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, Mycenaean from mainland Greece, and their eastern neighbours from southwestern Anatolia. Here we show that Minoans and Mycenaean were genetically similar, having at least three-quarters of their ancestry from the first Neolithic farmers of western Anatolia and the Aegean1,2, and most of the remainder from ancient populations related to those of the Caucasus3 and Iran4,5. However, the Mycenaeans differed from Minoans in deriving additional ancestry from an ultimate source related to the hunter-gatherers of eastern Europe and Siberia6–8, introduced via a proximal source related to the inhabitants of either the Eurasian steppe9,10 or Armenia9,10. 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 Eurasia4,6,8, 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’ ancestry6,10 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, obscurring 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 Greek13. 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 DNA14,15. 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 Europe4,6,8,16 and the Near East17–20? 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 1700–1300 bc; from the western coast of the Peloponnese, from Argolis, and the island of Samalas). 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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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 \(\sim 1.2\) 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...
Admixture modelling of Bronze Age populations

| Test | Ancestral sources | Mixture proportions | Standard errors |
|------|-------------------|---------------------|-----------------|
|      | A | B | C | D | A | B | C | D | A | B | C | D |
| Anatolia_BA | CHG | Anatolia_N | Levant_N | 0.319 | 0.618 | 0.063 | 0.029 | 0.078 | 0.063 |
| Minoan_Odigitria | CHG | Anatolia_N | Levant_N | 0.144 | 0.856 | 0.031 | 0.031 |
| Minoan_Odigitria | CHG | Levant_N | Anatolia_N | 0.137 | 0.863 | 0.032 | 0.032 |
| Minoan_Lasithi | CHG | Anatolia_N | Levant_N | 0.001 | 0.152 | 0.847 | 0.015 | 0.021 | 0.020 |
| Mycenaean | AfrotovaGora3 | CHG | Anatolia_N | 0.133 | 0.126 | 0.741 | 0.027 | 0.026 | 0.024 |
| Mycenaean | CHG | Anatolia_N | Levant_N | 0.004 | 0.154 | 0.842 | 0.024 | 0.026 | 0.020 |
| Mycenaean | CHG | Anatolia_N | Levant_N | 0.065 | 0.136 | 0.799 | 0.016 | 0.022 | 0.024 |
| Mycenaean | CHG | Anatolia_N | Levant_N | 0.044 | 0.176 | 0.780 | 0.016 | 0.023 | 0.024 |

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, a Chalcolithic northwestern Anatolian, and western Anatolians from Kumtepe. This component was maximized in the Mesolithic/Neolithic samples from Iran and hunter–gatherers from the Caucasus (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/Brone Age in mainland Europe, introduced there by migration from the Eurasian steppe.

Beyond the visual impressions of PCA and ADMIXTURE, we formally tested the relationships among populations from our study and the literature, using $f_2$-statistics of the form $f_2(X, Y; Test, Chimp)$ 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 $f_2$-statistics of the form $f_2(Ref_1, Ref_2; Test)$ 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 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’ (Caucasian/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; 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 (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 J1, 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 and a Mesolithic individual from Iran, 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 Peristera 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 3) and could model Mycenaeans as a mixture of the Anatolian Neolithic and Chalcolithic–Bronze Age populations from Armenia (Table 1). Populations from Armenia possessed some ancestry related to eastern European hunter–gatherers, 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
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 proportions4, by examining the correspondence between qpAdm estimates and PCA4 (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 occurred during the fourth to second millennium BC time window. Other proposed migrations, such as settlement by Egyptian or Phoenician colonists22, 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 admixture23. 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 Europeans1,24 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 eyes25. We used the HiRePlex26 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 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) Anatoliens. The same pattern also applies to Bronze Age populations from other regions of West Eurasia (Extended Data Fig. 5).
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\textsuperscript{17,28}.

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? Such a migration would support the idea that proto-Greek speakers\textsuperscript{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’\textsuperscript{30}.

Online Content Methods, along with any additional Extended Data display items and Online Content, can be found in the online version of the 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.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.P., performed bioinformatics analyses.

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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 aluminum 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 methods31.

Leipzig, Germany. As previously described32, sampling, extraction, and preparation of single-indexed, single-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 DNA33.

Enriched libraries were sequenced on an Illumina GAIIx platform for 2 × 76 + 6 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 of 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 protocol34.

Sequencing of shotgun and mitochondrial-DNA-enriched libraries took place at the laboratories of the Frauenklinik of the University of Tübingen, on an Illumina MiSeq for 2 × 150 + 8 cycles or on an Illumina HiSeq 2500 for 2 × 101 + 8 cycles (Supplementary Table 2).

Additional libraries were produced including full or partial15 repair with uracil-DNA glycosylase and endonuclease VIII to remove deaminated bases. In-solution enrichment was performed using previously reported protocols6-18.

Two SNP sets of 394,577 SNPs (‘390k capture’6) or 1,237,207 SNPs (‘1240k capture’6) were targeted. Sequencing took place in the facilities of the Frauenklinik, University of Tübingen, on an Illumina HiSeq 2500 for 2 × 101 + 8 cycles and at the facilities of the University of Kiel on a HiSeq 4000 for 2 × 150 + 8 cycles. One uracil-DNA glycosylase-treated library (10071) 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 were performed. Without uracil removal were performed in the Harvard Medical School cleanroom following previously described protocols34-36. After the screening stage, libraries were (1) shotgun sequenced and (2) sequenced after enriching for the human mitochondrial DNA together with some nuclear loci to approximate the nuclear coverage and mitochondrial contamination.

All four libraries (barcoded) prepared in Boston, three libraries (indexled) 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 (MAPQ ≥ 10), sites with a minimum sequence quality (≥20), and removing two bases at the ends of reads.

Testing for contamination. Modern human contamination of the mitochondrial DNA was assessed using the software snuclenti18, 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 ANGSD33 (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 pedigrees, as previously described15.

Testing for admixture. 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 setting the genotypes of 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 $f_2$ (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 smartpca30 with the default parameters inbred: YES31, and fstonly: YES. Phenotypic inference. The ancient samples had low coverage (median 0.87×) and the modelled ancestry from ‘right’ to ‘left’ and estimating mixture proportions.

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 setting the genotypes of 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 $f_2$ (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.

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 setting the genotypes of 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 $f_2$ (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.

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per individuals and submitted them to HiRePlex26, 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 $\leq 5$ are shown with thicker lines.
Extended Data Figure 2 | Symmetry testing of Aegean Bronze Age populations. The statistic $f(X, Y; \text{Test, Chimp})$ 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 $f_1(X, Y; \text{Test, Chimp})$ 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 Gündürle than with a Chalcolithic Anatolian from Barcin. 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 $\pm 3$ 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 $f$(Mycenaean, Simulated; Outgroup1, Outgroup2) 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 shows an affinity to present-day populations from Armenia, Anatolia, the Caucasus, and Iran, as does (b) Middle/Late Bronze Age Armenia. c, The Bronze Age Levant has an affinity to Levantine and Arabian populations. d, Late Neolithic/Bronze Age Europeans most resemble present-day northern/central Europeans, as do (e) Early/Middle Bronze Age steppe populations, who also resemble populations of the northeast Caucasus, while (f) Middle/Late Bronze Age steppe populations resemble central/northern Europeans. 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; b, Greeks from Thessaloniki; c, Cypriots. Whole-genome data: d, Cretans; e, Greeks from Thessaly; f, Greeks from central Greece; g, Greeks from the study in ref. 27.
## Extended Data Table 1 | Information on ancient samples reported in this study

| Individual ID | Genomic_ID | Other_ID | Source | Date | Population_Lable | Location | Country | Latitude | Longitude | Sex | Coverage | Ancient SNP | mDNA | Y-chromosome |
|---------------|------------|----------|--------|------|------------------|----------|---------|----------|-----------|-----|----------|-------------|------|-------------|
| 29837         | A2197      | 1240K    | 5418±41 cal BC | Greece, N | Dirós, Apeirþypa Cave | Greece | 36.64 | 22.38 | 0.870 | 481948 | K1a2a |
| 90701         | LXXXV      | 1240K    | 2300-1700 BCE | Minoan_Lewiti | Hagios Charalambos Cave, Lewiti, Crete | Greece | 35.95 | 25.83 | 7.312 | 953157 | JJx1 |
| 90707         | LXXXVI     | 1240K    | 2000-1700 BCE | Minoan_Lewiti | Hagios Charalambos Cave, Lewiti, Crete | Greece | 35.95 | 25.83 | 1.267 | 611797 | K3a1 |
| 90737         | LXXXVII    | 1240K    | 2000-1700 BCE | Minoan_Lewiti | Hagios Charalambos Cave, Lewiti, Crete | Greece | 35.95 | 25.83 | 1.485 | 643380 | K2a1 |
| 90744         | LXXXVIII   | 1240K    | 2000-1700 BCE | Minoan_Lewiti | Hagios Charalambos Cave, Lewiti, Crete | Greece | 35.95 | 25.83 | 0.874 | 506438 | K5 |
| 90055         | LXXXIX     | 1240K    | 2000-1700 BCE | Minoan_Lewiti | Hagios Charalambos Cave, Lewiti, Crete | Greece | 35.95 | 25.83 | 1.351 | 368659 | K1 |
| 90009         | 0006       | Salamis31 | 1411-1282 cal BCE | (887-201 BP, BCBA-3869) | Mycenaean | Agía Kyriaki, Salamis | Greece | 37.97 | 23.50 | 1.387 | 361190 | K2d |
| 89123         | 9123       | S-EVA 1203 | 1240K | 1370-1340 BCE | Crete, Armeroi | Armeroi, Crete | Greece | 35.45 | 24.17 | 0.041 | 45105 | J1a1 |
| 89127         | 9127       | 1240K    | 2000-1900 BCE | Minoan_Odighira | Moni-Odighira, Heraklion, Crete | Greece | 35.05 | 24.85 | 0.035 | 36475 | J2b1a |
| 89128         | 9128       | 1240K    | 2000-1900 BCE | Minoan_Odighira | Moni-Odighira, Heraklion, Crete | Greece | 35.05 | 24.85 | 0.016 | 17408 | X |
| 89129         | 9129       | 1494/12 | 1240K | 2000-1900 BCE | Minoan_Odighira | Moni-Odighira, Heraklion, Crete | Greece | 35.05 | 24.85 | 0.020 | 36896 | H—163 |
| 90130         | 9130       | 1495/12 | 1240K | 2000-1900 BCE | Minoan_Odighira | Moni-Odighira, Heraklion, Crete | Greece | 35.05 | 24.85 | 0.080 | 52186 | J2b3 |
| 89131         | 9131       | 1912/12 | 1240K | 2000-1900 BCE | Minoan_Odighira | Moni-Odighira, Heraklion, Crete | Greece | 35.05 | 24.85 | 0.005 | 96946 | K1a2 |
| 90010         | 9010       | Galatas19 | 1240K | 1700-1200 BCE | Mycenaean | Galatás Apothia, Paloponessos | Greece | 37.50 | 23.45 | 0.370 | 242238 | K2 |
| 90033         | 90033      | Peristera4 | 1240K | 1416-1260 cal BCE | (887-241 BP, BCBA-3869) | Mycenaean | Peristera Tryfíka, Paloponessos | Greece | 36.92 | 21.70 | 0.439 | 246913 | K |
| 90041         | 90041      | Galatas2d | 1240K | 1700-1200 BCE | Mycenaean | Galatás Apothia, Paloponessos | Greece | 37.50 | 23.45 | 1.558 | 417898 | K2a |
| 24955         | 2495      | A4-1     | 1240K | 3558-2285 cal BCE | Anatolia BA | Harmanören-Görünlü Höyük, Isparta | Turkey | 37.92 | 30.71 | 1.981 | 637146 | J1a |
| 24999         | 24999     | UC1      | 1240K | 2676-2472 cal BCE | Anatolia BA | Harmanören-Görünlü Höyük, Isparta | Turkey | 37.92 | 30.71 | 0.285 | 243348 | K1a2 |
| 24683         | 24683     | I3-S5   | 1240K | 2500-1800 BCE | Anatolia BA | Harmanören-Görünlü Höyük, Isparta | Turkey | 37.92 | 30.71 | 3.896 | 749308 | T2b |

Dates marked simply as BCE (Before Common Era) are based on the associated archaeology of the samples. Dates marked as calBC are based on radiocarbon dating of the samples (Supplementary Information section 1).
## Phenotypic inference of ancient individuals

| ID    | Population | BlueEye | PaleBlueEye | PBrownEye | PBrownHair | PRedHair | PBlackHair | PLightHair | PDarkHair | Hair Color | Eye Color |
|-------|------------|---------|-------------|-----------|------------|----------|------------|------------|-----------|------------|-----------|
| i2459 | 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 (1.5) | 2.2 (1.9)   | 97.4 (3.7) | 30.4 (5.1) | 60.4 (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) | 97.8 (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 (6.5) | 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)  | 95.6 (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) | 1.6 (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 HiResPlex® 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).