancestry. Both the general transformation across all sampled populations, and the more specific steppe-related ancestry in the Mycenaeans, could have been instruments of linguistic transformation. Further sampling of populations north and east of the Aegean may clarify the role that migration may have played in linguistic change in the region.

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Supplementary Information 3

Y-chromosome haplogroup determination

We determined that there were five males in the newly described data using the ratio of sequences aligning to the X and Y chromosomes[1]; for sequences with MAPQ≥30, the ratio of Y/(X+Y) was ≥0.13 for the group of five males, but ≤0.02 for the remaining individuals. For the five males we used ANGSD[2] to estimate their nuclear contamination based on the presence of heterozygosity on the X-chromosome (of which males have only one copy). Using the same parameters used for calling alleles as were used to analyze this data (MAPQ≥10 and base quality≥20), we determined that none of the males had evidence of substantial contamination (≤1.2%; Table S3.1), except perhaps I9130 (4±3.1% for this lower-quality sample).

Table S3.1: X-chromosome based estimates of contamination in 5 male samples (using new_llh and MoM estimate in ANGSD)

Individual	Estimate of contamination	Standard Error
I2495	0.012	0.003
I0070	0.003	0.002
I0073	0.005	0.002
I9041	0.012	0.004
I9130	0.040	0.031

Haplogroup determination

We used the haplogroup terminology of the International Society of Genetic Genealogy (http://www.isogg.org) v. 9.129 (accessed Dec. 08, 2014). We called genotypes using reads with MAPQ and base quality ≥30, omitting 2 bases at the ends of reads, and taking the majority allele (as only one allele should occur at each position of the Y-chromosome in males, minority alleles may represent ancient DNA damage, sequencing error, or low-level contamination). For each sample, we determined the most derived SNP as well as downstream SNPs for which the sample was ancestral. The results are summarized in Table S3.2.

Table S3.2: Y-chromosome haplogroups of male samples

Individual	Population	Haplogroup
I2495	Anatolia_BA	J1a(xJ1a2b)
I0070	Minoan_Lasithi	J2a1d
I0073	Minoan_Lasithi	J2a1(xJ2a1a, J2a1b1a, J2a1b2, J2a1c, J2a1e, J2a1h, J2a1i)
I9130	Minoan_Odigitria	G2a2b2a(xG2a2b2a1b1a2a, G2a2b2a1c1a)
I9041	Mycenaean	J2a1(xJ2a1a, J2a1b1, J2a1b2, J2a1c, J2a1e, J2a1g, J2a1h, J2a1i)

We discuss the haplogroup assignments in greater detail below.

I2495 (Bronze Age Anatolia)

Haplogroup J is supported by numerous mutations for this individual (CTS687, PF4505, PF4513, F1167, F1181, PF4519, PF4521, PF4524, FGC1604, FGC3271, PF4530, L60, F1744, F1826, CTS4349, F2114, CTS5628, CTS5678, CTS5934, CTS7229, F2502, CTS7483, PF4567, F2746, PF4575, F2769, CTS8974, F2973, CTS10446, F3119, F4299, S22619, F4300, PF4591, PF4594, PF4595, PF4598, Z7829, CTS10858, L778, CTS11571, PF4619, CTS12047). One read supports placement in haplogroup J1a (mutation CTS5368/Z2215:16227302G->A). This individual was ancestral for the major subclade[3] P58 (J1a2b; previously designated[3] J1e) and could thus be designated as J1a(xJ1a2b).

I0070 (Minoan from Lasithi)

This individual was derived for mutation M319:15467785T->A (J2a1d) as well as upstream mutations L26:22942897T->C (J2a1) and M410:2751678A->G, L212:22711465T->C (J2a). He was not found to be ancestral for any downstream mutations and could be designated as J2a1d. Haplogroup M319 was found[4] at a frequency of 8.8% in one sample set of 193 present-day Cretans (95% confidence interval from the binomial distribution 5.2-13.7%) and 5.4% in another set[5] of 168 Cretans (95% C.I.: 2.5-10%), but no examples were found in a combined sample set of 171 Greeks from three locations near early Neolithic settlements in mainland Greece (95% C.I: 0-2.1%). A re-analysis[4] of large set of 523 present-day Anatolian males[6] revealed only 2 examples of M319 in this population (95% C.I.: 0-1.4%). Thus, it appears plausible that this represents a Y-chromosome lineage that existed in Minoan Crete but was at a lower (or absent) frequency in neighboring mainland Greece and Anatolia and its occurrence in present-day Cretans represents continuity with those of the Bronze Age.

I0073 (Minoan from Lasithi)

This individual was derived for mutation L26:22942897T->C (J2a1) as well as upstream mutations M410, L559, L152 (J2a). He was ancestral for several downstream haplogroups: M322:15469740C-

>A (J2a1a), L560:21899860C->T (J2a1b1a), M166:21764694C->T (J2a1b2), M68:21878700A->G (J2a1c), M339:2881367T->G (J2a1e), L24:14286528G->A (J2a1h), L88.2:17595842T->C and L198:17595861A->C (J2a1i). He could thus be designated as J2a1(xJ2a1a, J2a1b1a, J2a1b2, J2a1c, J2a1e, J2a1h, J2a1i).

I9130 (Minoan from Moni Odigitria)

This individual was derived for mutations CTS946:7100848A->G (G2a2b2a) and upstream mutations F3088:20813445G->A and M3397:21605685G->C (G2a). He was ancestral for downstream mutations CTS4803:15833180G->A (G2a2b2a1b1a2a) and Z3423:19251438G->T (G2a2b2a1c1a). He could thus be designated as G2a2b2a(xG2a2b2a1b1a2a, G2a2b2a1c1a). G2a2 Y-chromosomes were common in Neolithic Europe[7], western Anatolia[8,9], and Neolithic mainland Greece[9]. We have also re-analyzed data from a recent study of central Anatolian Neolithic genomes[10], determining that they were present there during both the Aceramic phase at Boncuklu (2 G2a2b2b samples) and later at Tepecik-Çiftlik (1 G2a2a sample). Plausibly, the Minoan from Moni Odigitria who belonged to this lineage was also related to the same group of early Neolithic farmers as those from Europe, mainland Greece, and Anatolia.

I9041 (Mycenaean from Galatas Apatheia in the Peloponnese)

This individual was derived for mutations L26:22942897T->C and F4326:23021978A->G (J2a1) as well as upstream mutations M410:2751678A->G, L559:21674327A->G, L152:22243566C->T, L212:22711465T->C (J2a). He was ancestral for M322:15469740C->A (J2a1a), M260:15025506G->A and M92:21904023T->C (J2a1b1), M166:21764694C->T (J2a1b2), L210:16492197A->T (J2a1b3), M68:21878700A->G (J2a1c), M339:2881367T->G (J2a1e), P81:6739856G->A (J2a1g), L207.1:6753448A->G and L24:14286528G->A (J2a1h), L88.2:17595842T->C and L198:17595861A->C (J2a1i). He could thus be designated as J2a1x(J2a1a, J2a1b1, J2a1b2, J2a1c, J2a1e, J2a1g, J2a1h, J2a1i).

Discussion

Our results highlight the importance of haplogroup J chromosomes during the Bronze Age in mainland Greece, Crete, and Anatolia, in contrast to the earlier Neolithic populations that were dominated by haplogroup G2a2. We cannot exclude an earlier presence of haplogroup J chromosomes in the region, but we note that in the large population sample from northwestern Anatolia[8] (*n*=15 males) we discovered a single J2a male which did not differ in his autosomal profile from other individuals in that population. By contrast 4 of 5 individuals from the Bronze Age in our study belonged to haplogroup J. Both Caucasus hunter-gatherers of Paleolithic-to-Mesolithic time depth belonged[11] to haplogroup J, as did a Mesolithic and a Chalcolithic sample from Iran[12] and a hunter-gatherer from northeast Russia[8]. Haplogroup J (and especially J2) chromosomes are today common in present-day Anatolia[6] and Greece (including the mainland and Crete)[4,5,13-16]. It was previously associated (based on its present-day phylogeography) with the diffusion of Neolithic farmers into Europe[17] and its J2 and J1 clades with agriculturalist vs. pastoralist Neolithic pioneers (based on geographical/climatic correlations)[18]. Our results suggest a later westward dispersal than the Neolithic farming expansion and raise questions about the cause of this dispersal.

More sampling of ancient populations is needed to establish the presence (and frequency) of haplogroup J in the Aegean and neighboring regions). However, (i) the great time depth of its presence in the Caucasus/Iran, together with (ii) its low frequency/absence in Neolithic Greece/Anatolia, and (iii) its appearance in the samples of our study, lead us to believe that it may have accompanied the genetic admixture (Neolithic Iran/Caucasus-hunter-gatherer related) that seems to have affected all populations in our study (Supplementary Information, section 2). Thus, the Y-chromosome turnover that occurred in central Europe during the Bronze Age[7,19] may also have occurred in the Aegean, with a different set of incoming lineages.

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Supplementary Information 4

Phenotypic inference

We determined the alleles carried by the ancient individuals in 22 of the 24 HIrisPlex[1] SNPs (except rs86insA and Y152OCH that were not captured). We also examined the rs1426654 SNP in SLC24A5[2] which is a major determinant of skin color in present-day people (and which is not included in the HIrisPlex panel). The results are reported in Table S4.1.

Table S4.1: SNPs informative about pigmentation. For each SNP A, B we list the number of reads having A, B for each ancient individual.

				Anatolia_BA			Greece_N	Crete_Armenoi	Minoan_Lasithi					Minoan_Odigitria					Mycenaean			
	Gene	Alleles	GRCh37	I2495	I2499	I2683	I2937	I9123	I0070	I0071	I0073	I0074	I9005	I9127	I9128	I9129	I9130	I9131	I9006	I9010	I9033	I9041
rs1042602	TYR	C,A	88911696	1,0	1,0	6,0	1,0	0,0	0,5	13,8	0,0	0,0	7,2	0,0	0,0	0,0	1,0	0,1	0,11	0,3	0,3	1,4
rs1110400	MC1R	T,C	89986130	19,0	2,0	39,0	5,0	0,0	10,0	124,0	29,0	1,0	13,0	0,0	0,0	0,0	0,0	0,0	13,0	8,0	6,0	5,0
rs11547464	MC1R	G,A	89986091	16,0	1,0	38,0	5,0	0,0	3,3	61,0	19,0	2,0	14,0	0,0	0,0	0,0	0,0	0,0	12,0	3,0	3,0	6,0
rs12203592	IRF4	C,T	396321	2,0	0,0	3,0	0,0	0,0	4,0	16,0	7,0	5,0	12,0	0,0	0,0	0,0	0,0	0,0	4,0	2,0	1,0	3,0
rs12821256	KITLG	T,C	89328335	2,0	0,0	3,0	0,0	0,0	3,0	16,0	4,0	0,0	4,0	0,0	0,0	0,0	1,0	0,0	5,0	1,0	1,0	8,0
rs12896399	SLC24A4	G,T	92773663	0,0	0,0	0,1	0,0	0,0	0,0	6,0	4,0	1,0	5,0	0,0	0,0	0,0	0,0	0,0	3,0	0,0	0,0	7,0
rs12913832	HERC2	A,G	28365618	2,0	0,1	2,0	4,0	0,0	4,0	28,0	5,0	6,0	6,2	0,0	0,0	0,0	0,0	0,0	11,0	0,0	1,0	5,3
rs1393350	TYR	G,A	89011046	0,1	0,0	5,0	3,0	0,0	1,0	13,0	6,0	2,0	18,1	0,0	0,0	0,0	1,0	0,0	5,0	3,0	3,0	2,0
rs1426654	SLC24A5	A,G	48426484	2,0	0,0	0,0	0,0	0,0	2,0	10,0	4,0	4,0	5,0	0,0	0,0	0,0	0,0	0,0	9,0	4,0	5,0	9,0
rs16891982	SLC45A2	C,G	33951693	0,12	1,0	14,6	1,2	0,0	0,7	35,0	0,13	0,2	0,13	0,0	0,0	0,0	0,1	0,0	1,9	0,4	1,2	6,5
rs1800407	OCA2	C,T	28230318	6,0	0,0	11,1	4,1	0,0	10,0	15,0	3,0	9,0	24,0	0,0	0,0	0,0	0,0	0,0	10,0	2,1	4,0	4,0
rs1805005	MC1R	G,T	89985844	5,0	0,0	7,0	3,0	0,0	4,0	24,0	1,2	2,0	7,0	0,0	0,0	0,0	0,0	0,0	1,2	3,0	3,0	1,2
rs1805006	MC1R	C,A	89985918	6,0	1,1	18,0	9,0	4,0	11,0	42,0	22,0	2,0	12,0	0,0	0,0	0,0	0,0	1,0	8,0	1,0	13,0	4,0
rs1805008	MC1R	C,T	89986144	14,0	2,0	22,0	4,0	0,0	13,0	102,2	28,1	3,0	18,3	0,0	0,0	1,0	0,0	0,0	7,1	7,0	5,0	8,0
rs1805009	MC1R	G,C	89986546	16,0	3,0	36,0	6,0	0,0	8,0	40,0	10,0	4,0	17,0	0,0	0,0	0,0	0,0	0,0	18,0	5,0	5,0	12,0
rs2228479	MC1R	G,A	89985940	1,0	2,0	5,0	3,1	0,0	4,0	28,0	14,0	1,0	9,0	0,0	0,0	0,0	0,0	0,0	2,1	1,0	6,0	4,0
rs2378249	ASIP	G,A	33218090	0,1	0,0	0,0	0,0	0,0	0,5	0,18	0,4	0,4	0,2	0,0	0,0	0,0	0,0	0,0	0,6	0,0	0,1	0,3
rs2402130	SLC24A4	G,A	92801203	1,2	0,0	0,2	0,2	0,0	0,4	0,20	0,6	3,4	0,12	0,0	0,0	0,0	0,0	0,0	5,1	2,0	1,0	5,5
rs28777	SLC45A2	C,A	33958959	0,1	1,0	1,2	0,0	0,0	0,0	22,0	0,2	0,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	2,1
rs4959270	EXOC2	C,A	457748	8,0	0,0	16,0	0,2	0,0	1,0	4,5	4,1	2,0	5,0	0,0	0,0	0,0	0,0	0,0	1,4	2,1	0,0	2,2
rs683	TYRP1	C,A	12709305	0,0	0,0	0,0	0,0	0,0	0,0	2,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,0
rs885479	MC1R	G,A	89986154	9,1	2,1	16,1	4,0	0,0	12,0	95,0	28,0	3,0	23,0	0,0	0,0	1,0	0,0	0,0	8,0	5,0	3,0	8,0
snp_16_89986117	MC1R	C,T	89986117	19,0	1,0	42,1	3,0	0,0	8,0	110,2	25,0	1,0	8,1	0,0	0,0	0,0	0,0	0,0	9,0	4,0	8,0	4,0

We estimated allele frequency *p* in the combined dataset and the Bronze Age Aegean populations (Minoans and Mycenaeans) by maximizing for *p* the log likelihood[3]:

$$l(p|R,T) = \sum_{i=1}^{N} \{p^2\, B(R_i, T_i, 1-\varepsilon) + 2p(1-p)B(R_i, T_i, 0.5) + (1-p)^2 B(R_i, T_i, \varepsilon)\}$$

where $B(k,n,p) = \binom{n}{k} p^k (1-p)^{n-k}$ is the binomial probability distribution, and R_i, T_i are the number of reference alleles and the number of total alleles observed in the i^{th} individual. The parameter $\varepsilon = 0.001$ is useful to account for erroneous reads (due to sequencing error or ancient DNA damage). For example, individual I0071 has 102,2 reads for the two alleles at locus rs1805008 but is quite unlikely to be heterozygous at this C>T site. This method allows us to use the read data to estimate allele frequencies without calling genotypes, which is not possible for low-coverage data.

Estimated allele frequencies are shown in Table S4.2.

Table S4.2: Estimated allele frequency. The allele frequency p of the first allele is shown, together with a 1.9-log likelihood confidence interval.

	Gene	Alleles	Combined dataset			Minoans and Mycenaeans		
			p	C.I.		*p*	C.I.	
rs1042602	TYR	C,A	0.44	0.24	0.66	0.26	0.09	0.51
rs1110400	MC1R	T,C	1.00	0.92	1.00	1.00	0.89	1.00
rs11547464	MC1R	G,A	0.96	0.83	1.00	0.94	0.76	1.00
rs12203592	IRF4	C,T	1.00	0.90	1.00	1.00	0.89	1.00
rs12821256	KITLG	T,C	1.00	0.90	1.00	1.00	0.88	1.00
rs12896399	SLC24A4	G,T	0.91	0.67	1.00	1.00	0.83	1.00
rs12913832	HERC2	A,G	0.85	0.66	0.96	0.86	0.64	0.98
rs1393350	TYR	G,A	0.95	0.81	1.00	1.00	0.89	1.00
rs1426654	SLC24A5	A,G	1.00	0.90	1.00	1.00	0.89	1.00
rs16891982	SLC45A2	C,G	0.29	0.14	0.49	0.24	0.08	0.47
rs1800407	OCA2	C,T	0.92	0.76	0.99	0.95	0.77	1.00
rs1805005	MC1R	G,T	0.87	0.69	0.96	0.82	0.59	0.95
rs1805006	MC1R	C,A	0.97	0.85	1.00	1.00	0.90	1.00
rs1805008	MC1R	C,T	0.95	0.81	1.00	0.93	0.74	1.00
rs1805009	MC1R	G,C	1.00	0.93	1.00	1.00	0.90	1.00
rs2228479	MC1R	G,A	0.91	0.75	0.99	0.94	0.75	1.00
rs2378249	ASIP	G,A	0.00	0.00	0.12	0.00	0.00	0.13
rs2402130	SLC24A4	G,A	0.30	0.13	0.52	0.33	0.13	0.58
rs28777	SLC45A2	C,A	0.41	0.17	0.69	0.37	0.11	0.71
rs4959270	EXOC2	C,A	0.68	0.46	0.86	0.65	0.39	0.86
rs683	TYRP1	C,A	1.00	0.45	1.00	1.00	0.45	1.00
rs885479	MC1R	G,A	0.96	0.84	1.00	1.00	0.90	1.00
snp_16_89986117	MC1R	C,T	1.00	0.91	1.00	1.00	0.87	1.00

Discussion

Present-day Europeans are almost fixed for the derived (light pigmentation) allele G at rs1426654, but the ancestral allele occurred in western European hunter-gatherers[3,4]. We record no copy of the ancestral allele in 9 individuals with at least one sequence. We also examined the rs16891982 SNP in SLC45A2, the second strongest signal of selection in Europeans discovered in a genome-wide scan[3]. The overall frequency of the C allele could be estimated as 24% (C.I.: 8-47%) in the Aegean Bronze Age. The frequency of the minor C allele in present-day Greeks is 14% (95% C.I.: 11-17%)[5]. The C allele has decreased in frequency in eastern Europe[6] or Europe in general[3] due to likely selection since the Bronze Age, but with the available data, the Bronze Age frequency is consistent with its modern prevalence.

The rs12913832 SNP in HERC2 is a major determinant of blue eye color in humans[7]. The frequency of the A allele could be estimated as 86% (C.I.: 64-98%) in the Bronze Age Aegean. The G allele was present in Anatolia since Neolithic times[3] and our results suggest its presence in all studied Bronze Age groups at a low frequency. The “blue-eye” haplotype BEH2 is tagged by the G allele at rs12913832 which occurs at a frequency of ~40% in a sample of present-day Greeks[8], near the edge of the confidence interval for the Bronze Age Aegean populations, suggesting a possible increase in frequency to the present.

Classic blond hair has been associated with the C allele in the rs12821256 SNP in KITLG[9]. We have reads covering this site in 11 individuals and do not detect the C allele.

We also examined the rs1042602 SNP in TYR[10], the A allele of which is associated with light skin, eyes, and freckles[10-12]. The estimated frequency of the C allele is 26% (C.I.: 9-51%) in the Bronze Age Aegean. The C allele occurs at a frequency of 46% in present-day Greeks[5], at the high end of the confidence interval for the Bronze Age Aegean populations, suggesting a possible increase in frequency to the present. The A allele has increased in frequency from a very low ~4% in populations of the steppe to a present-day frequency of ~37% in eastern Europe (Ukraine)[6].

Phenotypic inference for individuals

HIrisPlex[1] allows inference of pigmentation (hair, eye, and skin) phenotypes in humans, but it relies on specifying the genotypes of individuals at a panel of SNPs. Since we do not have diploid genotypes for our low coverage ancient data we cannot use it directly to infer phenotypes in the ancient samples. A possible way of circumventing this difficulty is to use the most probable genotypes for each individual with the caveat that these may be inaccurate due to errors or low coverage. Instead, we explore the variability of the phenotypic inferences by generating 100 replicates from each ancient individual, drawing their genotypes randomly according to the distribution:

$$P(g|r,t) = \frac{P(r,t|g)P(g)}{P(r,t)} \propto \frac{1}{2^t}[(2-g)\varepsilon + g(1-\varepsilon)]^r[(2-g)(1-\varepsilon) + g\epsilon]^{t-r} \cdot \binom{g}{2} \hat{p}^g(1-\hat{p})^{2-g}$$

The first of the factors is a genotype likelihood[13] for g=0, 1, 2 reference alleles, with r reference alleles observed out of t total. The second factor is a prior set using the estimated reference allele frequency $\hat{p}$ in all the ancient individuals under study (from Table S4.2). (We ignore the normalizing factor $P(r, t)$ in the denominator as this is the same for all g.)

We submitted the 100 random replicates to HIrisPlex (http://hirisplex.erasmusmc.nl/; submitted on 8 Sep. 2016). In order not to give undue influence to the prior (which would effectively fill in missing data with a random genotype from the population), we do not call a random genotype at sites not covered by any reads, entering “NA” for such sites in the input format required by HIrisPlex. We record the mean and standard deviation of the reported phenotype probabilities for each individual, and add columns of an assessment of the phenotype (Extended Data Table 4).

These results suggest that ancient Bronze Age individuals from the Aegean and southwestern Anatolia had mostly dark (brown or black) hair and brown eyes. Blue eyes were uncommon as predicted by the lack of homozygotes for the G allele at rs12913832 which is the major predictor of this trait, however, this allele did occur in all studied populations (Table S4.1), thus the phenotype would have been uncommon but not unknown in the region. The brown eye phenotype is still the most common in present-day Greeks occurring in ~3/4 of them, with the remainder split between blue and intermediate shades[1]. Similarly, ~79% of present-day Greeks have light or dark brown hair, with the remainder split between blond and black.

While our inferences on ancient phenotypes are conditional on the availability of samples and their low coverage, they do seem to mirror the phenotypes depicted in visual art from the Aegean Bronze Age[14] and to suggest their relative stability in the region, in contrast to other parts of Europe where depigmentation seems to have occurred since the Bronze Age[6] or even more recently[15].

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Supplementary Table 1. Overview of processing steps for ancient samples

Individual ID	Other_ID	tissue sampled	mg sample powder in extract	extraction protocol	ul extract used for screening library preparation	protocol for screening library preparation	Shotgun sequencing for screening	protocol mtDNA capture for screening	mtDNA capture sequencing for screening	protocol for capture library preparation	ul extract in capture libraries	SNP set targeted	SNP capture sequencing
I2937	A2197	petrous	75	Dabney et al. 2013, Korlevic et al. 2015	1/3 of extract	Rohland et al. 2015, UDG-	NextSeq500 2x76+2x7	Rohland et al. 2015	NextSeq500 2x76+2x7	same as screening		1240k	NextSeq500 2x76+2x7
I0071	Lasithi4	tooth	400	Hughey et al. 2013	5ul	Meyer & Kircher 2010, UDG-	MiSeq 2x150+2x8	Maricic et al. 2010	MiSeq 2x150+2x8	Briggs et al. 2010, UDG+	20ul	390k+840k	390k:HiSeq2500 2x100+2x7; 840k:NextSeq500 2x76+2x7
I0070	Lasithi2	bone	390	Rohland&Hofreiter 2007	20ul	Meyer & Kircher 2010, UDG-	none	Maricic et al. 2010	GA IIx 2x76+2x7	Briggs et al. 2010, UDG+	50u	390k+840k	390k:HiSeq2500 2x100+2x7; 840k:NextSeq500 2x76+2x7
I0073	Lasithi7	bone	495	Rohland&Hofreiter 2007	20ul	Meyer & Kircher 2010, UDG-	none	Maricic et al. 2010	GA IIx 2x76+2x7	Briggs et al. 2010, UDG+	40ul	390k+840k	390k:HiSeq2500 2x100+2x7; 840k:NextSeq500 2x76+2x7
I0074	Lasithi9	bone	500	Rohland&Hofreiter 2007	20ul	Meyer & Kircher 2010, UDG-	none	Maricic et al. 2010	GA IIx 2x76+2x7	Briggs et al. 2010, UDG+	50ul	390k+840k	390k:HiSeq2500 2x100+2x7; 840k:NextSeq500 2x76+2x7
I9005	Lasithi17	tooth	100	Rohland&Hofreiter 2007	5ul	Meyer & Kircher 2010, UDG-	MiSeq 2x150+2x8	Maricic et al. 2010	MiSeq 2x150+2x8	Briggs et al. 2010, UDG+	2x25ul	390k	HiSeq2500 2x101+2x8
I9006	Salamis31	tooth	100	Dabney et al. 2013	5ul	Meyer & Kircher 2010, UDG-	MiSeq 2x150+2x8	Maricic et al. 2010	MiSeq 2x150+2x8	Briggs et al. 2010, UDG+	2x35ul	390k	HiSeq2500 2x101+2x8
I9123	S-EVA 1263 Armenoi 503	tooth	106	Dabney et al. 2013	5ul	Meyer & Kircher 2010, UDG-	HiSeq2500 2x101+2x8	Maricic et al. 2010	HiSeq2500 2x101+2x8	Rohland et al. 2015, UDGhalf	60ul	1240k	HiSeq4000 2x150+2x8
I9127	12V t2 Tholos	tooth	230	Dabney et al. 2013	20ul	Meyer & Kircher 2010, UDG-	HiSeq2500 2x101+2x8	Maricic et al. 2010	HiSeq2500 2x101+2x8	Rohland et al. 2015, UDGhalf	60ul	1240k	HiSeq4000 2x150+2x8
I9128	13V t2 Tholos	tooth	121	Dabney et al. 2013	20ul	Meyer & Kircher 2010, UDG-	HiSeq2500 2x101+2x8	Maricic et al. 2010	HiSeq2500 2x101+2x8	Rohland et al. 2015, UDGhalf	60ul	1240k	HiSeq4000 2x150+2x8
I9129	14V t2 Tholos	tooth	250	Dabney et al. 2013	20ul	Meyer & Kircher 2010, UDG-	HiSeq2500 2x101+2x8	Maricic et al. 2010	HiSeq2500 2x101+2x8	Rohland et al. 2015, UDGhalf	60ul	1240k	HiSeq4000 2x150+2x8
I9130	16V Tholos	tooth	257	Dabney et al. 2013	20ul	Meyer & Kircher 2010, UDG-	HiSeq2500 2x101+2x8	Maricic et al. 2010	HiSeq2500 2x101+2x8	Rohland et al. 2015, UDGhalf	60ul	1240k	HiSeq4000 2x150+2x8
I9131	19V t2 Tholos	tooth	125	Dabney et al. 2013	20ul	Meyer & Kircher 2010, UDG-	HiSeq2500 2x101+2x8	Maricic et al. 2010	HiSeq2500 2x101+2x8	Rohland et al. 2015, UDGhalf	60ul	1240k	HiSeq4000 2x150+2x8
I9010	Galatas19	tooth	71	Dabney et al. 2013	5ul	Meyer & Kircher 2010, UDG-	MiSeq 2x150+2x8	Maricic et al. 2010	MiSeq 2x150+2x8	Briggs et al. 2010, UDG+	2x35ul	390k	HiSeq2500 2x101+2x8
I9033	Peristeria4	tooth	30	Dabney et al. 2013	5ul	Meyer & Kircher 2010, UDG-	MiSeq 2x150+2x8	Maricic et al. 2010	MiSeq 2x150+2x8	Briggs et al. 2010, UDG+	2x35ul	390k	HiSeq2500 2x101+2x8
I9033	Peristeria4	tooth #2	330	Dabney et al. 2013	5ul	Meyer & Kircher 2010, UDG-	MiSeq 2x150+2x8	Maricic et al. 2010	MiSeq 2x150+2x8	Briggs et al. 2010, UDG+	2x35ul	390k	HiSeq2500 2x101+2x8
I9041	Galatas4	tooth	47	Dabney et al. 2013	5ul	Meyer & Kircher 2010, UDG-	MiSeq 2x150+2x8	Maricic et al. 2010	MiSeq 2x150+2x8	Briggs et al. 2010, UDG+	2x35ul	390k	HiSeq2500 2x101+2x8
I2495	A4-1	petrous	57	Dabney et al. 2013, Korlevic et al. 2015	1/3 of extract	Rohland et al. 2015, UDG-	NextSeq500 2x76+2x7	Rohland et al. 2015	NextSeq500 2x76+2x7	same as screening		1240k	NextSeq500 2x76+2x7
I2499	UC1	petrous	58	Dabney et al. 2013, Korlevic et al. 2015	1/3 of extract	Rohland et al. 2015, UDG-	NextSeq500 2x76+2x7	Rohland et al. 2015	NextSeq500 2x76+2x7	same as screening		1240k	NextSeq500 2x76+2x7
I2683	G3-95	petrous	62	Dabney et al. 2013, Korlevic et al. 2015	1/3 of extract	Rohland et al. 2015, UDG-	NextSeq500 2x76+2x7	Rohland et al. 2015	NextSeq500 2x76+2x7	same as screening		1240k	NextSeq500 2x76+2x7

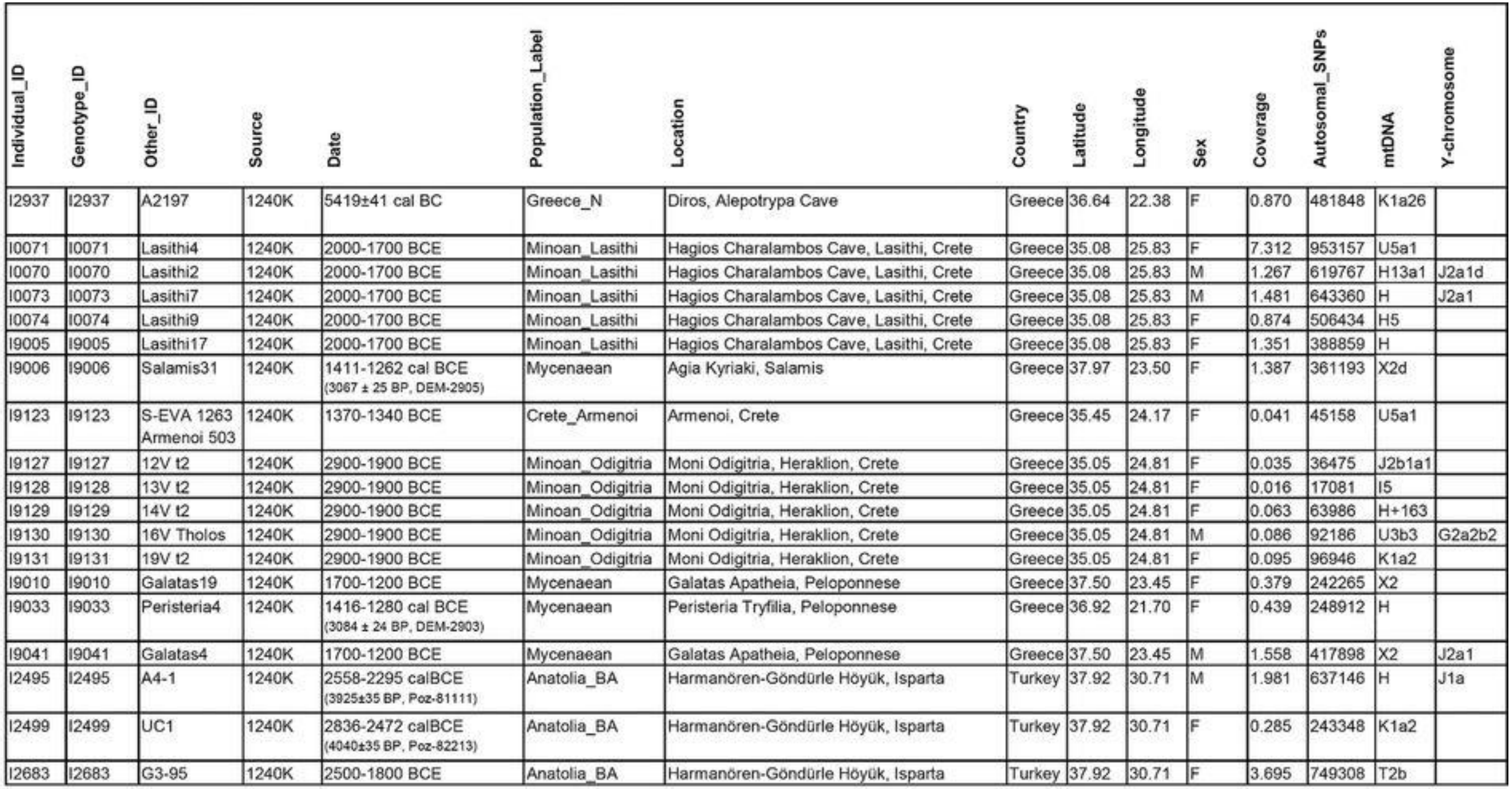
Processing lab
Dublin
Seattle
Leipzig
Tübingen
Boston
Kiel

Supplementary Table 2. Screening results

Individual_ID	Other_ID	shotgun sequencing				mtDNA capture sequencing				
		merged, quality filtered reads before mapping	unique reads mapping to hg19	% endogenous DNA	deamination at 5'-end	merged, quality filtered reads before mapping	unique reads mapping to rCRS	average coverage of mtDNA	deamination at 5'-end	contamination estimate
I2937	A2197	1710123	43743	2.56	35.8%	1915732	34123	92.5	51.1%	0-3%
I0071	Lasithi4	416193	74430	21.19	30.8%	1216951	23645	133.09	35.1%	0-2%
I0070	Lasithi2	n/a	n/a	n/a	n/a	1007119	43932	158.18	34.4%	0-2%
I0073	Lasithi7	n/a	n/a	n/a	n/a	1922701	28957	111.71	32.0%	0-2%
I0074	Lasithi9	n/a	n/a	n/a	n/a	191272	37313	139.40	32.5%	0-2%
I9005	Lasithi17	353836	31855	11.89	41.0%	1680149	149451	585.18	42.5%	0-2%
I9006	Salamis31	114047	4077	3.58	35.8%	48559	1275	4.66	38.0%	0-2%
I9123	S-EVA 1263 Armenoi 503	100606	333	0.50	52.1%	3411895	98947	374.90	44.9%	0-2%
I9127	12V t2 Odigitria	88826	138	0.20	46.9%	3230130	37835	128.09	44.7%	0-2%
I9128	13V t2 Odigitria	178544	367	0.27	18.8%	569715	15914	48.46	43.3%	1-3%
I9129	14V t2 Odigitria	124970	990	1.02	45.9%	1032940	4435	14.46	52.5%	1-3%
I9130	16V Odigitria	176785	1000	0.75	49.5%	1440950	37028	120.66	50.8%	1-3%
I9131	19V t2 Odigitria	195943	3034	1.96	33.6%	4571525	75329	230.65	47.9%	1-3%
I9010	Galatas19	17306	305	2.34	47.1%	33656	2420	7.88	50.1%	1-3%
I9033	Peristeria4	249258	9447	5.30	46.4%	24677	1236	5.76	37.0%	0-2%
I9033	Peristeria4 tooth #2	221	1	0.91	0.0%	102987	2285	8.98	48.4%	1-3%
I9041	Galatas4	393645	56416	21.10	35.5%	249346	1497	5.74	45.2%	1-3%
I2495	A4-1	284570	94485	33.2	31.4%	1969508	162151	357	29.5%	0-2%
I2499	UC1	284485	11459	4.03	13%	1776067	13069	33.3	45.8%	2-6%
I2683	G3-95	378422	114121	30.16	34.2%	1856542	157105	461	40.9%	0-1%

Extended Data Table 1: Information on ancient samples reported in this study

From: Genetic origins of the Minoans and Mycenaeans

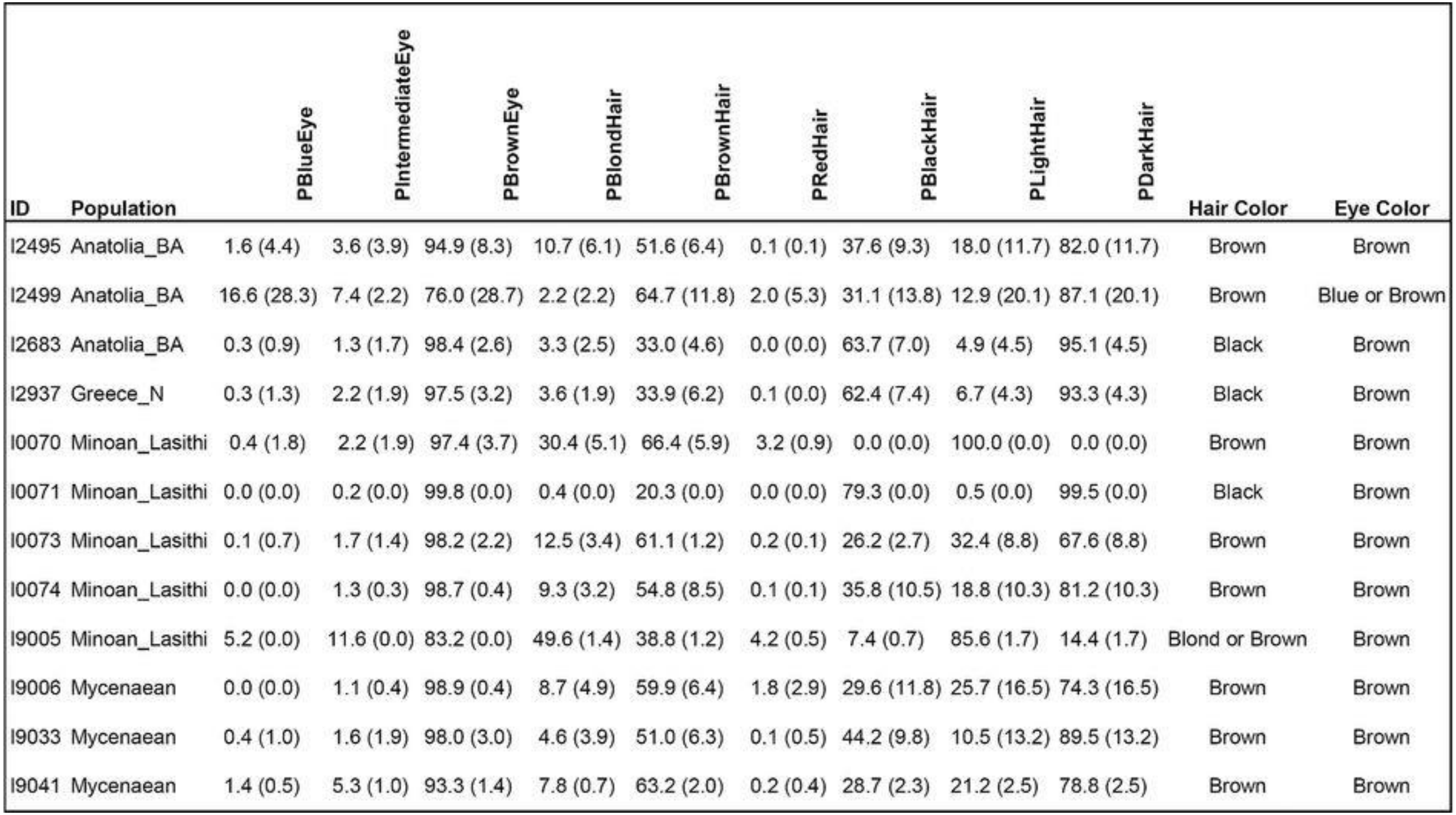


Individual_ID	Genotype_ID	Other_ID	Source	Date	Population_Label	Location	Country	Latitude	Longitude	Sex	Coverage	Autosomal_SNPs	mtDNA	Y-chromosome
I2937	I2937	A2197	1240K	5419±41 cal BC	Greece_N	Diros, Alepotrypa Cave	Greece	36.64	22.38	F	0.870	481848	K1a26	
I0071	I0071	Lasithi4	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	F	7.312	953157	U5a1	
I0070	I0070	Lasithi2	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	M	1.267	619767	H13a1	J2a1d
I0073	I0073	Lasithi7	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	M	1.481	643360	H	J2a1
I0074	I0074	Lasithi9	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	F	0.874	506434	H5	
I9005	I9005	Lasithi17	1240K	2000-1700 BCE	Minoan_Lasithi	Hagios Charalambos Cave, Lasithi, Crete	Greece	35.08	25.83	F	1.351	388859	H	
I9006	I9006	Salamis31	1240K	1411-1262 cal BCE (3067 ± 25 BP, DEM-2905)	Mycenaean	Agia Kyriaki, Salamis	Greece	37.97	23.50	F	1.387	361193	X2d	
I9123	I9123	S-EVA 1263 Armenoi 503	1240K	1370-1340 BCE	Crete_Armenoi	Armenoi, Crete	Greece	35.45	24.17	F	0.041	45158	U5a1	
I9127	I9127	12V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.035	36475	J2b1a1	
I9128	I9128	13V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.016	17081	I5	
I9129	I9129	14V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.063	63986	H+163	
I9130	I9130	16V Tholos	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	M	0.086	92186	U3b3	G2a2b2
I9131	I9131	19V t2	1240K	2900-1900 BCE	Minoan_Odigitria	Moni Odigitria, Heraklion, Crete	Greece	35.05	24.81	F	0.095	96946	K1a2	
I9010	I9010	Galatas19	1240K	1700-1200 BCE	Mycenaean	Galatas Apatheia, Peloponnese	Greece	37.50	23.45	F	0.379	242265	X2	
I9033	I9033	Peristeria4	1240K	1416-1280 cal BCE (3084 ± 24 BP, DEM-2903)	Mycenaean	Peristeria Tryfilia, Peloponnese	Greece	36.92	21.70	F	0.439	248912	H	
I9041	I9041	Galatas4	1240K	1700-1200 BCE	Mycenaean	Galatas Apatheia, Peloponnese	Greece	37.50	23.45	M	1.558	417898	X2	J2a1
I2495	I2495	A4-1	1240K	2558-2295 calBCE (3925±35 BP, Poz-81111)	Anatolia_BA	Harmanören-Göndürle Höyük, Isparta	Turkey	37.92	30.71	M	1.981	637146	H	J1a
I2499	I2499	UC1	1240K	2836-2472 calBCE (4040±35 BP, Poz-82213)	Anatolia_BA	Harmanören-Göndürle Höyük, Isparta	Turkey	37.92	30.71	F	0.285	243348	K1a2	
I2683	I2683	G3-95	1240K	2500-1800 BCE	Anatolia_BA	Harmanören-Göndürle Höyük, Isparta	Turkey	37.92	30.71	F	3.695	749308	T2b	

1. Dates marked simply as bce (Before Common Era) are based on the associated archaeology of the samples. Dates marked as calbce are based on radiocarbon dating of the samples (Supplementary Information section 1).

Extended Data Table 2: Phenotypic inference of ancient individuals

From: Genetic origins of the Minoans and Mycenaeans



ID	Population	PBlueEye	PIntermediateEye	PBrownEye	PBlondHair	PBrownHair	PRedHair	PBlackHair	PLightHair	PDarkHair	Hair Color	Eye Color
I2495	Anatolia_BA	1.6 (4.4)	3.6 (3.9)	94.9 (8.3)	10.7 (6.1)	51.6 (6.4)	0.1 (0.1)	37.6 (9.3)	18.0 (11.7)	82.0 (11.7)	Brown	Brown
I2499	Anatolia_BA	16.6 (28.3)	7.4 (2.2)	76.0 (28.7)	2.2 (2.2)	64.7 (11.8)	2.0 (5.3)	31.1 (13.8)	12.9 (20.1)	87.1 (20.1)	Brown	Blue or Brown
I2683	Anatolia_BA	0.3 (0.9)	1.3 (1.7)	98.4 (2.6)	3.3 (2.5)	33.0 (4.6)	0.0 (0.0)	63.7 (7.0)	4.9 (4.5)	95.1 (4.5)	Black	Brown
I2937	Greece_N	0.3 (1.3)	2.2 (1.9)	97.5 (3.2)	3.6 (1.9)	33.9 (6.2)	0.1 (0.0)	62.4 (7.4)	6.7 (4.3)	93.3 (4.3)	Black	Brown
I0070	Minoan_Lasithi	0.4 (1.8)	2.2 (1.9)	97.4 (3.7)	30.4 (5.1)	66.4 (5.9)	3.2 (0.9)	0.0 (0.0)	100.0 (0.0)	0.0 (0.0)	Brown	Brown
I0071	Minoan_Lasithi	0.0 (0.0)	0.2 (0.0)	99.8 (0.0)	0.4 (0.0)	20.3 (0.0)	0.0 (0.0)	79.3 (0.0)	0.5 (0.0)	99.5 (0.0)	Black	Brown
I0073	Minoan_Lasithi	0.1 (0.7)	1.7 (1.4)	98.2 (2.2)	12.5 (3.4)	61.1 (1.2)	0.2 (0.1)	26.2 (2.7)	32.4 (8.8)	67.6 (8.8)	Brown	Brown
I0074	Minoan_Lasithi	0.0 (0.0)	1.3 (0.3)	98.7 (0.4)	9.3 (3.2)	54.8 (8.5)	0.1 (0.1)	35.8 (10.5)	18.8 (10.3)	81.2 (10.3)	Brown	Brown
I9005	Minoan_Lasithi	5.2 (0.0)	11.6 (0.0)	83.2 (0.0)	49.6 (1.4)	38.8 (1.2)	4.2 (0.5)	7.4 (0.7)	85.6 (1.7)	14.4 (1.7)	Blond or Brown	Brown
I9006	Mycenaean	0.0 (0.0)	1.1 (0.4)	98.9 (0.4)	8.7 (4.9)	59.9 (6.4)	1.8 (2.9)	29.6 (11.8)	25.7 (16.5)	74.3 (16.5)	Brown	Brown
I9033	Mycenaean	0.4 (1.0)	1.6 (1.9)	98.0 (3.0)	4.6 (3.9)	51.0 (6.3)	0.1 (0.5)	44.2 (9.8)	10.5 (13.2)	89.5 (13.2)	Brown	Brown
I9041	Mycenaean	1.4 (0.5)	5.3 (1.0)	93.3 (1.4)	7.8 (0.7)	63.2 (2.0)	0.2 (0.4)	28.7 (2.3)	21.2 (2.5)	78.8 (2.5)	Brown	Brown

1. We list the probability assignments for different phenotypes by HIrisPlex[26] and an assessment of the phenotype. We generate 100 random replicates of the genotypes of each individual, listing the standard deviation in parentheses (Supplementary Information section 4).