Psonis *et al. Genome Biology* (2026) 27:96
https://doi.org/10.1186/s13059-026-03968-5

Genome Biology

RESEARCH Open Access

Genetic affinities between the ancient Greek colony of Amvrakia and its metropolis

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Abstract

Background: The complex historical phenomenon known as Greek colonization refers to the strategic establishment of new settlements (colonies) from the 8th to the early fourth century BCE. Unlike earlier migrations, this process was planned and driven by the need to expand trade, access resources, and develop economic as well as political networks. Corinth, a prominent commercial center in southern Greece, constitutes a prominent example for initiating colonization. By founding colonies, Corinth established a safe and continuous route for moving goods along the coasts of western mainland Greece and the Adriatic. Amvrakia was one of Corinth's principal colonies along this route in northwestern Greece. Founded in the seventh century BCE, Amvrakia was characterized by a strong dependence on its metropolis (Corinth). Here, we aim to investigate the genetic relationships between the Corinthian metropolis and the Amvrakia colony, the contribution of the local population to the founding genetic pool, as well as the demography of Amvrakia in subsequent periods.

Results: During its foundation in the Archaic period, Amvrakia appears to have been shaped by genetic influences from a single source. This source migrated from the Corinth territory, represented by the Archaic Tenea population and is supported via an Identity By Descent (IBD) analysis. A direct ancestry from Late Bronze Age (LBA) Greece, including a local LBA population represented by the Ammotopos site located in close proximity to Amvrakia, was not inferred despite conducting a plethora of independent population genomics analyses. During the subsequent Classical and Hellenistic periods, the population of Amvrakia appears to have only slightly differentiated and evidence of genetic continuity over time is observed.

Conclusions: The migration of Corinthians to Amvrakia was the major contributor to the initial genetic pool of the colony, indicating that the Corinthian colonization included both genetic and cultural transmission between the metropolis and its colony.

Keywords: Admixture, Amvrakia, Ancient Greek colonization, Archaeogenomics, Archaic period, Classical period, Hellenistic period, Tenea, Roman period, Whole genome sequencing

Background

Since the beginning of the Holocene, the Mediterranean region has witnessed the rise of extensive exchange systems among coastal societies, fostering intercultural interactions that eventually gave birth to the earliest trans-Mediterranean trade networks e.g. Aegean Neolithic cultures, Protopalatial Minoan Cultures [1]. These dynamics laid the groundwork for Bronze Age [2, 3] cultures. During the Bronze Age, particularly the Eastern Mediterranean exhibited signs of urban growth, complex societal hierarchies, and specialized craftsmanship that are indicators of widespread development and economic expansion [4]. During the Late Bronze Age, trade and communication networks became more expansive and efficient, enabling the large-scale movement of people, goods, and ideas across greater distances than ever before [5]. These trends intensified during the Iron Age, as pre-existing networks further expanded and mobility surged, leading to substantial migrations, predominantly initiated by Greeks and Phoenicians [6].

Within this context, the phenomenon of Ancient Greek colonisation emerged (see Additional file 1: Section 1.4). The term describes the establishment of hundreds of new Greek settlements throughout the Mediterranean, along the African coasts and around the Black Sea, in the course of but a few centuries [7, 8]. Many of these new settlements (e.g. Naucratis in Egypt, Cyrene in Libya, Calchedon and Byzantium on Bosporus, and Olbia, Sinope, and many others in Black Sea) developed into prominent urban centers where culturally and biologically diverse populations interacted. Over time, these interactions contributed to the development of new political structures —most notably, the emergence of the Greek city-state as an organized urban community of citizens— which played a substantial role in shaping sociopolitical, and economic affairs. Historians today generally categorize Ancient Greek colonisation into two main phases. The first occurred during the Iron Age or so-called Greek Dark Ages that followed the collapse of the Mycenaean palatial Bronze Age civilization (circa 1200–750 BCE) and focused on the Aegean islands and the coast of Asia Minor [9]. The second phase, which affected a substantially larger geographic region —including the entire Mediterranean and the Black Sea— and involved more pronounced population movements, dates to the Archaic period (approximately 8th to early fourth century BCE [7]). The search of colonizers for new homes had numerous reasons: necessity due to internal strife, social conflicts, political strategies, famine or poverty, and the pursuit of opportunities (e.g., new land to farm, more livestock to own, ampler natural resources to exploit).

The second wave of colonisation, which is the subject of this study, extended over a long period and encompassed vast areas [10]. The migrations/colonisations were systematically organized by parent cities (metropoleis), which selected colony sites based on strategic criteria, such as 1) proximity to the sea, including natural harbors or river mouths and 2) suitability of the surrounding land (chora) to support the settlers with essential resources [11].

Based on literary sources and archaeological evidence, the founding process began when a metropolis decided to dispatch a group of its citizens to form a new community abroad (*apoikia*; see also Additional file 1: Section 1.4). A designated leader, known as the *oikistes,* was selected to head the expedition and was granted elevated civic powers. This individual played a pivotal role in guiding the colony's establishment and future direction. The *oikistes* usually consulted the Delphic oracle, which offered guidance on various aspects of the foundation, including its location. After receiving the oracle's advice, the *oikistes* would lead the initial group of settlers, secure the territory, and institute the foundational laws and customs (*nomima*) of the new society. These customs typically included a legal framework, a calendar of religious festivals, protocols for worship, and a tribal organization of citizens. The *nomima* served as a unifying set of traditions that were of particular importance in colonies composed of settlers from diverse backgrounds [12], and became enduring features of a colony's civic identity [7]. Based on these elements (cults, temples, material culture), archaeologists and historians identify a colony in relation to the metropolis, although this connection is not always straightforward to establish.

While many Greek colonies were founded in areas already inhabited by indigenous populations [13], some were established entirely from scratch, such as Abdera (on the Thracian coast, Northern Greece). Over time, some of these colonial communities transformed into multicultural hubs (e.g. Abdera, Syracuse, Massalia) and, in numerous cases, flourished both politically and economically. The successful establishment of the colony was of considerable importance to the mother city, which often maintained ongoing interest and influence in its affairs. The relationship between a metropolis and its colony extended well beyond the initial act of foundation. These interactions were often bidirectional and mutually beneficial, with some colonies ultimately exceeding their metropoles in terms of cultural and political advancement [14].

The present study focuses on the colonization process of Amvrakia, a colony of ancient Corinth. Corinth as other Greek *poleis* (cities), from the mid-eighth century BCE onwards, started to expand in a more strategic and sustainable manner and evolved into one of the most powerful metropoles. Corinth established colonies (*apoikiai*) and trading posts across the Mediterranean (Syracuse in Sicily, Corcyra and Leukas in the Ionian Sea), the Adriatic (Epidamnus, Apollonia), the North Aegean (Potidaea in Chalcidice), and mainland Greece (Amvrakia in Epirus, Anaktorion and Sollion in the western part of the geographical unit of Sterea Ellada) (Fig. 1A). Through its colonies, Corinth developed a trade network encompassing the Aegean, the coasts of Western Greece, the Adriatic, and Sicily [6]. Corinth had a profound impact on the economy and lifestyle of its colonies, promoting a culture of cosmopolitanism. Its political strength, strategic ambition, and artistic as well as cultural significance, enhanced its prestige, while its influence shaped a secure urban public life for its citizens [7–9].

The colony of Amvrakia (also known as Ambracia) was part of this strategic colonization plan. It was founded on the banks of the Arachthos River [10], in the area of present-day northwestern Greece (Epirus regional unit; present-day city of Arta; Fig. 1A), in the second half of the seventh century BCE. In this region, Corinth had established a trading post, in as early as the eighth century BCE [11], which connected southern Greece with the mainland of Epirus and extended to Apollonia, another Corinthian colony on the

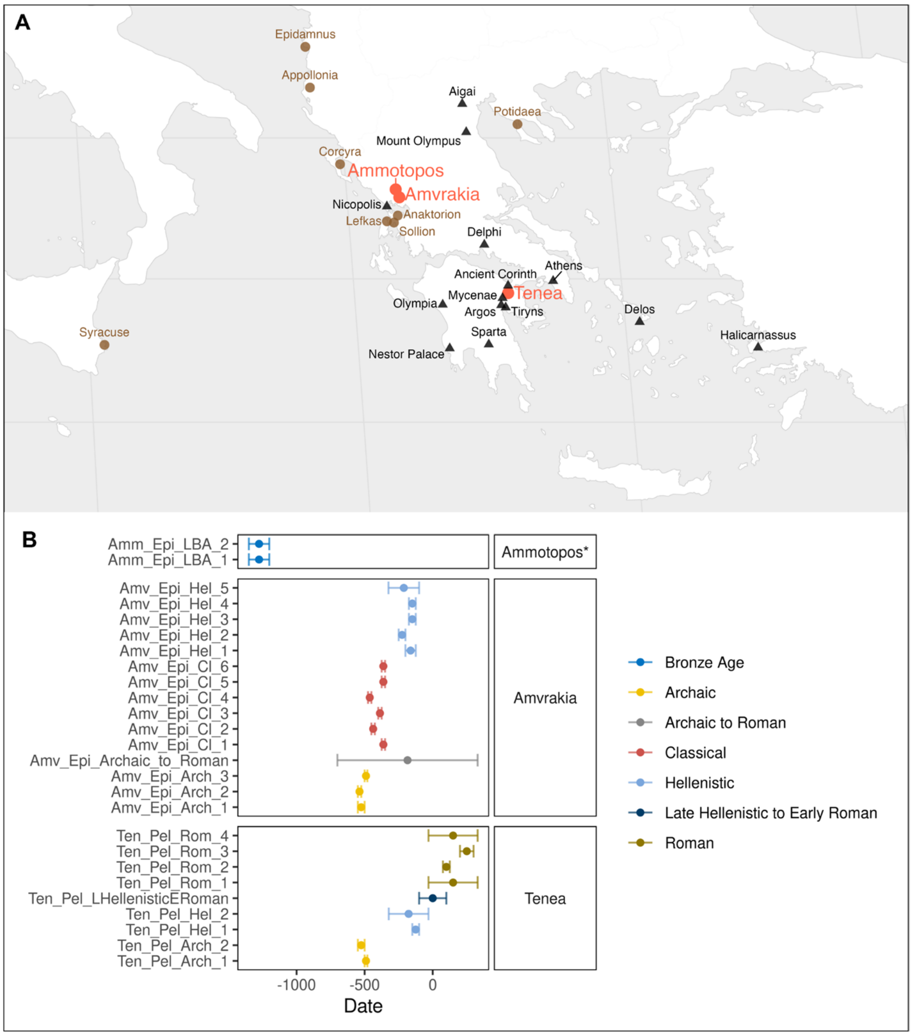

Fig. 1 **A** Location of Ammotopos, Amvrakia, and Tenea in the present-day geographical area of Greece. The main Corinthian colonies are displayed in brown color. Other important ancient locations, as well as locations mentioned in the text are displayed as black triangles. **B** Temporal coverage of the 26 ancient genomes reported for the first time in our study. The asterisk in Ammotopos denotes C-14 dating as opposed to archaeological dating

eastern Adriatic coast. The foundation of Amvrakia by Corinth is substantiated by the strong presence of Corinthian material culture, mythological traditions, and religious practices within the ancient city. Historical literature corroborates the early dependence of Amvrakia on its metropolis [12].

While many colonies have been excavated, the debate on the mode, intensity, and tempo of the migratory movements (e.g. [17, 18]) is still ongoing. Can we indeed identify biological, linguistic, religious, cultural, or social groups whose origins might as often have been merely invented to establish founding myths as they might have been real? What was the role of the local populations? Were they integrated into the new communities, or did they remain genetically and culturally distinct? Many of these open questions are anthropological and population genetic in nature and have been only addressed to a limited extent.

Nowadays, ancient colonization can be studied via modern methodological approaches, such as ancient DNA and strontium isotope studies in conjunction with archaeological evidence and literary sources. Up to now, archaeogenomic investigations of ancient Greek colonization are limited to two studies. The first included genome-wide data from inhabitants of the Greek colony of Empúries (*Εμπόριον* in Greek) in Iberia dated to the fifth century BCE, who display genetic proximity to both, Late Bronze Age (LBA) Aegean people, and indigenous populations [19]. The second study focused on soldiers who fought for the army of the Greek Sicilian colony of Himera, along with representatives of the civilian population, where both groups included individuals with an LBA Aegean ancestry [20]. Both studies used prehistoric Aegean individuals as a proxy for the ancestral profile of ancient Greeks. This is due to the scarcity of available ancient genomes or genome-wide data from the Eastern Mediterranean covering the period from the Greek Archaic era to Roman Imperial times. The first historical genome-wide data from Greece were generated only recently including four Iron Age (IA) individuals from mainland Greece (Kastrouli near Delphi) [21, 22] and the Peloponnese (Palace of Nestor and Tiryns) and one individual from Roman times (Marathon, Attica) [21].

In our study, we focus on the Corinthian colony of Amvrakia to investigate the genetic relationships between a metropolis and its apoikia. For the first time, we assess the contribution of the local population and the colonists to the genetic pool of the founded city. We further examine its demographic evolution from its foundation during the Archaic period until its complete independence in Hellenistic times. Moreover, the assembly of genomes from these yet unsampled periods in the area of present-day Greece also allows for a comparison with preceding prehistoric genetic data from the Eastern Mediterranean, as well as to get insights on their phenotypic characteristics and identify ancient DNA traces from their commensal or pathogenic microbes. Therefore, we sampled ancient bones and teeth from 24 individuals from Archaic, Classical, and Hellenistic Amvrakia (Fig. 1), as well as from two individuals from the LBA site of Ammotopos (Fig. 1), located approximately 16 km north of the modern city of Arta (Ancient Amvrakia). The findings of Ammotopos represent the first tangible Mycenaean evidence identified within the present-day regional unit of Arta. As Ammotopos reflects the local ancestral background prior to the foundation period, the anthropological material from the site was included in the present study. Moreover, as a proxy for the genetic pool of Corinth, we sampled 13 individuals from Archaic up to Roman times from the ancient city of Tenea (Fig. 1), an important settlement located in the eastern periphery of Corinth and in a key strategic position controlling *Kontoporeia*, the shortest path leading from Corinth to Mycenae, and to Argos. For centuries, Tenea was the largest *kome* (see Additional file 1: Section 1.4) of the Corinthia area, thriving under Corinth's influence. Though not an independent *polis*, it grew into a prosperous community, noted by Strabo and Pausanias and linked to the Corinthian royal house through the myth of Oedipus. In the Archaic and Classical periods, its citizens identified themselves as Corinthians, and in 734 BCE Teneans joined Corinth in founding Syracuse [23].

Results

We performed pre-screening shotgun NGS analysis on 41 samples from 39 individuals of Amvrakia, Ammotopos, and Tenea burials (Additional file 2). Based on the useful human endogenous content of each sample/library, we performed deep whole genome sequencing on 26 out of the 41 samples (Additional file 3). All individuals' genetic data were characterized by an ancient-like DNA signature (i.e., deamination damage and short fragments length; Additional file 4). The final dataset included 15 individuals from Archaic (3), Classical (6), Hellenistic (5), and Archaic-to-Roman (1) Amvrakia, two individuals from LBA Ammotopos, and nine individuals from Archaic (2), Hellenistic (2), Late Hellenistic-to-Early Roman (1), and Roman (4) Tenea (Fig. 1 and Additional file 2). The mean coverage depth exceeded 0.05 × (0.07—6.31 ×) for all 26 individuals (Additional file 3), nine individuals were males and 17 were females (Additional file 4), and no aneuploidies were detected. Contamination evaluation resulted in > 98.49% estimated average authenticity levels using ContamMix, a contamination estimate below 4% using schmutzi, negative estimates in ContamLD, and ANGSD contamination estimates below 1.62% based on the X-chromosome in males (Additional file 4). Various haplogroups were detected (Additional file 4) regarding both the mitochondrial DNA and the Y-chromosome. We further discovered a few cases of close genetic relatedness (see details in Additional file 1: Section 3.1). We detected one in Classical Amvrakia [second degree genetic kinships between a female individual (Amv_Epi_Cl_1) and two other individuals that were sisters (Amv_Epi_Cl_5 and Amv_Epi_Cl_6)], one in Hellenistic Amvrakia (mother and daughter: Amv_Epi_Hel_3 and Amv_Epi_Hel_4), and one in Archaic Tenea (mother and son: Ten_Pel_Arch_2 and Ten_Pel_Arch_1). In all downstream kinship-affected analyses (i.e. ADMIXTURE, F-statistics, IBDs), we controlled for the aforementioned relatedness cases by only keeping one single individual with higher coverage for each genetically related group of individuals at first and second degree.

Comparison between historical and prehistoric genomes from the geographic area of present-day Greece

We grouped the ancient individuals (newly sequenced and "Dataset 1") primarily according to their main cultural chronology and geography (countries and main regions within) (Additional file 5; see also details and rationale about grouping in Additional file 1: Sects. 3.5.7–3.5.9). We computed principal components (PCs) on the Human Origins (HO) SNP set data ("Dataset 3") [24] using 888 modern genomes from West Eurasia and projected the 26 newly generated as well as 670 published ancient genomes onto the first two PCs (Fig. 2). Our new genomes are projected among other ancient eastern Mediterranean genomes. However, the new genomes do not form a tight cluster as they are distributed among several prehistoric (Neolithic to Iron Age) and historical (Archaic to Roman times) individuals from a wide geographical area (Italy, Balkans, Anatolia) with two main clusters emerging (see Additional file 1: Section 3.5.7 for a detailed presentation of the PCA results). The first cluster includes the majority of the Amvrakia samples (one of the three Archaic, all six Classical, and four of the five Hellenistic samples), the two BA Ammotopos samples, and some of the Tenea samples (both Archaic, two of the three Hellenistic, and the Late Hellenistic-Early Roman). This cluster is primarily close to LBA (1700–1050 BCE) genomes from across present-day Greece, Early Iron Age (1100–500 BCE) genomes from present-day Bulgaria, and the locals of the Ancient Greek colony of Himera in Sicily (780–400 BCE). The second cluster comprises all four Roman Tenea individuals and one of the three Hellenistic Amvrakia individuals. It is placed close to Archaic (750–480 BCE), Roman (27–476 CE), and other

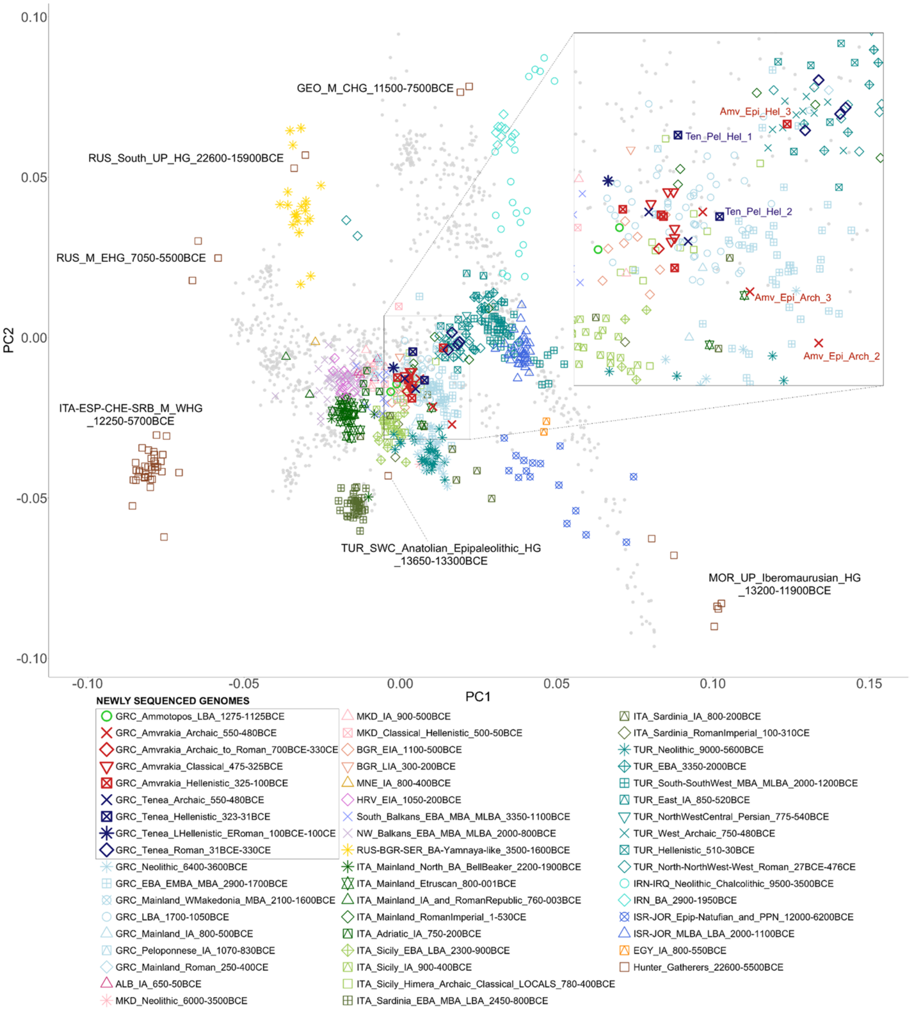

Fig. 2 PCA projection of the 26 newly generated ancient genomes of the present study and 670 other ancient published genomes into the two first PCs (PC1 variance: 7.6%, PC2 variance: 3.5%) generated using 888 genomes from modern West Eurasians ("Dataset 2"). Hunter-Gatherers are indicated, separately, within the plot. South_Balkans includes Albania, North Macedonia, and Bulgaria, whereas NW_Balkans includes Croatia, Montenegro, and Serbia. The analysis was based on 597,573 genomic sites of the Human Origins SNP array. GRC = Greece; ALB = Albania; MKD = North Makedonia; BGR = Bulgaria; MNE = Montenegro; HRV = Croatia; RUS = Russia; SER = Serbia; ITA = Italy, TUR = Türkiye, EGY = Egypt, IRN = Iran, IRQ = Iraq, ISR = Israel, JOR = Jordan; BA = Bronze Age; EBA = Early Bronze Age; MBA = Middle Bronze Age; MLBA = Middle-Late Bronze Age; LBA = Late Bronze Age; IA = Iron Age; EIA = Early Iron Age; LIA = Late Iron Age; PPN = Pre-Pottery Neolithic; Epip = Epi-Paleolithic

Anatolian genomes [including a Hellenistic (510–30 BCE) and an Early Bronze Age (EBA, 3350–2000 BCE) genome], a Roman Imperial (1–530 CE) genome from Italy, and a few Greek genomes from the Roman (250–400 CE), EBA_MBA (2900–1700 BCE), and LBA (1700–1050 BCE) periods. Between these two clusters, the remaining of the two Hellenistic Tenea individuals are placed, whereas the two remaining Archaic Amvrakia individuals are closer to the first cluster, but more differentiated towards the upper left of the PC space and the Levant Neolithic—BA-Yamnaya-like axis. We executed an unsupervised ADMIXTURE analysis on "Dataset 2" [25] for a set of 686 ancient individuals on the 1240 K SNP set data [24], including 22 of our newly reported genomes (22 remain after removing close relatives) and 664 ancient genomes, for K = 2…10 clusters, where K is the number of putative admixture sources. We display the results for K = 3, which is the K with the second lowest cross validation errors (only slightly higher than K = 2; see Additional file 1: Supplementary Figure S34). The setting of K = 3 is at the same time the lowest K that allows to differentiate among genetic clusters associated with three key European ancestral components, namely, Western hunter-gatherers (WHGs), early European farmers (EEFs), and Caucasus hunter-gatherers (CHGs), shown in red, orange, and blue color, respectively, in Fig. 3. The majority (18 out of 22) of the newly generated genomes have ancestry proportions that resemble those of previously published LBA and IA genomes from mainland Greece and the Peloponnese, whereas the remaining ones (Roman Tenea) resemble that of Roman times Greece and Italy.

We performed ancestry modeling on a per-group and per-individual basis, using ADMIXTOOLS2 [26] and rotating qpAdm using three distinct sets of putative source populations ("Ultimate", "More_proximate", and "Most_proximate"; see Additional file 1: Section 3.5.9 for details), and for a given target population/individual we tested from one up to four possible sources (1-way to 4-way admixture). The "Ultimate" set of sources include a, *common to all tested targets*, set of individuals assembled into groups that may be considered a distal ancestor to them, whereas the same applies for the "Most_proximate" set of sources, albeit the groups are dated more recent, and may have a less distal ancestry to the targets. Similarly, the "Most_proximate" set of sources include groups of individuals that are, spatiotemporally, as close as possible to the target, and by definition, each target has *a unique, target-specific* set of individuals and assembled groups. The results indicate that when using the Ultimate set of sources, Epipaleolithic/Neolithic Anatolia appears as the more frequent major source to the ancient Ammotopos, Amvrakia, and Tenea individuals (Additional file 1: Supplementary Figure S36). Similarly, when using the "More_proximate" set of sources, all of our newly sequenced individuals have potential source populations closely related to prehistoric groups from the southern Balkans (Additional file 1: Supplementary Figure S37), particularly those from the area of present-day Greece (see Additional file 1: Section 3.5.9 for a more detailed presentation).

Genetic discontinuity of Archaic Amvrakia from local prehistoric Greek populations?

Due to limitations in sample availability, we used the LBA Ammotopos individuals (1275–1125 BCE) as proxy for the local population inhabiting the Archaic Amvrakia area, before the foundation of Amvrakia. In PC space, we find that the two LBA Ammotopos individuals are projected close to other LBA Greek individuals (1700–1050 BCE) and in close proximity to earlier EBA to MLBA individuals from the South Balkans (Albania, North Macedonia, and Bulgaria) (Fig. 2). These observations are also supported by ADMIXTURE results (Fig. 3), where the two Ammotopos individuals share analogous proportions of the genetic components that are maximized in WHGs, CHGs, and EEFs (red, blue, and orange in Fig. 3, respectively) with LBA individuals from mainland Greece and the Peloponnese. Ammotopos inferred to be in rotating qpAdm using its "Most_proximate" set of sources as a two-way admixture between MBA mainland Greece (2100–1600 BCE; 56%) and LBA Crete (1700–1250 BCE; ~ 44%); in three-way admixture MBA Sardinia is also inferred as an additional source although with negligible contribution (0.004%)(Fig. 5A and Additional file 1: Supplementary Figure S38A). The

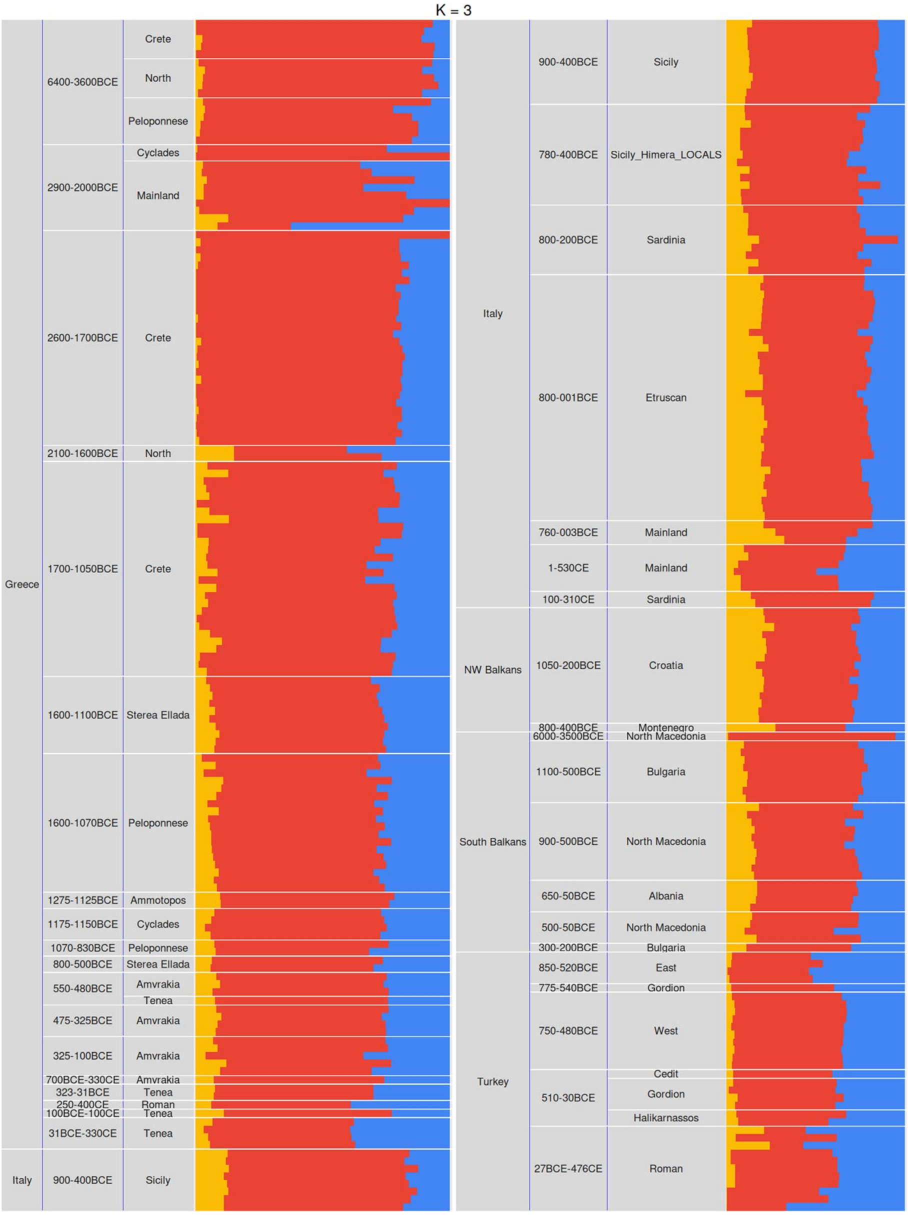

Fig. 3 Unsupervised ADMIXTURE analysis of 22 newly generated ancient genomes of the present study (four individuals were excluded due to genetic kinship) and 664 published ancient genomes ("Dataset 1" without six Upper Paleolithic Moroccans) using K = 3, a Linkage Disequilibrium (LD) r^2 threshold of 0.80, and allele missingness threshold of 40%. A setting of K = 3 differentiates genetic clusters associated with three key European ancestral components, namely, Western hunter-gatherers (WHGs), early European farmers (EEFs), and Neolithic Iran/Caucasus hunter-gatherers (CHGs), depicted with orange, red, and blue color, respectively. The analysis was based on 343,068 genomic sites of the 1240 K list. Our plot only shows individuals from the current geographical area of Greece (Neolithic period to Roman times), as well as historical individuals (Iron Age to Roman times) from adjacent areas (Italy, Balkans, and Türkiye). The full plot is available in Additional file 1: Supplementary Figure S35B, as well as at Zenodo (https://doi.org/10.5281/zenodo.10848927)

LBA Ammotopos genomes show the closest genetic distance, as estimated by Outgroup f3 tests when using the "Most_proximate" to LBA Ammotopos set of sources, with earlier MBA and LBA individuals from Italy, Crete, and mainland Greece, and to a lesser degree with earlier LBA individuals from the Peloponnese and MBA individuals from the western Balkans (Additional file 1: Supplementary Figure S39A-B).

In the PCA, the two LBA Ammotopos individuals are only placed relatively close to one out of the three Archaic Amvrakia individuals (Amv_Epi_Arch_1). The ADMIXTURE results and the genetic components maximized in WHGs, CHGs, and EEFs (red, blue, and orange in Fig. 3, respectively), support a common genetic background between Ammotopos and Archaic Amvrakia (at least for two out of the three Amvrakians). However, LBA Ammotopos (as well as any LBA population from Mainland Greece or IA populations from western or northern Balkans) is not inferred as a potential source for Archaic Amvrakia when using the "Most_proximate" to Archaic Amvrakia set of sources in qpAdm analyses (Fig. 5 and Additional file 1: Supplementary Figure S38B). Moreover, no shared Identity By Descent (IBD) fragments (Fig. 4) can be observed between them either. This appears plausible as they are separated by almost 550–750 years. Finally, we do not observe any common mtDNA haplogroups between these two groups.

Overall, based on the aforementioned results, Archaic Amvrakia appears to not have a genetic continuity from an LBA source within the area of present-day Greece, including LBA Ammotopos or a similar genetic pool. The same applies for IA central Greece (Sterea Ellada). However, we cannot speculate if this is the case for the IA populations of western Greece or Albania, too, due to lack of available genomic data.

Genetic affinities between Amvrakia and its metropolis during the Archaic times foundation

Our Archaic Amvrakia and Tenea individuals (550–480 BCE) can be considered as the closest representatives (subset) of the populations involved in the foundation of Amvrakia during the last half of the seventh century BCE. We found that the sampled sixth century BCE individuals from Amvrakia and Tenea, share strong genetic links of recent ancestry, albeit not distant genetic kinship, as demonstrated by the shared IBD segments (yellow, green, petrol, and blue colors in Fig. 4B; bottom-left plot). These shared IBD segments with a length of 8–12 cM indicate a shared ancestry several generations ago, perhaps when the ancestors of these individuals were part of the same local population in the Corinthian territory. If we assume a human generation length of 27 years [27] and that the probability of an IBD segment of length l cM persisting for t generations rapidly decreases as $\exp(-t \times l/50)$ according to Ringbauer et al. [28] (50 denotes the distance in cM of two independent loci), then, a 8–12 cM range of segments persists, on average, for approximately 110–170 years. This coincides well with the historically documented Amvrakia foundation time, about 1–1.5 centuries prior to the estimated age of the Archaic individuals. The Archaic Amvrakia and Archaic Tenea populations display analogous proportions of the genetic components that are maximized in WHGs, CHGs, and EEFs based on the ADMIXTURE analysis (red, blue, and orange in Fig. 3, respectively). When using Archaic Tenea as one of the sources and additional sources from its "Most_proximate" set of sources in qpAdm analyses, Archaic Amvrakia is either inferred to be a non-admixed descendant population of either Archaic Tenea or IA Peloponnese (includes two individuals, one from Nestor Palace near Pylos and one from Tiryns near Tenea), or a two-way admixture between Archaic Tenea (97%) as major source and IA Sardinia (3%) as a minor source; IA Egypt is also inferred as a potential minor source,

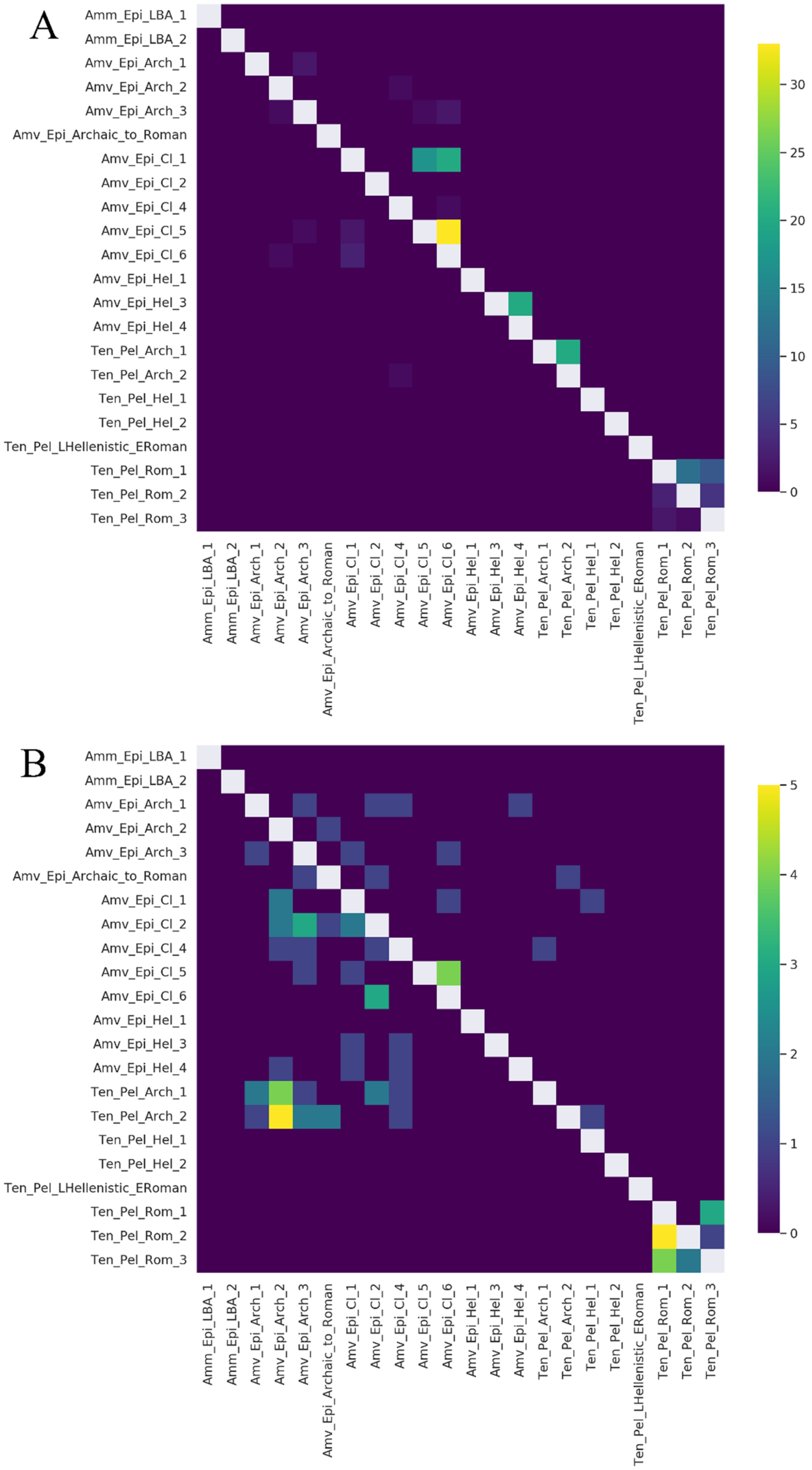

Fig. 4 The number of shared IBDs for our newly sequenced WGS data with at least 0.25 × coverage (imputed 1240 K list of genomic sites) in a pairwise fashion within the > 20 cM (**A**; upper right), 16–20 cM (**A**; lower left), 12–16 cM (**B**; upper right), and 8–12 (**B**; lower left) length bins

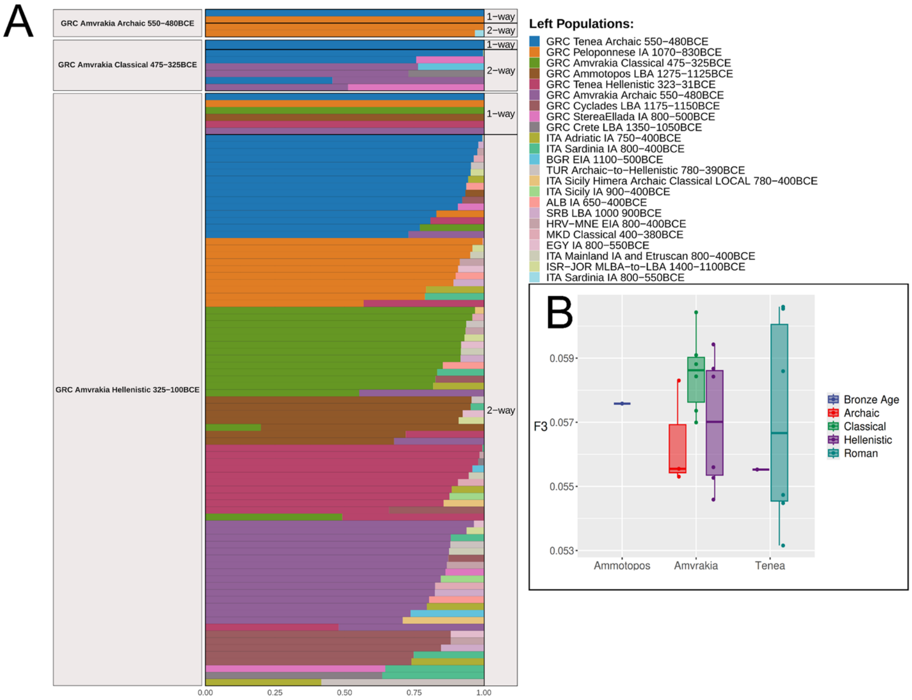

Fig. 5 A Horizontal stacked bar chart of qpAdm analysis results with Amvrakia (Archaic/Classical/Hellenistic) as target population. Only the feasible models with a p-value > 0.05 (accepted models) are shown with the points representing the populations involved and the color indicating their admixture proportions. The models were sorted based on the number of involved sources (1–4). **B** Boxplot of intrapopulation similarity levels estimated by calculating pairwise Outgroup f3 values within each population and within a given period

although with negligible contribution (0.1%) (Fig. 5A and Additional file 1: Supplementary Figure S38B). Compared to other populations, Archaic Amvrakia and Archaic Tenea are shown to be highly related based on the genetic distances in Outgroup f3 analyses, when calculated either by using the "Most_proximate" to Archaic Amvrakia set of sources (Additional file 1: Supplementary Figures S39C-D) or by using the "Most_proximate" to Archaic Tenea set of sources (Additional file 1: Supplementary Figures S39I-J). Finally, as an additional evidence of their common genetic origin, the two groups share a common mtDNA haplogroup (T1a4) represented by Amv_Epi_Arch_2 and Tenea_Pel_Arch_1.

On the other hand, in the PC space, the Archaic Amvrakia and Archaic Tenea are placed in distinct positions, mostly due to the position covered by two of the three Amvrakia Archaic individuals (Fig. 2). The two Archaic Tenea and one of the three Archaic Amvrakia individuals (Amv_Epi_Arch_1) are placed among the earlier LBA Greek individuals (1700–1050 BCE). The remaining Archaic Amvrakia individuals are more differentiated towards the upper left of the PC space and the Levant Neolithic—BA-Yamnaya-like axis. One of them (Amv_Epi_Arch_3), which is the closest to the Greek LBA cluster, overlaps with an Etruscan individual from Italy (800–001 BCE) and is surrounded by Greek genomes mostly from the EBA_MBA (2900–1700 BCE) and the LBA (1700–1050 BCE). The other Archaic Amvrakia individual (Amv_Epi_Arch_2) is placed even further away from the Greek LBA cluster and in close proximity to EBA_MBA

(2900–1700 BCE) Greece and a few Greek Neolithic (6400–3600 BCE) and Anatolian Neolithic (9000–5600 BCE) individuals.

Overall, based on PCA, Outgroup f3, qpAdm, and more importantly, on the IBD analyses, Amvrakia and Tenea appear to have a common past, just prior to the foundation of Amvrakia. Interestingly, only one out of the three Amvrakia individuals appears (by visual inspection of the PCA plot) to have a genetic affinity with the Tenean individuals, despite the fact that two out of the three Archaic Amvrakia individuals share IBDs exceeding 20 cM. This indicates that they had a common ancestor several generations ago. The different localization of the other two individuals from Archaic Amvrakia on the PCA plot, is not due to PCA instability as all three individuals exhibit Pandora Stability support values between 0.80 and 0.86. Could, however, be a methodological artifact (batch effect), as the two aforementioned individuals are the only ones, for whom their DNA was not treated enzymatically to reduce *post-mortem* deamination damage in the sequences. Indeed, when performing an additional PCA (only projecting the newly generated genomes onto modern ones) using only transversions (see plot at Zenodo: https://doi.org/10.5281/zenodo.10848927) and thus removing the effect of possible deamination and treatment biases, these two Archaic Amvrakia individuals are grouped within the first cluster that includes the third -UDG-treated- Archaic Amvrakia individual.

Evolution of the Amvrakia population during the Classical and Hellenistic times

The Classical Amvrakia individuals appear to form a homologous cluster in the PC space, with a comparatively low variability among the individuals, placed in between the LBA Ammotopos and one of the Archaic Amvrakia individuals (Fig. 2). The high similarity among the Classical Amvrakia individuals is apparent also a) when comparing the proportions of the genetic components maximized in WHGs, CHGs, and EEFs in the ADMIXTURE analysis (red, blue, and orange in Fig. 3, respectively), b) by considering the shared IBD segments among the Classical Amvrakia individuals (Fig. 4A), and by the within-population, pairwise Outgroup f3 values (Fig. 5B). Further, the homozygosity analyses revealed the presence of “long ROH” ($sROH_{>20}$ above 50 cM; Fig. 6), as termed by [29] and indicating increased inbreeding levels, only during the Classical period in the Amvrakia population, although a degree of consanguinity practices is indicated by the presence of shared $sROHs_{12-20}$ for the earlier Archaic Amvrakia population, too (Fig. 6). The IBD analyses also yielded distant kin relationships (several generations apart) between Archaic and Classical Amvrakia individuals (Amv_Epi_Arch_3 with Amv_Epi_Cl_−5 and −6; Amv_Epi_Arch_2 with Amv_Epi_Cl_4) (Fig. 4A). Classical Amvrakia inferred to be in rotating qpAdm using its “Most_proximate” set of sources: either a non-admixed descendant of Archaic Tenea or b) a two-way admixture between either the -almost equally contributed- pairs of Archaic Tenea-Archaic Amvrakia, and Archaic Amvrakia-IA central Greece, or a pair with one source being the major contributor and the other source being the minor contributor (i.e. the Archaic Tenea-IA central Greece pair and the Archaic Amvrakia -IA Bulgaria/LBA Crete pairs) c) a three-, or four-way admixture, in which Archaic Amvrakia is always present (either a an equal contributor or as a major one) (Fig. 5A and Additional file 1: Supplementary Figure S38C). Classical Amvrakia shows the closest Outgroup f3 genetic distances, when calculated by using the “Most_proximate” to Classical Amvrakia set of sources, with preceding Greek

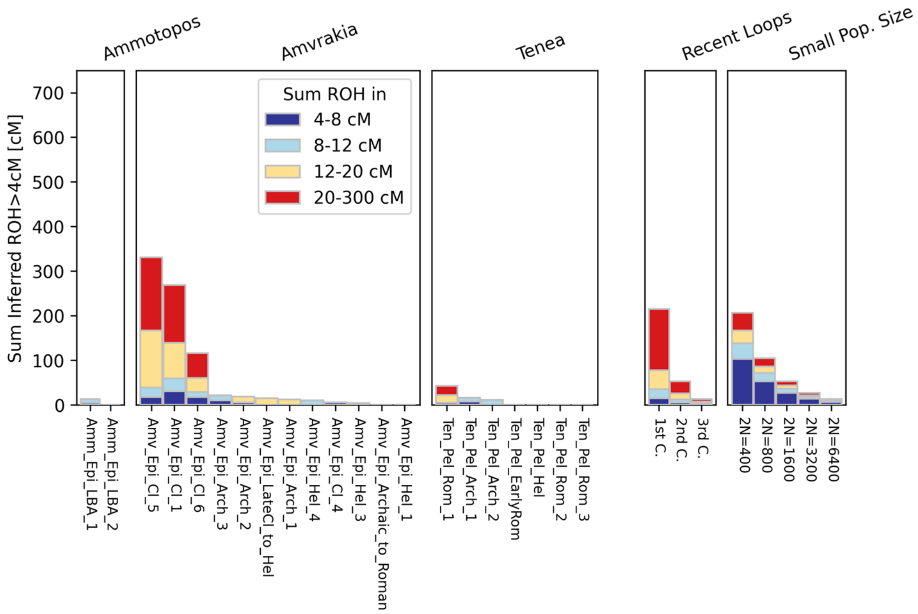

Fig. 6 Sums of inferred runs of homozygosity (sROH) per individual in four length bins (4–8 cM, 8–12 cM, 12–20 cM, and above 20 cM). All individuals had more than 300,000 genomic sites covered by the 1240 K list. We also show the expected ROH for offspring of close kin (recent loops) or in small populations as provided by hapROH

populations, including Archaic Amvrakia and LBA Ammotopos (Additional file 1: Supplementary Figures S39E-F). The closer genetic proximity between Classical Amvrakia and Archaic Amvrakia, compared to Archaic Tenea, is also worth noting when examining Outgroup f3 genetic distances. Overall, a genetic continuity from the Archaic times to the Classical times is suggested for Amvrakia.

On the other hand, and when considered as a group, the Hellenistic Amvrakia individuals cover a larger area of the PC space than earlier Classical ones (Fig. 2). This might be due to the low Pandora Stability support values (0.65 and 0.53, respectively) estimated for two out of the four Hellenistic Amvrakia individuals, albeit the Hellenistic Amvrakia individual that is placed far away from the rest (Amv_Epi_Hel_3) has good stability support. More importantly, the Hellenistic Amvrakia individuals are also characterized by slightly different proportions of genetic components maximized in WHGs, CHGs, and EEFs in the unsupervised ADMIXTURE analysis (red, blue, and orange in Fig. 3, respectively), both, with respect to each other, as well as with respect to Classical Amvrakia individuals, and compared to Classical Amvrakia a decreased mean, within-population, pairwise Outgroup f3 value (Fig. 5B). Notably, according to the Outgroup f3 genetic distances (Additional file 1: Supplementary Figure S42G-H), Hellenistic Amvrakia individuals retain strong genetic links with the preceding Classical Amvrakia, as also manifested by the shared IBDs between two pairs of individuals from these periods (Fig. 4B). Note that IBD sharing is *not* observed between Hellenistic Amvrakia and Hellenistic Tenea. We also observe a high Outgroup f3 measured genetic affinity with the Classical population living in the geographical area of present-day North Macedonia, albeit their ADMIXTURE proportions are slightly different (Fig. 3). Given the unavailability of an Ancient Macedonian genome from Hellenistic times, the latter observation may be considered as testimony of genetic affinity between Ancient Macedonian territory and Amvrakia, corresponding to the creation of connections during the occupation of Amvrakia by the Macedonians or its subsequent rise as a capital of the Epirus Kingdom [30]. Hellenistic Amvrakia inferred to be in rotating qpAdm using its "Most_proximate" set of sources: a non-admixed descendant of a single source (i.e., Archaic Amvrakia, Classical Amvrakia, LBA Ammotopos, Hellenistic Tenea, Archaic Tenea, IA Peloponnese) or as a two-way admixture with a major source being one of the aforementioned populations; in three-way and four-way admixture models, several other sources with lower contribution appear (Fig. 5 and Additional file 1: Supplementary Figure S38D).

Overall, only a slight population differentiation is apparent in Amvrakia between the Archaic period and the subsequent Classical and Hellenistic periods; thus, genetic continuity over time is observed.

Evolution of the Tenean population from Archaic to Roman times

As mentioned above, Archaic Tenea (or at least a closely related population) contributed genetically to the foundation of Amvrakia, and has a close genetic proximity to Archaic Amvrakia, as well as to other preceding LBA and IA Mainland Greek and Peloponnese populations (Additional file 1: Supplementary Figures S39I-J). Archaic Tenea inferred to be in rotating qpAdm using its "Most_proximate" set of sources: a non-admixed descendant of IA/LBA single sources (IA Peloponnese, LBA Sterea Ellada, LBA Cyclades) or a two-, three-, four-way admixture among, one of the above (plus LBA Crete) as, frequently, the major source and one (or more) additional minor source(s) from Eastern Mediterranean and Italy (Fig. 5 and Additional file 1: Supplementary Figure S38E). The above shows that Archaic Tenea has a LBA/IA southern Greek genetic ancestry.

Compared to Archaic Tenea, the subsequent Hellenistic Tenea has also its closest Outgroup f3 genetic distances, when calculated by using the "Most_proximate" sources to Hellenistic Tenea, with preceding Greek populations, including Archaic Tenea, indicating a degree of local continuity (Additional file 1: Supplementary Figures S39M-N). In contrast to the Archaic Tenea individuals, Hellenistic Tenea individuals are not placed very close to each other in the PC space (Fig. 2), although in the unsupervised ADMIXTURE analysis, the Hellenistic Tenea individuals are characterized by homogeneous proportions of the genetic components maximized in WHGs, CHGs, and EEFs (red, blue, and orange in Fig. 3, respectively). In the same plot (Fig. 3), when comparing the Archaic and the Hellenistic Tenea, the latter shows a lower EEFs proportion, but a higher CHGs proportion. Finally, Hellenistic Tenea is inferred to be in rotating qpAdm using its "Most_proximate" set of sources: a direct descendant of either Archaic Tenea or Hellenistic Amvrakia, or as a two-way admixture between a major source (Archaic Tenea, Archaic Amvrakia, Classical Amvrakia, Hellenistic Amvrakia, LBA Ammotopos) and a minor source (various populations mostly from the Eastern Mediterranean, with BA Levant and Anatolia having frequently a larger contribution compared to other); in three-way and four-way admixture models, several other sources with lower contribution appear (Fig. 5 and Additional file 1: Supplementary Figure S38F).

One of Tenea individuals is dated in the transitional phase of the Late Hellenistic period to the Early Roman times, hence it was not grouped within either the Hellenistic or the Roman Tenea. In the PCA, this individual is placed close to Classical and Hellenistic Amvrakia individuals, as well as close to Archaic and Hellenistic Tenea individuals (Fig. 2). In the unsupervised ADMIXTURE analysis, this individual has similar proportions of the genetic components maximized in WHGs, CHGs, and EEFs (red, blue, and orange in Fig. 3, respectively) with the earlier dated Archaic, Classical, and Hellenistic individuals from Amvrakia and Tenea. It also shows the closest Outgroup f3 genetic distances, when calculated by using its "Most_proximate" set of sources, with preceding and/or contemporary to it Greek and south Balkan populations rather than NW Balkan, Anatolian, Italian, and Levant populations (Additional file 1: Supplementary Figures S39K-L). It does not share large IBDs with any other newly sequenced individual, though, indicating that it is not sharing a relatively recent common ancestor with any of them.

We found that the Roman Tenea individuals form a cluster on the PCA plot that is distinct from most of the preceding Archaic, Classical, and Hellenistic Amvrakia and Tenea individuals. More specifically, they are projected among a) contemporary to them Roman individuals from Türkiye, Italy, and Greece, b) earlier prehistorical (EBA, MBA, and LBA) Greek and Anatolian individuals, and c) historical (Archaic and Hellenistic) Anatolian genomes (Fig. 2). Roman Tenea individuals are homogeneous regarding the proportions of the unsupervised ADMIXTURE genetic components, which are maximized in WHGs, EEFs, and CHGs (red, blue, and orange in Fig. 3, respectively). As shown in Fig. 3, these components appear in analogous proportions in other published Roman genomes from Greece and mainland Italy (Imperial Roman times). According to the Outgroup f3 analyses using the "Most_proximate" sources to Roman Tenea, earlier LBA and IA Greek populations are among the most closely related to the Roman Tenea ones, together with the Late Hellenistic—Early Roman Tenea individual, in contrast to earlier Hellenistic populations from Greece and Türkiye or to preceding Tenea time periods (Additional file 1: Supplementary Figures S39O-P**)**. Roman Tenea is inferred to be in rotating qpAdm using its "Most_proximate" to Roman Tenea set of sources: a two-way admixture between BA Levant and either Hellenistic Tenea or Hellenistic Amvrakia; in three-way admixture model IA Egypt is added as a potential third source, whereas in four-way admixture LBA Ammotopos is included and the Hellenistic sources are replaced with Archaic Amvrakia (Fig. 5 and Additional file 1: Supplementary Figure S38G). The above shows that Roman Tenea has an eastern influence, but also a local continuity. Noteworthily, according to the shared IBDs analyses, that we conducted on three out of the four Roman Tenea individuals (Ten_Pel_Rom_−1, −2, and −3; Fig. 4) due to coverage issues, they exhibit an intermediate genetic kinship relationship that is a few generations apart, albeit exceeding the 3rd degree as they were not inferred as being closely related (Additional file 1: Section 3.5.3). In addition, these three individuals have the same matrilineality, as they belong to the same mtDNA haplogroup (N1a1a + 152 or N1a1a2 depending on the software used) in contrast to the fourth individual, whereas two of these aforementioned three male individuals have distinct Y-chromosome haplogroups (Additional file 4). Given that these three individuals were children with intermediate genetic relatedness, same matrilineality, and different patrilineality, we can assume that they were members of an extensive family that also displayed a degree of matrilocality.

Phenotypic and microbial metagenomic insights on ancient Greek historical populations

We estimated eye color, skin color, and hair shade for all individuals. Hair color was estimated for 19 out of 26 individuals due to coverage (Additional file 6). All newly sequenced individuals from a) LBA Ammotopos, b) Archaic, Amvrakia, and Hellenistic Amvrakia, and c) Archaic, Hellenistic and Roman Tenea showed the highest probability for brown eyes (average p-value: 0.95, 95% CI: 0.92–0.98). Most individuals likely had an intermediate skin tone (average p-value: 0.64, 95% CI: 0.58–0.70), whereas three of them had a darker skin color (two from Classical Amvrakia and one from Roman Tenea). The individuals from Classical Amvrakia showed the highest probability for dark skin (~ 0.93) and dark to black (note that our newly sequenced individuals are not of African genetic origin as shown above) skin color (~ 0.50) categories, respectively. The individual from Roman Tenea had a notable probability for dark skin (~ 0.58). Similarly, most individuals likely had brown hair (average p-value: 0.62, 95% CI: 0.59–0.65) with a dark shade (average p-value: 0.80, 95% CI: 0.74–0.86). Notably, the Late Hellenistic—Early Roman individual from Tenea still exhibited a high probability for red hair (~ 0.64). Among the ancient individuals analyzed so far, only four have shown a high probability of having red hair. Three of these cases were located in central and northern Europe, specifically in present-day Hungary and Latvia, dating between 1500 and 4000 years BP [31]. The sole case in southern Europe, dating to approximately 2500 years BP, was discovered in the Bezdanjača cave in present-day Croatia [31]. Overall, these results are in line with previously published archaeogenomics results, stating that in antiquity, darker skin tones (most often associated with the "Intermediate" skin category in the HIrisPlex-S model) were typically found in southern Europe, whereas lighter skin tones were more prevalent in northern Europe [31]. In addition, we examined the *TYR* variant rs1042602, which has been associated with the absence of freckles [32, 33]. Among the 26 individuals analyzed, eight were homozygous for the allele linked to absence of freckles, 13 were heterozygous, and five did not carry the allele.

Regarding lactase persistence, none of the individuals (for whom the specific SNPs were covered, 14/26; Additional file 6) were found to be lactose tolerant, even the more recent ones, suggesting a different evolutionary history for this phenotype in the Greek region compared to Central Europe. In previous studies on Greece, lactose tolerance-associated alleles were found to be virtually absent in the Aegean's first Neolithic farmers [34–36] and remained so until the Bronze Age [35]. Therefore, our results further indicate the absence or at least the low frequency of the lactase persistence phenotype in ancient Greece. In Central Europe however, lactose tolerance was detected at low, but noticeable frequencies (~ 7%) as early as ~ 5000 BCE, with strong selection pressures continuing over the last 3000 years from around 1500 BCE onwards [37].

Regarding sensitivity to fats (15/26 individuals covered the specific SNP), as well as the muscle contraction type (15/26 individuals covered the specific SNP) and muscle performance (11/26 individuals covered the specific SNP), seven individuals showed a moderately increased sensitivity to fats, eight individuals had an *ACTN3* genotype associated with improved muscle performance typically seen in sprinters, whereas seven individuals likely had impaired muscle performance. Lastly, five individuals had higher muscle strength associated with the *ACVR1B* gene (Additional file 6). The *ACTN3* gene has been previously studied due to its potential influence by the cultural transition from hunter-gatherer to farming societies [38]. Although some results suggest positive selection acting on this gene (particularly in Europe), the evidence remains inconclusive [39].

Regarding beta thalassemia (and malaria resistance), the most common genetic disorder in modern Greece [40, 41], none of the newly sequenced Greek individuals were found to carry associated alleles on the 29 SNPs examined (Additional file 6; only one individual had zero SNPs coverage). Despite its high modern day frequency, previous aDNA studies investigating beta thalassemia variants in Greece have not identified any alleles associated with the disorder either [34, 42].

No microbial DNA belonging to ancient systemic pathogens was detected in any of the samples examined (Additional file 1). Given that most of our bone samples were petrous bones, this is not surprising as this bone material is not well-suited for this purpose (e.g. [43]), despite its utility in human archaeogenomics analyses due to its high human endogenous DNA content. In dental samples, however, we did observe DNA traces belonging to ancient human oral bacteria, including those associated with severe forms of periodontal disease, such as *Porphyromonas gingivalis* and *Tannerella forsythia*.

Discussion

Insights in the genetic profile of historical Greece

Our study is among the first to produce whole-genome sequencing (WGS) archaeogenomic data -and one of the earliest when considering non-targeted genome-wide SNP approaches- from individuals dating to the historical periods of modern-day Greece, specifically from the Archaic to Roman eras. By assembling genomes from these previously unsampled periods, we can compare them with earlier prehistoric genetic data from the Eastern Mediterranean, gain insights into their phenotypic traits, and identify traces of ancient DNA from associated commensal or pathogenic microbes.

The consensus of our findings (PCA, ADMIXTURE, qpAdm using the “Most_Proximate” set of sources) shows that the Amvrakia and Tenea individuals can be considered as descendants of the LBA and IA populations of the southern Balkans, especially the area of present-day Greece. In addition, the Roman Tenea individuals appear to have an additional minor contribution from the east, represented by BA Levant and IA Egypt in the “Most_proximate” qpAdm analysis. Overall, a local genetic continuity is suggested from the LBA/IA Greece to the Archaic, Classical, and Hellenistic Greece, as well as in a lower degree to Roman Greece, albeit for the latter the spatial sampling is inadequate to justify such a generalization.

Regarding their external phenotypes, our newly sequenced individuals most likely had brown eyes, an intermediate or a darker skin tone, and brown hair with a dark shade, similar to the preceding LBA and IA individuals from Greece [21, 22, 44, 45]. While the phenotypic results are intriguing, aligning them with artistic representations from the focal areas should be conducted with caution. Artistic depictions of humans from the relevant regions are limited, and in the rare cases where they do exist, they often reflect symbolic or idealized imagery, rather than realistic portrayals. For example, in Amvrakia, a mosaic composed of white and black pebbles from the Small Theater depicts mythological scenes featuring human figures (young Eros). The use of white pebbles to suggest fair skin tones emphasizes the predominantly symbolic and narrative expression as opposed to physical realism. Analogously, in Tenea, a rare example of monumental funerary painting from the early sixth century BCE also depicts mythological themes without the inclusion of any human figures. These artistic works, while culturally significant, do not offer reliable evidence for physical appearance, as they prioritize imaginative and symbolic representations over realism. Additionally, there is almost no surviving sculpture or clay modeling from the area retaining pigment traces that would be sufficient for a phenotypic analysis. For the above reasons, direct correlations between our phenotypic findings and artistic documentation are unfortunately not feasible.

Regarding the other phenotypes examined, they display an intermediate frequency in fats sensitivity and muscle-related traits, a low frequency of having freckles, as well as no occurrence of lactase persistence or Beta thalassemia. Finally, no systematic pathogen DNA was found in any of the individuals, albeit we detected taxa associated with severe forms of periodontal disease.

Manifestation of the genetic links between Amvrakia and its metropolis and the contribution of the locals

The ancient Greeks employed the term "apoikia" (*Αποικία*), best translated as "home away from home", to highlight the separation and/or connection between the metropolis and the new "oikos" (see Additional file 1: Section 1.1 for definitions of oikos, apoikia, metropolis, polis, kome) [46]. According to the founding myth, people from the metropolis were participating in the foundation of an apoikia; a process that could have had occurred in the form of either a single or multiple migration (translocation) events, at various points in time and with a plethora of socioeconomic (e.g. population increase, lack of farmland, better life opportunities due to competition) and political (e.g. political exiles) drivers and characteristics (e.g. organized military expedition, male-oriented) [47, 48]. For instance, in the case of Amvrakia, the Corinthians had already established an "Emporion" (trading post) prior to founding Amvrakia [16]. Emporia, however, were not characterized by the permanent translocation of a group(s) of people in contrast to an apoikia that implies permanent settlement to the new city [49, 50]. Admittedly, in archaeology there is a clear cultural connection between the apoikia of Amvrakia and the metropolis of Corinth [16]. In Greek literature, there are references to the relocation of groups of people, such as the oracle tablets from Dodona asking the god for guidance on whether it was a wise decision to move to Amvrakia [51]. However, there is no direct biological evidence, though not disputed either, that people migrated *en masse* and to what extent this had an impact on the local population (that had developed by that point).

Although the presence of imported Corinthian ceramics indicates cultural interaction and exchange, such consuming patterns also reflect broader developments in production and trade networks, rather than direct evidence for colonization. Since material culture is influenced by multiple factors beyond colonization, it was not considered as primary evidence in this study. Accordingly, imported grave goods were not employed as a basis for interpreting the colonization of Amvrakia. In the present study, our primary research goal was to identify genetic affinities and study the consequences of Corinthian colonization in the demography of the population of Amvrakia. Overall, Amvrakia and Tenea seem to share a common history just before the establishment of Amvrakia, based on analyses such as PCA, Outgroup f3, qpAdm, and especially IBD (see main figures). Two of the three Archaic Amvrakia individuals share multiple IBD segments (8–12 cM) with the two Archaic Tenea individuals, indicating a common ancestor several generations back, to a date coinciding with the colonization period. These observations constitute direct genetic evidence of the affinity that the Amvrakia has with its metropolis during its foundation period of Amvrakia and its early years, supporting the scenario that Corinth contributed, both culturally and genetically, during the foundation of Amvrakia. Shared IBD segments in the 8–16 cM range suggest relatively recent shared ancestry. These segments typically persist for only a few tens of generations due to rapid breakdown by recombination. Therefore, while we acknowledge that third-source ancestry is possible (although not backed up by the literature), the presence of these long segments suggests that the shared ancestry between the groups we compare is likely to reflect more recent and potentially direct contact, rather than deeper shared ancestry from ancient population events. This is corroborated by the outgroup f3 statistic which indicates that Archaic Amvrakia and Archaic Tenea are, on average, genetically closer to each other than to any preceding IA or LBA population of Greece or neighboring area. Analogously, a lack of shared IBD does not exclude the existence of genetic affinities because limited sample sizes or historically large population sizes may obscure IBD signals. However, there may also exist a third source that independently mixes with the others which results in the populations to appear more distant (e.g. [27]). Overall, given the extensive historical (written sources) and archaeological evidence of Amvrakia being a colony of Corinth, the fact that we find such a genetic connection is most parsimoniously explained by a movement of people from the area of Corinth to the area of Amvrakia. There is no archaeological or literary evidence of either a massive migration of Amvrakians moving into Tenea, or a third population contributing to both of them.

One may consider that Archaic Tenea constitute a suboptimal population to be used as representative of the Corinthian genetic pool, given the lack of genomes from the polis of Corinth per se. Tenea was a “kome” (politically may be a subdivision of a larger polis) of Corinth, belongs to the region of Corinthia, and has participated in the Corinthian colonization efforts (records survive only for Syracuse). Therefore, while there is no ancient text or other source or inscriptions indicating that the people of Tenea were actively involved in the colonization process of Amvrakia, we cannot exclude the presence of individuals from Tenea in the foundation of Amvrakia either. Indeed, the elevated shared IBDs (Fig. 4) between Amvrakia and Tenea constitute evidence that closely related individuals to the Tenea ones, may have been members of the group(s) that translocated to Amvrakia.

One of the main challenges in our study is to determine the genetic influence and contribution of the local and neighboring people of the pre-colonial area of Amvrakia, in the initial formation of Amvrakia and its population composition. Whereas Greek colonies were the meeting grounds of culturally and genetically diverse people [46], as for example has been found for Sicilian Himera [20], in the case of Amvrakia the indigenous people are expected to have similar ancestry with the newcomers. The potential recent common ancestry, coupled with the increased gene-flow that someone may expect in such a small spatial scale, and the common cultural (e.g. worship) and linguistic elements, hinder the identification of their differentiation. Indeed, we were not able to infer a local contribution from LBA Ammotopos (or other LBA population) to the genetic composition of Archaic Amvrakia. However, given that there are no available IA western Greek individuals and that LBA Ammotopos includes only two individuals we do not proceed to generalizations.

The evolution of Amvrakia and Tenea in the post-Archaic times

One important question is how much different genetically, if any, was Amvrakia, during the Classical and Hellenistic periods compared to the Archaic period, and if the genetic links between the metropolis and the colony remained the same or not during these subsequent periods. We found that during the Classical and Hellenistic periods, the population of Amvrakia seems to be only slightly differentiated genetically (during Hellenistic times) when compared to the Archaic period (according to qpAdm, IBD, Outgroup f3, ADMIXTURE), providing evidence of genetic continuity over time. Importantly, no shared IBDs are observed during Hellenistic times between the two areas, in contrast to the Archaic and Classical periods.

Evidently, in the Greek literature there are records of the dependency and close relationship between Amvrakia and Corinth during Classical times, at least in the political sense [48]. For example, Amvrakia, together with nearby sister-colonies, became an ally of Sparta during the Peloponnesian War (431–404 BCE) according to Thucydides [52, 53]. Amvrakia also joined Corinth in the anti-Spartan alliance that was formed after the Peloponnesian War and before the Corinthian War in 394 BCE [54]. On the other hand, during the Hellenistic times, there is archeological evidence that Corinth lost its influence into Amvrakia, following a general trend for the Corinthian colonies in Western Greece [55]. Importantly, at the end of the Classical times, Amvrakia came under the rule of Macedonians under Philip II (338 BCE), although it maintained a semi-autonomous status [30]. During Hellenistic times, the Macedonians ceded it to the Kingdom of Epirus. King Pyrrhus, the king of Mollosians, established it as the capital of the Epirus Kingdom in 294 BCE and Amvrakia experienced notable prosperity during the century to follow [56].

Hence, we may conclude that Amvrakia retain its genetic ancestry from the Archaic times during the subsequent Classical times, a period characterized, however, by lower diversity and population size in Amvrakia [as also manifested by the increased consanguinity practices (see ROH results; Fig. 6)]. Nonetheless, this may also be attributed to a purely culturally-related practice. Nevertheless, during Hellenistic times, although genetic continuity from Classical times is observed, a higher diversity characterizes Amvrakia, which during that time has become totally independent politically from Corinth, a fact that is also translated into the genetic level. We should note, though, that the lack of shared IBDs between Amvrakia and Hellenistic Tenea could additionally or alternatively mean a genetic change in the "pool" of Tenea. Indeed, Tenea shows also a differentiation in ADMIXTURE between Archaic and Hellenistic times, which is moderated if we include the Late Hellenistic to Early Roman times individual in the comparison.

In the case of Tenea, the most striking differentiation (see main figures with IBD, ADMIXTURE, and PCA results) happens during Roman times, during which, despite that genetic continuity is observed from the Hellenistic times, a gene flow is also inferred to had been occurred from an east source (see qpAdm and Outgroup f3 results).

Conclusions

Local genetic continuity is suggested from the LBA/IA Greece to the subsequent historical periods of Greece. Amvrakia and Tenea display strong genetic affinities indicating a recent shared genetic past, even before the foundation of Amvrakia by the Corinthians. The latter procedure is characterized by the major genetic contribution of the metropolis in the genetic pool of the newly founded apoikia of Amvrakia.

Methods

Ancient DNA laboratory work

All analytical procedures, that is sample processing, DNA extraction, and genomic library preparation were performed in the cleanroom facilities of the Ancient DNA Lab at the Institute of Molecular Biology and Biotechnology at the Foundation for Research and Technology—Hellas (IMBB-FORTH). Laboratory work details are provided in Supplementary Information (Additional file 1: Section 3.1). In brief, DNA extraction was performed using optimized protocols for ancient DNA [57–59]. Double-stranded, blunt-end libraries without pretreatment were constructed according to published protocols [60, 61] with some minor modifications (see supplement for details), and pre-screening shotgun whole genome sequencing was performed on an Illumina NextSeq500 platform. Deeper sequencing on the 26 selected samples/libraries was performed on freshly-produced, double-indexed libraries, that were partially pre-treated [62] -except for two samples- with the USER™ enzyme (New England BioLabs Inc., USA), in an Illumina Novaseq6000 platform (2 × 150 bp).

Sequence data processing and initial analyses

Data processing was performed using the ancient DNA analysis pipeline mapache v.0.3.0 [63] at three levels: (a) at the FastQ level corresponding to the sequence reads in each FastQ file, (b) at the library level, corresponding to multiple BAM files from the same (PCR amplified) library, and (c) at the level of individuals, corresponding to multiple BAM files from the same individual. Data processing details are provided in Supplementary Information (Additional file 1: Sects. 3.2). Analyses at the FastQ level included quality control, residual adapter trimming and filtering, pair-end read merging, mapping to a human reference genome (hs37d5), read group incorporation, sorting and quality filtering of mapped reads, and statistical reports. Analyses at the library level included BAM file merging (of the same indexed library) and de-duplication, post-mortem DNA damage profiling, soft-clipping of damaged bases, and statistical reports. Finally, analyses at the individual level included BAM file merging (of the same individual), local indel realignment, final BAM file generation, statistics reporting, and genetic sex inference.

Contamination was assessed by using four distinct contamination estimation approaches (see details in Additional file 1: Section 3.3); contamMix v.1.0–10 [64], schmutzi v.1.5.6 [65], ContamLD [66], and the *contamination* function of ANGSD v.0.941–6-g67b6b3b [67]. The classification to mitochondrial haplogroups was performed with HaploGrep3 v.3.3.2.1 [68] and HaploCart v.1.0 [69] and to Y-chromosome haplogroups with Yleaf v.3.1 [70] and Yhaplo v.1.1.2 [71] (see details in

Additional file 1: Section 3.4). The genetic relatedness analyses included Relationship Estimation from Ancient DNA (READ) [72] and KIN v.3.1.3 [73] (see details in Additional file 1: Section 3.5.3).

Population genomics analyses

The 26 newly whole-genome-sequenced ancient individuals were studied at the population level, both by assembling them into a distinct stand-alone dataset, but also in the context of previously published modern and ancient data as different analyses required the assembly of appropriate, distinct datasets (Additional file 1: Section 3.5.6 and Additional file 5).

For the analyses as a distinct stand-alone dataset (see details in Additional file 1: Sects. 3.5.4–5), we first performed Runs Of Homozygosity (ROHs) analysis on 1240 K pseudo-haploidised data using the hapROH v.64 [29] software and the 1000 Genomes Project as a reference panel (see details in Additional file 1: Section 3.5.4). Then, we imputed the 26 newly produced ancient genomes of this study by using the 1000 Genomes phase 3 [74] dataset as a reference and GLIMPSE v.1.1.1 [75], as well as the ATLAS pipeline v.0.9 [76] and HapMap phase II NCBI b37 genetic map [77] (see details in Additional file 1: Section 3.5.5). Finally, we performed Identity-by-Descent (IBD) segments screening using the ancIBD v0.5 tool [28] (see details in Additional file 1: Section 3.5.5).

For the analyses in the context of previously published modern and ancient data (see details in Additional file 1: Sects. 3.5.7–10), three datasets were assembled and merged with our data: "Dataset 1" that includes 663 ancient individuals with collected data over a list of ~ 1.24 million genomic sites, known as 1240 K [24], "Dataset 2" that included all the individuals of "Dataset 1" except of six Upper Paleolithic Iberomaurusian hunter-gatherers from Tafolrat, Morocco, as two-thirds of their ancestry originates from sub-Saharan Africa [78], and "Dataset 3" that includes 888 modern West Eurasian individuals genotyped on the Human Origins SNP (HO; 597,573 sites) array [24] and the data from the ancient individuals of "Dataset 1", albeit restricted to the HO sites.

PCA projection of ancient data onto modern ones (newly generated genomes and "Dataset 3") was performed with the smartpca function of EIGENSOFT v.7.2.1 [79], using default parameters and the lsqproject: YES option (see details in Additional file 1: Section 3.5.7). The stability of the PCA was assessed using Pandora v.2.0.0 [80]. Clustering of ancient genomes was performed using unsupervised ADMIXTURE v.1.3.0 [25] with K = 2, 3,…,10 after filtering the dataset (newly generated genomes and "Dataset 2") for linkage disequilibrium (LD) and allele missingness (see details in Additional file 1: Section 3.5.8).

For the F-statistics analyses, we grouped the ancient individuals (newly sequenced here and "Dataset 1") according to geographical, chronological, and cultural contexts, and performed the analysis on a per-group (closely related individuals were omitted) and per-individual basis (see details in Additional file 1: Section 3.5.9). Ancestry modeling was performed with qpAdm in a rotating fashion (when a given population is not included in the test as one of the putative source populations, then it used as a reference population) as recommended by [81], using ADMIXTOOLS2 v.2.0.0 [26] and three different sets of potential sources: a) distant genetic sources ("Ultimate") that characterize the general ancestry of ancient Western Europeans following Lazaridis et al. [21], b) spatiotemporally, more proximate sources ("More-proximate"), and c) spatiotemporally, as close as possible sources, by limiting the temporal range only to individuals dated earlier than each target, and the spatial range only to the Eastern Mediterranean and adjacent areas ("Most-proximate"). Outgroup f3 (using, separately, the modern Yoruba and Han populations as outgroups) analyses were performed with ADMIXTOOLS2. Within-population genetic similarity levels were estimated by calculating the pair-wise Outgroup f3 values within each population and within a given period.

Additional genetic analyses: phenotype estimation and microbial metagenomics

Phenotypic estimation was performed for hair, eye, and skin color prediction using HirisPlex-S [82], as well as for specific metabolic traits (lactase persistence and sensitivity to fats), human muscle characteristics (muscle contraction type and muscle performance), and the genetic disorder of beta thalassemia (resulting to malaria resistance). Details can be found in Additional file 1: Section 3.6.

Ancient microbial DNA screening analyses were performed with the v.1.0.0 aMeta [83] metagenomic pipeline (see details in Additional file 1: Section 3.7), by using the aMeta-provided, pre-built, microbial NCBI non-redundant *nucleotide* (microbial-NT) database containing records of microbial organisms, as well as a few representative eukaryots (including human).

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13059-026-03968-5.

Additional file 1. Detailed information on archaeological background, samples, methodology, and results including supplementary figures [15, 17, 18, 22, 25, 28, 34, 36, 41, 45, 46, 57, 58, 60, 68, 75, 78, 82, 87–270].

Additional file 2. Information about the individuals and the samples used in this study, including wetlab details.

Additional file 3. Sequencing and mapping statistics at the fastQ, library, and individual levels.

Additional file 4. Post mortem DNA damage profiling, contamination estimates, karyotype inference, and haplogroup assignments.

Additional file 5. Sample assignment per analysis and associated population labels.

Additional file 6. Phenotype reconstruction results.

Additional file 7. Metagenomics analysisheatmap scores.

Acknowledgements

We thank the Genomics Facility of IMBB-FORTH for the pre-screening library sequencing.

Peer review information

Andrew Cosgrove and Claudia Feng were the primary editors of this article and managed its editorial process and peer review in collaboration with the rest of the editorial team. The peer-review history is available in the online version of this article.

Authors' contributions

Nikolaos Psonis: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing—Original Draft, Writing—Review & Editing, Visualization, Project administration Eugenia Tabakaki: Conceptualization, Writing—Original Draft, Writing—Review & Editing, Project administration Despoina Vassou: Investigation, Validation, Writing—Original Draft, Writing—Review & Editing, Project administration Stefanos Papadadonakis: Formal analysis, Writing—Review & Editing, Software, Visualization Angelos Souleles: Formal analysis, Writing—Original Draft, Writing—Review & Editing, Visualization Argyro Nafplioti: Formal analysis, Investigation, Writing—Original Draft, Writing—Review & Editing Georgios Kousis Tsampazis: Writing—Review & Editing, Visualization Angeliki Papadopoulou: Writing—Review & Editing, Visualization Kiriakos Xanthopoulos: Writing—Review & Editing Panagiotis Panailidis: Writing—Review & Editing Angeliki Georgiadou: Writing—Review & Editing Dimitra Papakosta: Writing—Review & Editing Sevasti Koursioti: Writing—Review & Editing, Investigation Maria Evangelinou: Software Varvara Papadopoulou: Resources, Writing—Review & Editing Paraskevi Evageloglou: Resources, Writing—Review & Editing Elena Korka: Resources, Writing—Review & Editing Ioannis Christidis: Writing—Review & Editing Michael Ioannou: Writing—Review & Editing Theodora Kontogianni: Writing—Review & Editing Athanasios Arkoumanis: Writing—Review & Editing Alexandros Stamatakis: Resources, Writing—Review & Editing Nikos Poulakakis: Writing—Review & Editing, Supervision Christina Papageorgopoulou: Writing—Original Draft, Writing—Review & Editing, Supervision Pavlos Pavlidis: Formal analysis, Writing—Review & Editing, Software, Supervision. All authors read and approved the final manuscript.

Funding
This study was supported by the project "APOIKIA" implemented within the framework of the special actions "AQUACULTURE"—"INDUSTRIAL MATERIALS"—"OPEN INNOVATION IN CULTURE" and co-financed by the European Regional Development Fund (ERDF) of the European Union and Greek national funds through the Operational Program "Competitiveness, Entrepreneurship & Innovation (EPAnEK) of the NSRF 2014–2020 under the supervision of the General Secretariat for Research and Innovation (GSRI) of Greece (Project code: Τ6ΥΒΠ-00191). Alexis Stamatakis was funded by the European Union (EU) under Grant Agreement No 101087081 (CompBiodiv-GR).

Data availability
The genetic data in raw FastQ formatted files are accessible in NCBI Short Read Archive (SRA) under the BioProject accession PRJNA1143893 [84]. The mapache configuration (for runs 1 and 2) and samplelist files that were used in the present study, the SNPs lists (1240 K, 5 M), the assembled datasets in EIGENSTRAT format, as well as various software outputs are accessible at Zenodo (https://doi.org/10.5281/zenodo.10848927) [85]. Scripts used are available under GPL3 license in (https:/github.com/Himsself1/APOIKIA_Analysis) [86].

Declarations

Ethics approval and consent to participate
Permissions for sampling and analysis of the biological excavation findings of the present study have been acquired by the Directorate of Conservation of Ancient and Modern Monuments, Ministry of Culture, Greece, (protocol numbers ΥΠΠΟΑ/ΓΔΑΠΚ/ΔΣΑΝΜ/ΤΕΕ/Φ77/281858/183008/2818/254, ΥΠΠΟΑ/ΓΔΑΠΚ/ΔΣΑΝΜ/ΤΕΕ/Φ77/250940/175997/2927/179, ΥΠΠΟΑ/Φ77/225862, ΥΠΠΟΑ/Φ77/342765, ΥΠΠΟΑ/Φ77/225402, ΥΠΠΟΑ/80102/22–3-2022). This study has been approved by the Research Ethics committee of the Foundation for Research and Technology Hellas (FORTH; Institutional Review Board Information: IRB00014620) with protocol number 89/17–7-2020. All research was conducted in accordance with the principles of the Declaration of Helsinki. The research involved archaeological human skeletal remains and no living individuals/participants. Therefore, informed consent was not required, as the study did not recruit living human participants.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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Received: 11 September 2024 Accepted: 20 January 2026

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