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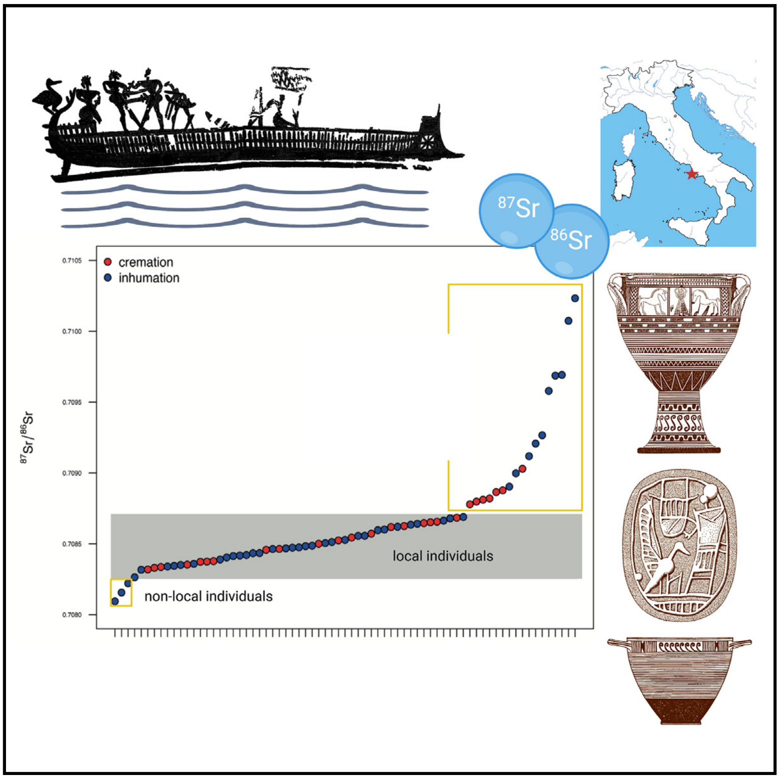
Where Typhoeus lived: $^{87}Sr/^{86}Sr$ analysis of human remains in the first Greek site in the Western Mediterranean, Pithekoussai, Italy

Graphical abstract



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In brief

Archeology; Human geography; Isotope.

Highlights

- Reconstruction of biocultural interactions in the first Greek settlement in the West
- Different patterns of geographic mobility of males, females, and across generations
- Exploring the effectiveness of isotope analyses on human remains from a volcanic environment
- Critical contribution to the debate on defining of $^{87}Sr/^{86}Sr$ baselines for mobility studies

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Article

Where Typhoeus lived: $^{87}Sr/^{86}Sr$ analysis of human remains in the first Greek site in the Western Mediterranean, Pithekoussai, Italy

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SUMMARY

The archaeological heritage of Pithekoussai offers a unique insight into the dynamics of human mobility and biocultural interactions at the dawn of the Magna Graecia during the Iron Age Mediterranean. Pithekoussai was founded by Greeks on the volcanic island of Ischia in southern Italy in the mid-eighth century BC, marking the earliest Greek settlement in the western Mediterranean. The archaeological evidence suggests that Pithekoussai was an emporium where local communities, Greeks, Phoenicians, and people from the mainland lived together and interacted. Despite the challenges posed by the active volcanic burial environment, which affected the preservation of human remains, this study successfully applied strontium isotope analysis ($^{87}Sr/^{86}Sr$) to n = 71 inhumed and cremated individuals. Integrating biogeochemistry and (bio) archaeology, this research enriches the narrative of human mobility by providing a nuanced reconstruction of the life histories of the individuals who participated in a crucial moment in Mediterranean history that shaped societies at the emergence of Magna Graecia.

INTRODUCTION

The history of Mediterranean peoples is a history of mobility and migration, of ethnic and cross-cultural interactions, and of maritime interconnections and networks.[1–6] Long-distance maritime trade and exchange of raw materials and goods took place in the Mediterranean Sea since early prehistory.[1,7–10] During the Bronze Age, the archaeological record proves the existence of significant maritime contacts between the Aegean and Mycenaean worlds and the West.[11–14] These first expeditions were followed by more intensive mobility of people during the early Iron Age until the Archaic Age. From the ninth to the sixth century BC, numerous permanent settlements and *emporia* (i.e., trading settlements) were established along the coasts of Spain, Italy and Sicily, North Africa, Asia Minor, and the Black Sea.[15,16] These settlements formed part of the "colonization movements" instigated by Greek, Phoenician, and Levantine colonists.[15,17–20] In particular, the Greek *oikistes* (i.e., "founders of a colony") played a significant role in the sophisticated and elaborate process of relocating people and customs from their *poleis* (i.e., the Greek city-state) to new overseas "colonies."[19] These latter were referred to as *apoikiai* (i.e., "a settlement away from home") in ancient Greek historiography.[15,19,21] The settlement of Greek *apoikiai* in the indigenous areas of southern Italy and Sicily resulted in the emergence of heterogeneous communities with native inhabitants, culminating in the intricate cultural and historic phenomenon traditionally referred to as Magna Graecia.[15,16,19,22,23]

The ancient site of Pithekoussai, located on the Ischia Island in the Gulf of Naples (southern Italy; see Figure 1), is the ideal case study for a deeper understanding of the early Greek movements in the Iron Age western Mediterranean.

Although their accounts are retrospective, the ancient historians Strabo (Geographia, V.4.9, first century AD) and Livy (Ab Urbe Condita, VIII.22, first century AD) remain the most significant sources for understanding the Greek settlement of Ischia. Pithekoussai was founded by Greeks from Euboea, an island located to the east of the Attic peninsula. Archaeological evidence—e.g., the presence of Phoenician and Greek inscriptions, exotic items mixed with indigenous grave goods, and different funerary customs at the Pithekoussai necropolis—supports the

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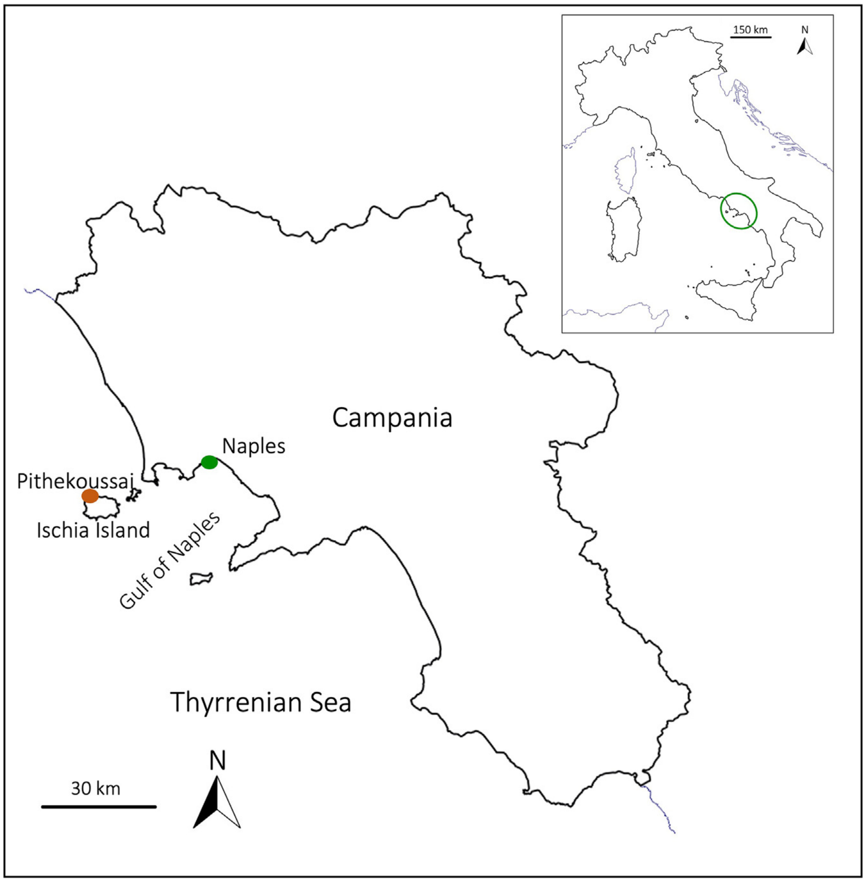

Figure 1. The geographic location of the ancient Pithekoussai (Ischia Island, Gulf of Naples, Italy)

idea that Pithekoussai was a community in which individuals with diverse cultural and ethnic identities and different geographic provenance were integrated.

According to scholars, this site functioned as an *emporium*, catalyzing contacts between Greeks, Phoenicians and indigenous from the Tyrrhenian and Adriatic regions of the Peninsula, while contributing to the spread of alphabetic writing across the West, the knowledge of Homeric poetry, and the exchange of luxury goods, social customs and practices from the Near East.[18,24–39]

Evidence of mixed cultural identities at the Pithekoussai necropolis

The Pithekoussai necropolis is one of the most important discoveries of Mediterranean archaeology. The tombs are placed in the Valley of San Montano (present-day town of Lacco Ameno), in the north-western corner of Ischia Island (Figure 1). The archaeologist Giorgio Buchner discovered the first tombs in 1952. Subsequently, from 1952 to 1982, he brought to light approximately 1,300 tombs dated from the mid-eighth century BC to the first century AD.[30,34,36] The majority of the tombs dated from the mid-eighth to the seventh century BC (see Table S1).

Pithekoussai's people adopted different funerary practices, along with significant heterogeneity in the grave good sets, which included Euboean geometric pottery, Corinthian, Levantine, Rhodian and Phoenician grave goods, exotic small finds, and artifacts from Italic and Etruscan areas.[21,24,30,34,36]

As for burial customs, three distinct practices were identified as follows: (1) secondary cremation covered by a cairn (i.e., a burial mound of stones); (2) primary inhumation in a supine or—less frequently—crouched position; (3) primary inhumation in amphora known as *enchytrismos*.[30] According to Buchner and Ridgway,[30] the adult cremation ritual was representative of the burial practice used by the Greek "colonizers" while most of the adult inhumations, particularly those without grave goods, were interpreted as a possible marker of diverse ethnicity and/or a social lower-ranking position. The inhumation was commonly in use at the indigenous contemporary necropolises of the Iron Age *fossa-kultur* people and widely attested across the Italian peninsula.[40] In particular, in some areas of the Tyrrhenian and Adriatic coasts, such as Daunia, the inhumation practice foresaw the crouched position of the body as opposed to the supine or prone position. The crouched position in some of the Pithekoussai inhumations led to the suggestion that also people from the Tyrrhenian and Adriatic indigenous centers were buried at the site. Further archaeological studies on the Pithekoussai material culture also supported this hypothesis.[33,34,36,41]

Where Typhoeus lived: The geological background of Ischia Island

Ischia is an active volcanic island situated at the north-western corner of the Gulf of Naples, in southern Italy (for a geological map of the Ischia Island, see Figure S1). The island is part of the Phlegrean Volcanic District (PVD), along with the Procida Island and Phlegrean Volcanic Fields.[42–44]

Ancient written sources (e.g., Pherecydes of Athens and Strabo) attributed the island's volcanic and seismic activities to the reckless movements of the giant Typhoeus, who was trapped in the depths of Ischia's abysses by Zeus. Condemned to suffer and unleashing his wrath in the form of earthquakes, flames and scalding water, Typhoeus became a symbol of enduring anger and instability.

The geological history of the island is characterized by a complex interplay of tectonism, volcanism, erosion, and sedimentation phenomena.[45–49] Volcanic eruptions are attested prior to 150 ka BP and continued, with long quiescence periods, until the last eruption in AD 1302. The later phase of activity—from

10 ka to AD 1302—concentrated volcanic eruptions primarily within the last 2.9 ka, exhibiting effusive, extrusive and explosive characteristics.[42] These eruptions produced diverse pyroclastic fall and flow deposits containing hydrothermally altered lithic clasts.

Presently, Ischia exhibits the highest heat flow ranging from 200 to 400 mW m-2,[50] making it one of the most thermally active regions in Italy, with the highest temperature of 250°C recorded at 1,051 m deep on the island's western side.[51] Further insights into the hydrothermal system have come from geochemical studies of thermal waters and fumaroles. These studies estimated temperatures ranging from ~200°C–370°C.[51–53]

The north-western part of the island, from the valley of San Montano to the Gulf of Lacco Ameno, is well-known for its fumaroles and thermal waters. The area between the valley of San Montano and the coast of Lacco Ameno is recognized for its great archaeological interest, as the necropolis of Pithekoussai was located there.

The discovery of this necropolis in a fumarolic-volcanic environment presented archaeologists with many difficulties in excavating the tombs. Buchner and Ridgway recorded a temperature of around 63°C at a depth of around 8 m from the surface when the tombs were opened.[30,54]

$^{87}Sr/^{86}Sr$ isotope ratio signature of the Ischia geology

$^{87}Sr/^{86}Sr$ isotope ratio analyses previously performed on the whole rock tephra samples from Molara, Vataliero, and Cava Nocelle volcanic centers, located in the south-eastern area of Ischia Island, yielded values between 0.70631 and 0.70648.[42] These values are slightly different from those reported in Civetta et al.[55] for the three volcanic centers, which ranged between 0.70620 and 0.70635.

Since its discovery, scholars have recognized the importance of studying Pithekoussai to gain a deeper understanding of the historical context of Iron Age Mediterranean societies.

Many studies have investigated the catalytic role that Pithekoussai played in the political and cultural dynamics at the dawn of Magna Graecia.[56–60] In this context, researchers have re-evaluated the interactions between indigenous inhabitants and foreign settlers, while adopting a more intricate method of interpreting archaeological findings, portraying indigenous populations as active participants rather than passive recipients of foreign political and cultural influences.[6,17,18,21,32,34,57,61–74]

Despite the extensive research conducted over the past 70 years to define this "*atypical apoikia*,"[21] there is still much to be understood regarding the social, cultural, and biological profiles of the individuals who lived in the melting pot site of Pithekoussai.

This paper provides a more in-depth and nuanced understanding of the biocultural interactions and human mobility at Pithekoussai by applying an interdisciplinary approach through archaeology, human osteology and strontium ($^{87}Sr/^{86}Sr$) isotope ratio analysis in human teeth and bone.

The main aims of this study are as follows: (1) to determine the $^{87}Sr/^{86}Sr$ isotope profile of the individuals buried at the Pithekoussai necropolis and to assess the presence of mobile and non-mobile individuals; (2) to reconstruct the variability in the funerary representation at the light of individual osteobiographies, grave goods and ritual treatment of the bodies; and (3) to characterize whether and how human mobility patterns have changed at Pithekoussai during the different chronological phases (i.e., from the mid-eighth century BC to the first century AD). Furthermore, to investigate the possible intake of marine food consumption, which may have influenced the individuals $^{87}Sr/^{86}Sr$ values, a sub-set of n = 11 individuals is sampled for stable carbon and nitrogen isotope analysis ($\delta^{13}C$, $\delta^{15}N$).

Overall, this research tests from a methodological perspective the applicability and effectiveness of biogeochemical analyses ($^{87}Sr/^{86}Sr$, $\delta^{13}C$, $\delta^{15}N$ on human dental tissues from inhumations and $^{87}Sr/^{86}Sr$ on bone tissues from cremations) in archaeological individuals that were buried in a volcanic environment. The unique location of Pithekoussai's tombs provides a valuable opportunity for a critical assessment of the constraints and potentialities of isotope methods in investigating human mobility in the past. Finally, the analytic limitations and possible solutions for characterizing a local strontium baseline in a volcanic and marine-influenced isotope environment are here discussed.

RESULTS

Biologically available strontium (BASr) at Pithekoussai

Table S2 includes the $^{87}Sr/^{86}Sr$ isotope ratio results from the Ischia environmental samples (n = 11; see STAR Methods). Shallow-rooted plant samples (n = 7) collected in a catchment area of about 10 km from the Pithekoussai necropolis (see Table S2) yield $^{87}Sr/^{86}Sr$ values ranging from 0.7074 to 0.7091 (mean = 0.7080; median = 0.7078; SD = 0.0006). The vegetation sample BASR_PTH/09, collected closer to the coastline, gave the most radiogenic value of 0.7091. This value is close to the modern seawater $^{87}Sr/^{86}Sr$ isotope ratio value of 0.7092.[75] The fauna enamel sample BASR_PTH/03 from an archaeological *Ovis* exhibits an $^{87}Sr/^{86}Sr$ value of 0.7088, while the fauna enamel BASR_PTH/01 from a modern wild rabbit gives a value of 0.7074. Acetic acid leachate sediment samples from the Pithekoussai burial environment yield $^{87}Sr/^{86}Sr$ isotope values of 0.70835 (BASR_PTH/10) and 0.7084 (BASR_PTH/11). If we disregard the result from the plant BASR_PTH/09 due to the large impact of the sea spray effect (see limitations of the study), the range of $^{87}Sr/^{86}Sr$ values in the Pithekoussai environment can be estimated between 0.7074 and 0.7088.

Human $^{87}Sr/^{86}Sr$ isotope ratio values at Pithekoussai

Table S3 lists individuals' $^{87}Sr/^{86}Sr$ isotope ratio values (n = 71) for the human odonto-skeletal remains from Pithekoussai. The range of the human $^{87}Sr/^{86}Sr$ values is between 0.7081 and 0.7102 (mean = 0.7086; median = 0.7085; SD = 0.0004) and it is broader than the Pithekoussai environmental $^{87}Sr/^{86}Sr$ isotope range.

Figure 2 compares the isotope values of the environment (i.e., vegetation, archaeological and modern fauna, and burial sediment) with those from the human odonto-skeletal remains, considering the two mineralized tissues analyzed (i.e., tooth enamel for inhumed individuals and bone for cremated individuals; see Table S3).

$\delta^{13}C_{VPDB}$ and $\delta^{15}N_{AIR}$

Of the sub-set of inhumed individuals (n = 11) analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in dentine collagen

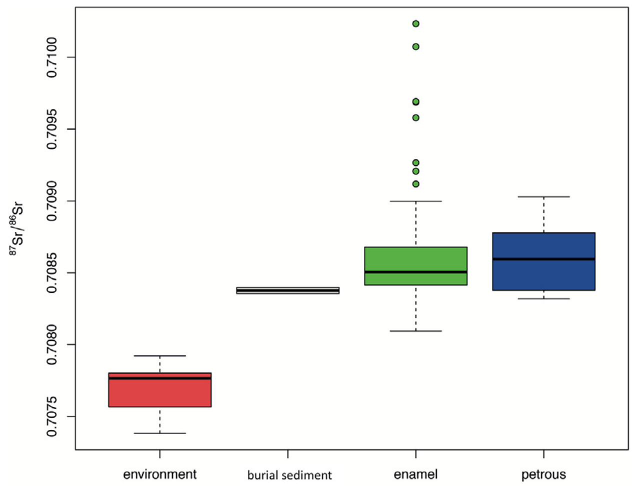

Figure 2. $^{87}Sr/^{86}Sr$ isotope ratio values from the Pithekoussai environmental and human odonto-skeletal samples

Boxplots comparing the $^{87}Sr/^{86}S$ Sr isotope ratios from n = 9 environmental samples collected at 0 to ~10 km from the Pithekoussai necropolis, $^{87}Sr/^{86}Sr$ isotope ratio in burial sediment (n = 2), 87Sr/86Sr isotope ratio in humans (n = 71) are shown as tooth enamel samples (inhumations, n = 45), and petrous bone samples (cremations, n = 26). Environmental samples included shallow-rooted plants (n = 7), modern and archaeological fauna enamel (n = 2). Due to the severe sea-spray effect affecting BASR_PTH/09, this sample is not considered here (see limitations of the study). Dots outside the whiskers represent outliers, lower whisker is equal to minimum value (excluding outliers), lower hinge equals to first quartile, thick line represents the median value, upper hinge equals to third quartile and upper whisker to maximum value (excluding outliers).

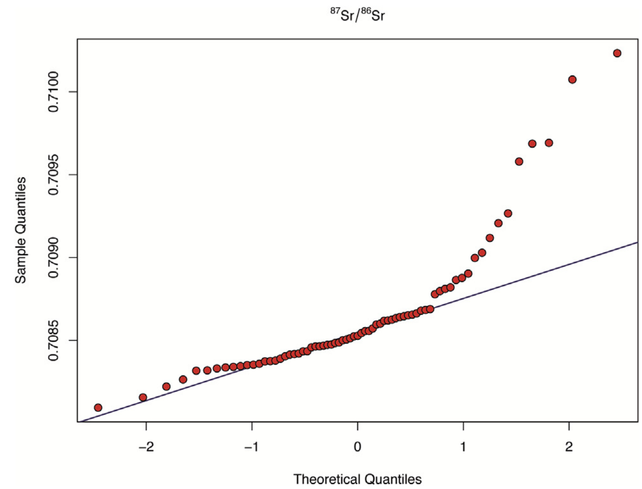

Figure 3. Normal probability plot—quantile-quantile plot (QQ plot)—of the human $^{87}Sr/^{86}Sr$ isotope distribution from Pithekoussai

The Q-Q plot compares the expected normal data (blue line) with the quantile data (red dots). Out of n = 71, n = 17 individuals visibly stand out from the expected normal distribution.

(see STAR Methods), none produced an adequate quantity of collagen to fulfill the laboratory analysis[76] (see limitations of the study).

DISCUSSION

As highlighted in the results, BASr values range from 0.7074 to 0.7088, considering that the vegetation sample BASR_PTH/09 (0.7091) was removed due to its high value likely contaminated by modern seawater $^{87}Sr/^{86}Sr$ value (0.7092).[75] If these BASr values are considered, this would result in n = 15 human individuals falling outside the local range. Nonetheless, it is important to make further considerations on the remaining BASr samples. The sample BASR_PTH/03 is the only one yielding a higher value of 0.7088 compared to the less radiogenic results from vegetation, modern fauna and burial soil samples (see Table S2 and Figure 2). BASR_PTH/03 was sampled from the tooth of an archaeological *Ovis*, whose remains were found mixed with human fragments from Cremation 1120. This tomb is dated to last quarter of eighth-early seventh century BC.[34,35] In prehistory and protohistory, transhumance, food trade, and the export and import of raw food sources and finished food products were widespread practices.[77–79] In this context, it cannot be excluded that the *Ovis* from Cremation 1120 itself may have been reared and traded from elsewhere to become sacrificial offerings or ceremonial meals during the funerary practices at Pithekoussai.[80,81] However, due to the paucity of animal remains attested at the necropolis and, thus, of faunal samples suitable for $^{87}Sr/^{86}Sr$ isotope ratio analysis, the animal mobility at the site cannot be further investigated (see limitations of the study).

Given the aforementioned difficulties in assessing a consistent BASr at Pithekoussai, this research considers the distribution of human $^{87}Sr/^{86}Sr$ isotope data[82–85] to obtain a proxy for the local baseline.

The normal quantile-quantile plot of human $^{87}Sr/^{86}Sr$ isotope data at Pithekoussai (Figure 3) shows that there are n = 17 values deviating from the theoretically expected normal distribution and located in the upper part of the plot.

The shape of the sample distribution of $^{87}Sr/^{86}Sr$ values can aid the identification of possible outliers and age-related patterns. The kernel density estimate of the Pithekoussai individuals (Figure 4) has a multimodal distribution with a dominant mode, representing the core values and skewed tails toward both lower and higher radiogenic values.

Applying the Tukey's 1.5× inter quartile range (IQR) to the entire sample distribution for the identification of outliers (Lightfoot and O'Connell[86] for $\delta^{18}O$ isotope analysis; Esposito et al; [83] for $^{87}Sr/^{86}Sr$ isotope analysis), only n = 8 individuals out of n = 71 can be considered as possible outliers.

The density line in Figure 4 shows that $^{87}Sr/^{86}Sr$ values for the infant and child classes are distributed in a narrow range, within which a significant portion of adult and adolescent individuals fall. The use of $^{87}Sr/^{86}Sr$ data in infants and children as a proxy of the isotope local signature[87–89] assumes that infants and children were generally less involved in mobility phenomena,[89] although this cannot be completely ruled out.[87,88,90]

At Pithekoussai, infants (i.e., aged one to five years at death) and children (i.e., aged five years to ten years at death) (for age-classes definition *see* study by White et al.[91]) yield values ranging from 0.70834 to 0.70864, which fall within the main peak of the

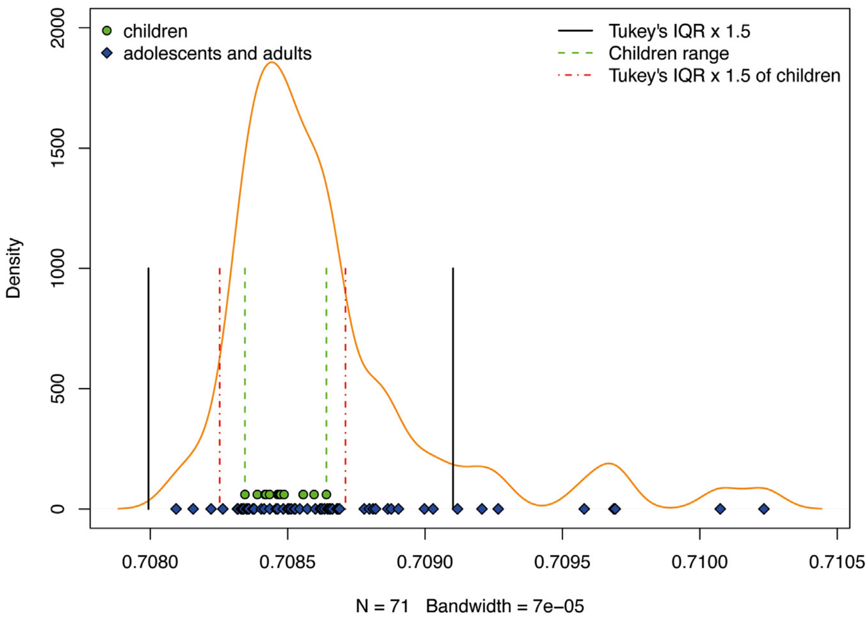

Figure 4. Kernel density plot of the human $^{87}Sr/^{86}Sr$ distribution from Pithekoussai

Tukey's IQR 1.5× criterion to statistically detect outliers within a given human $^{87}Sr/^{86}Sr$ isotope ratio distribution is applied to the whole sample (black line) and to infants and children (red dash-dotted line). Children range in green dashed lines.

kernel density (Figure 4). If these values are adopted as a proxy of the local range,[89,92] a larger number of outliers (n = 35) is identified. Nonetheless, if this method is adopted, many adults that are within the central core of the kernel density plot should be considered outliers.

For this reason, it seems more appropriate and cautious to apply a more conservative approach that considers the "core" distribution of the isotope data as the Pithekoussai local range. The core distribution of the values can be described as the Tukey's 1.5× IQR of the infants and children $^{87}Sr/^{86}Sr$ values that range from 0.70823 to 0.70875. This range allows for the identification of n = 20 mobile and n = 51 non-mobile individuals, in agreement with what was observed for the "core" distribution of the data in the Kernel density plot (Figure 4). Of the n = 20 mobile individuals (28.2% of the sample), n = 17 present isotope values more radiogenic than the local range, while n = 3 individuals (4.2% of the sample) yield ones that are less radiogenic (see Table 1). This latter represents the lowest values at Pithekoussai (individuals PTH 890, PTH 1057a, and PTH 1116; see Table S3).

Figure 5 shows the human $^{87}Sr/^{86}Sr$ isotope values divided by funerary practices, indicating different mobility patterns for secondary cremations and inhumations in the sub-set of tombs here analyzed.

Even if the ratio between the cremated vs. inhumed individuals varies through time, this variation is not significant given the sample size (Pearson's Chi-squared test with simulated p value, based on 10,000 replicates, X-squared = 9.9635, df = NA, p value = 0.08).

The isotope values for human cremated remains range from 0.70832 to 0.70903, with 26.9% of the individuals (n = 7) identified as mobile. Of these mobile individuals, n = 4 belong to single secondary cremations (PTH 154; PTH 159; PTH 203; PTH 985), while n = 3 (PTH 199a; PTH 199b; PTH 944a) belong to double secondary cremations (see Table S3). Only in n = 2 out of n = 4 double cremations, it was possible to identify and sampling both the individuals from the same tomb (i.e., Cremation 199 and 208). Interestingly, by combining the sex assessment of the individuals[80,81] (see also STAR Methods) with their $^{87}Sr/^{86}Sr$ isotope profiles, it was possible to define that Cremation 208 contained the remains of a non-mobile male and a non-mobile female, while Cremation 199 yielded a mobile male along with a mobile female.

The isotope values for inhumed individuals range from 0.70809 to 0.71023. This suggests a larger variability and more radiogenic values for inhumations than cremations. Thirteen inhumed individuals (28.9% of the inhumation sub-set) were defined as mobile. Overall, the wider variation in $^{87}Sr/^{86}Sr$ profiles across inhumations might indicate a diverse provenance for the sub-set of tombs here analyzed. These results seem to confirm for the inclusiveness of the inhumation ritual as a funerary custom adopted not only by individuals of different age-at-death,[30,34,80,81] but also by people from various geographic origins.

Finally, as for inhumed individuals, it is also important to clarify that enamel sampling was conducted from the first permanent molar (M1) in n = 35 individuals out of n = 45, while n = 9 individuals and n = 1 individual were sampled from the second permanent molar (M2) and the third permanent molar (M3) respectively (see STAR Methods and Table S3). While bulk strontium isotope analysis on M1 samples reflects an isotope signature attributable to early infancy (from the perinatal period up to around two years of age[91]), sampling the second and third permanent molar crowns provides isotope values corresponding to later life stages, specifically early to late childhood in the case of M2, and late childhood to early adolescence for M3. By analyzing the $^{87}Sr/^{86}Sr$ values in M2 tooth samples, n = 5 out of n = 9 individuals are mobile, suggesting that they arrived at the site after the period of the crown formation of the M2s (after the eighth year of life); the only individual sampled for the M3 was a young female (age at death 15–20 years), who was non-mobile, at least after early adolescence.

Figure 6 shows the human $^{87}Sr/^{86}Sr$ isotope values divided by sex.

The range of $^{87}Sr/^{86}Sr$ isotope values for adult females is from 0.70809 to 0.70921, whereas males have higher values, ranging from 0.70822 to 0.71023 Overall, these results indicate n = 8 males (PTH 199b; PTH 203; PTH 957; PTH 985; PTH 1052; PTH 1089; PTH 1097; PTH 1166c) and n = 8 females (PTH 154; PTH 159; PTH199a; PTH 653; PTH 755; PTH 768; PTH

Table 1. Summary statistics of the $^{87}Sr/^{86}Sr$ ratio by ritual, sex, chronological phase

	range	mean	median	SD	*N*	*N* mobile	% mobile
Cremation	0.70832–0.70903	0.70859	0.70859	0.0002	26	7	26.9%
Inhumation	0.70809–0.71023	0.70868	0.70851	0.0005	45	13	28.9%
Adult females	0.70809–0.70921	0.70862	0.70860	0.0003	21	8	38.1%
Adult males	0.70822–0.71023	0.70879	0.70864	0.0006	26	8	30.8%
Phase A	0.70832–0.70903	0.70862	0.70858	0.0002	12	4	33.3%
Phase B	0.70832–0.70921	0.70860	0.70854	0.0002	17	4	23.5%
Phase A-B	0.70842–0.70969	0.70881	0.70865	0.0004	11	4	36.4%
Phase C	0.70809–0.70958	0.70861	0.70851	0.0005	6	2	33.3%
Phase D	0.70822–0.71007	0.70859	0.70842	0.0005	12	3	25.0%
Phase E	0.70816–0.71023	0.70861	0.70848	0.0006	11	2	18.2%

Range, mean, median, standard deviation (SD) of the $^{87}Sr/^{86}Sr$ ratio values, *N* = number of individuals, % = percentage of mobile individuals.

944a; PTH 1123) as mobile. Out of *n* = 8 adults with no sex determinations, *n* = 4 can be considered as mobile individuals (PTH 783; PTH 842; PTH 997b; PTH 1184).

When considering the different chronological phases (phases A–E; see Table S1)—from the mid-eighth century BC to the first century AD—the human $^{87}Sr/^{86}Sr$ isotope values indicate different mobility patterns across generations (Figure 7).

In individuals from phase A (i.e., third quarter of the eighth century BC), the $^{87}Sr/^{86}Sr$ isotope values range from 0.70832 to 0.70903. For this phase, $^{87}Sr/^{86}Sr$ isotope values indicate that *n* = 8 out of *n* = 12 individuals analyzed were non-mobile; as for the *n* = 4 outliers identified, their $^{87}Sr/^{86}Sr$ isotope values range from 0.70881 to 0.70903.

During phase B (i.e., last quarter of eighth – early seventh century BC), the distribution of the human $^{87}Sr/^{86}Sr$ isotope values is comprised between 0.70832 and 0.70921, with *n* = 4 mobile out of *n* = 17 individuals from this period. Interestingly, in this phase mobile individuals are represented by both more radiogenic (as for the previous phase) and less radiogenic $^{87}Sr/^{86}Sr$ isotope values than the baseline range. The mobile individual PTH 755 (0.70809) has the lowest $^{87}Sr/^{86}Sr$ isotope ratio value of the whole human sample distribution.

As for the tombs between phase A and phase B (i.e., the tombs for which was not possible to determine archaeologically a more precise chronology than between the third quarter of the eighth century and the early seventh century BC[30,34–36]), the distribution of the human values falls between 0.70842 and 0.70969. Four out of *n* = 11 individuals are mobile, showing $^{87}Sr/^{86}Sr$ isotope values from 0.70890 to 0.70969.

Overall, for the second half of the eighth century until the early seventh century BC, the total of mobile individuals at Pithekoussai is *n* = 12 (30%), which is more than what recorded for other Greek settlements for the same period.[93]

During phase C (i.e., seventh century BC), the human $^{87}Sr/^{86}Sr$ profiles range from 0.70809 to 0.70958, yielding *n* = 2 mobile individuals out of *n* = 7 samples, while phase D (i.e., sixth–fourth century BC) gives a range of $^{87}Sr/^{86}Sr$ isotope values from 0.70822 to 0.71007, yielding *n* = 3 mobile out of *n* = 12 individuals analyzed for the Archaic-Classic period.

The Hellenistic-Roman period (phase E, i.e., third century BC–first century AD) at Pithekoussai is characterized by higher radiogenic human $^{87}Sr/^{86}Sr$ isotope values compared to the early stages of the necropolis. The human $^{87}Sr/^{86}Sr$ isotope data show values from 0.70816 to 0.71023 and *n* = 2 outliers out of *n* = 11 samples available. The mobile individual PTH 1052 (0.71023) has the highest $^{87}Sr/^{86}Sr$ isotope value of the whole human sample distribution.

Finally, the mobile male PTH 1097 pertains to an inhumation for which it was not possible to determine any archaeological chronology; thus this has been excluded from any other consideration.

By integrating the two main burial practices attested at Pithekoussai (i.e., cremation and inhumation) with relative chronology, osteological data (sex and age-at-death) and individual $^{87}Sr/^{86}Sr$ isotope signatures, this research identified a potential correlation among sex, the mobility of the individuals and funerary customs adopted during the different phases of the Pithekoussai necropolis.

Overall, within the sub-set of tombs considered in this study, all mobile individuals from phase A sub-set adopted the cremation ritual, while all non-mobile individuals practiced the inhumation of the body. The only exception is Cremation 177, which belongs to a non-mobile male (PTH 177; 0.70852). Despite the uncertainties, it is possible that Cremation 177 contains the remains of a second-generation foreigner of Greek origin. As is often the case in hybrid societies with cultural permeability and cross-cultural interactions,[66] it is also worth considering the possibility of local individuals adopting foreign customs or different geographic areas reflecting similar isotope values.

During phase B, the arrival at Pithekoussai of new people who practices cremation persisted, with *n* = 3 out of *n* = 9 cremated individuals identified as mobile. Cremation became also more common among individuals born on the Island, possibly indicating an adoption of foreign customs. As for the case of Cremation 177, it is also possible that some of them represent the later generations of the first Greek settlers on the Island.

More interestingly, from the transition to phase B onwards, the inhumation of the body is practiced also by mobile people. When comparing the $^{87}Sr/^{86}Sr$ isotope values of mobile cremated individuals with mobile inhumed individuals, it is evident that during phase B inhumations have significantly higher radiogenic $^{87}Sr/^{86}Sr$ isotope values than contemporary cremations. The

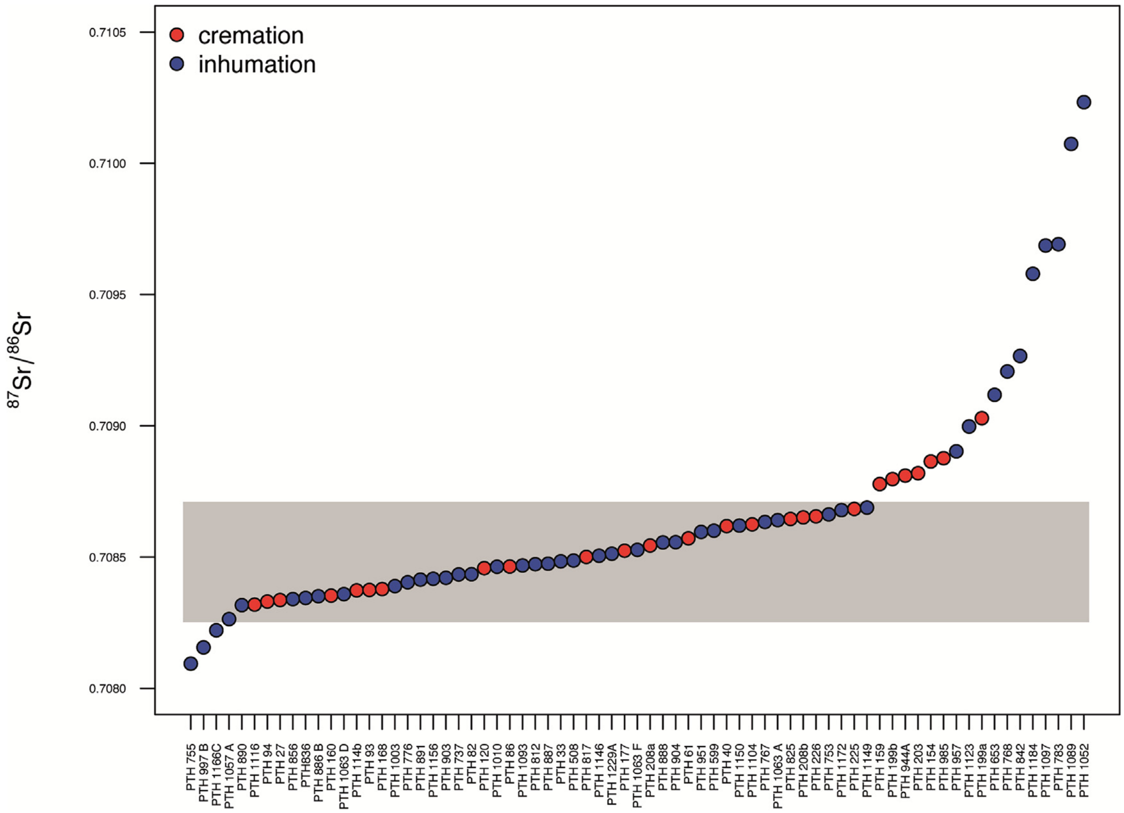

Figure 5. The human $^{87}Sr/^{86}Sr$ isotope ratio values divided by funerary practices

The gray region indicates the local $^{87}Sr/^{86}Sr$ range; $n = 7$ out of $n = 26$ cremations and $n = 13$ out of $n = 45$ inhumations fall outside the $^{87}Sr/^{86}Sr$ isotope local range.

range of $^{87}Sr/^{86}Sr$ isotope variability for mobile cremated individuals is between 0.70878 and 0.70886, while for the $n = 2$ mobile inhumations (PTH 755 and PTH 768) the $^{87}Sr/^{86}Sr$ isotope values are respectively of 0.70809 and 0.70921. This suggests that foreign cremated and inhumed individuals here analyzed might have arrived at Pithekoussai from regions with a different environmental isotope background.

Among the inhumations dated between phase A and phase B, the $^{87}Sr/^{86}Sr$ isotope values identify $n = 2$ mobile individuals (i.e., PTH 783 and PTH 842), the bodies of which were discovered in a crouched position. The results of $^{87}Sr/^{86}Sr$ isotope analysis suggest a positive correlation between the funerary behavior and allogeneity of the deceased, thus supporting previous archaeological interpretations.[30,34]

Overall, $^{87}Sr/^{86}Sr$ isotope values in humans at Pithekoussai reveal a complex scenario of mobility that involved both males and females, highlighting the complexity of social and cultural dynamics at the site, where the coexistence of different ethnic and cultural groups led to the creation of a unique social milieu.

Mobile women were attested at Pithekoussai since the earliest phase of the necropolis. In Phase A, $n = 2$ out of $n = 4$ sampled females (i.e., PTH 199a and PTH 944a) are identified as mobile cremations. These females pertained to the double Cremations 199 and 944, which contained the commingled remains of a male along with a female.[80,81] As for the double Cremation 199, both the male and female were sampled and reported to be mobile (see Table S3).

Conversely, the poor state of preservation of the double Cremation 944[80,81] allowed for the sampling of the female PTH 944a only. The double Cremation 944 is an important case for understanding the connection between the elites of Pithekoussai and the ones from the Etruscan-Latium areas, on the mainland.[34,94] This case also helps to reconstruct the choices made by the Pithekoussai people in the adoption of funerary customs. The analysis of archaeological evidence has suggested that Cremation 944 contained the remains of a mobile female, likely coming from the Tyrrhenian regions.[34,35] Nonetheless, despite not being of Greek origin, the female was believed to be integrated into the higher social rank at Pithekoussai as evidenced by the funerary choice to cremate her body.[34,35]

The $^{87}Sr/^{86}Sr$ isotope ratio result confirms the allogeneity of PTH 944a.

The female Cremation 159 (phase B) shows similarities to Cremation 944 grave goods, including—among the grave goods set—the presence of a small impasto amphora from the Etruscan-Latium area and similar $^{87}Sr/^{86}Sr$ isotope ratio values. The $^{87}Sr/^{86}Sr$ isotope ratio for the female PTH 159 is 0.70877, slightly lower than the value of PTH 944a, which is 0.70881, and however possibly indicating a common geographic origin.

Although the human $^{87}Sr/^{86}Sr$ isotope values for males do not support archaeological and historical assumptions of possibly

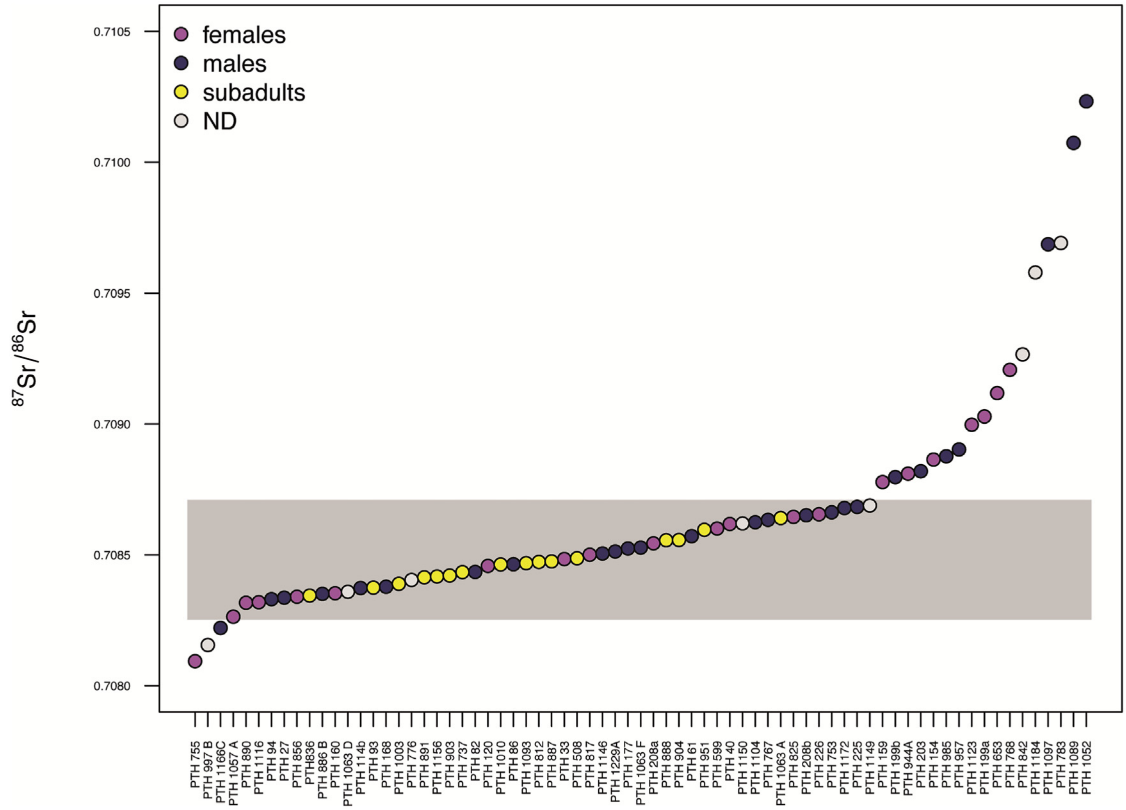

Figure 6. The human $^{87}Sr/^{86}Sr$ isotope ratio values divided by sex (for adult individuals)
The gray region indicates the local $^{87}Sr/^{86}Sr$ range.

greater mobility of men compared to women, the $^{87}Sr/^{86}Sr$ isotope ratio profiles here characterized reveal a wider range of $^{87}Sr/^{86}Sr$ values for males (0.70888, 0.71023), in particular during phase B and later on, during the Archaic-Classic (phase D) and Hellenistic-Roman (phase E) periods of the necropolis.

To conclude, the focus of this discussion is placed on one of the most noteworthy discoveries within the Pithekoussai necropolis, namely the so-called Tomb of Nestor's Cup (Cremation 168).[30,37] As an emblematic find within Mediterranean archaeology, this cremation and its grave goods provide critical insights into the interconnectivity and biocultural integration dynamics at the site during the second half of the eighth century BC. Its significance within the broader archaeological context of Pithekoussai justifies its role here as the final case study in our analysis.

The tomb is named after a Rhodian *kotyle* (i.e., a wine cup) that was part of the grave goods set. The cup, decorated in geometric style, bears on one of its sides a three-line inscription evoking the legendary cup of the Homeric hero Nestor.[30,95] Although the interpretation of the inscription is still controversial,[95,96] it represents the oldest evidence for the Euboic Greek alphabet and one of the earliest pieces of evidence of Homeric and symposiac culture in the Mediterranean.[30,97] Recently, Gigante and colleagues[37] have re-examined the osteological assemblage of Cremation 168, discussing the mixed nature of the human remains, while highlighting the presence of faunal remains and rejecting the previous hypothesis of the tomb as a child cremation. This research sampled a human *pars petrosa* from the Cremation 168 skeletal assemblage (see Table S3). Although considering the evidence of at least three adult individuals[37,81,98] in taphonomic association with the sherds of the exotic and extraordinary cup, this study indicates the presence of a non-mobile individual buried in the Tomb of Nestor's Cup.

Limitations of the study

The present study has some limitations that require consideration when interpreting the results.

The first limitation is the sample size. Although the number of individuals sampled (n = 71) is large for isotope studies of archaeological specimens, it is important to note that all these individuals represent different chronological phases of the Pithekoussai necropolis, spanning from the mid-eighth century BC to the first century AD ca. The size of this sample is also related to the poor state of preservation of the skeletal and dental remains from Pithekoussai,[80,81] which has had consequences on the number of individuals suitable for biogeochemical analyses. The peculiar burial environment—characterized by the presence of fumaroles and hot volcanic sediments—played a key role in not preserving both biological and inorganic materials.[30,80] This is particularly evident in inhumed skeletal and dental remains, which were strongly affected by the burial conditions.[80,81]

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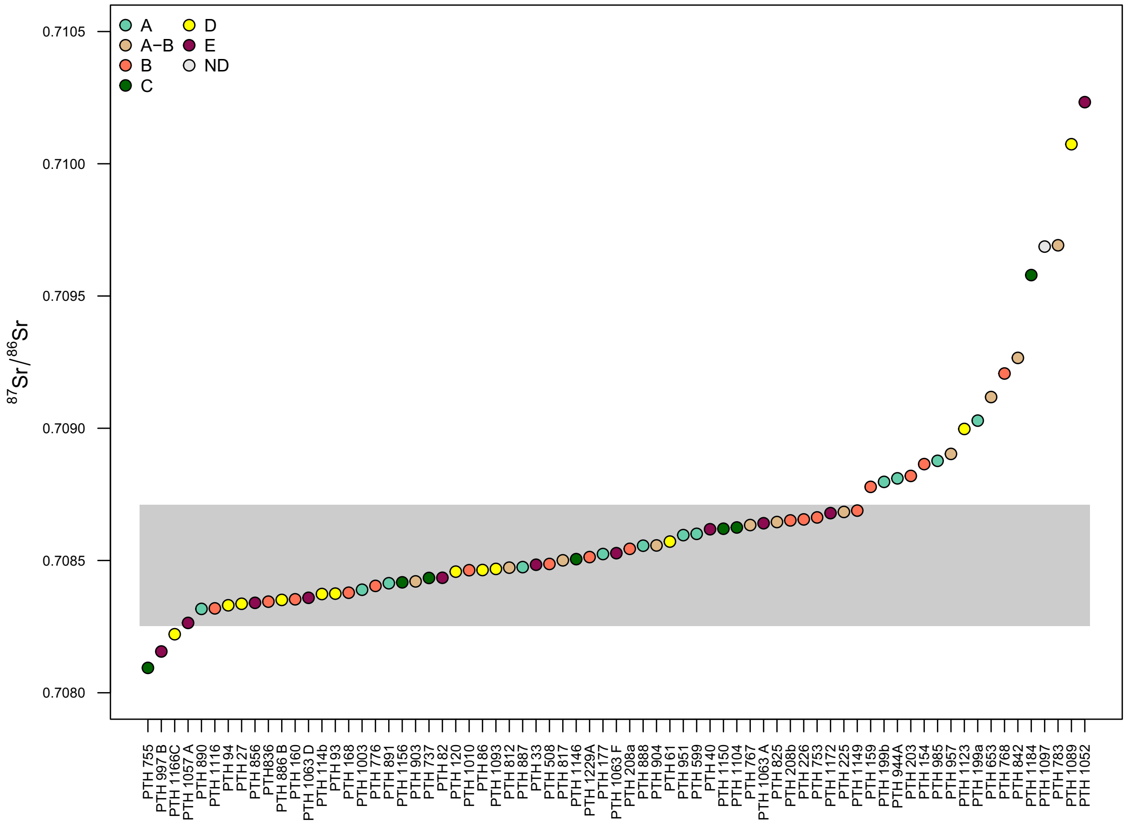

Figure 7. The Human $^{87}Sr/^{86}Sr$ isotope ratio values by chronological phases (A–E)

For a detailed definition of relative and absolute chronology at the Pithekoussai necropolis considered in this manuscript, please refer to Table S1. The gray region indicates the local $^{87}Sr/^{86}Sr$ range.

A significant limitation in this study is also represented by the lack of yielded collagen in dentine for stable isotope analysis, making the exploration of dietary patterns impossible. Although $\delta^{13}C$ and $\delta^{15}N$ isotopic analysis can only be applied to a subset of the inhumations, a study on dietary habits could have helped clarifying potential reliance on a marine diet. This would have influenced individuals' $^{87}Sr/^{86}Sr$ isotope ratios,[99] making them closer to the marine baseline value of approximately 0.7092.[75] Given Pithekoussai's significant proximity to the coast, it is not possible to discount the possibility of a marine food contribution to the isotopic signatures. It is important to note, however, that at other coastal sites in the western Mediterranean, including contemporaneous settlements, $\delta^{13}C$ and $\delta^{15}N$ analyses have often indicated limited reliance on marine resources and a greater emphasis on terrestrial protein consumption.[100–102] This indicates a potential pattern where marine consumption may have been less prevalent than anticipated. However, estimating marine intake at Italian sites remains challenging due to isotopic overlap with other food sources.

Another potential source of issues may be the lack of reliable data on the consumption of drinking water from different sources. With regard to the potential impact of drinking water on the isotope composition of the human dataset and/or local baseline, it is noteworthy that the plant samples collected in Lacco Ameno exhibited a relatively homogeneous range of isotope values, consistent with the narrow range observed in vegetation.[103] This suggests that, as plants biometabolize strontium from groundwater,[103] the isotope composition of drinking water may not significantly influence the isotope composition of plants in the vicinity.

The use of statistical approaches based on the distribution of $^{87}Sr/^{86}Sr$ isotope values in human samples to differentiate between mobile and non-mobile individuals at Pithekoussai represents a potential limitation of this study, particularly given the site inherent characteristics, which, according to historical sources (e.g., Strabo and Livy), are expected to have a high proportion of non-mobile individuals. Furthermore, the human sample here analyzed encompasses a temporal range of several centuries, from the mid-eighth century BC to the first century AD,[30,34–36] posing an additional challenge in interpreting the data. However, following a critical evaluation of the baseline samples (n = 11) and their $^{87}Sr/^{86}Sr$ isotope values, many of which appear unconvincing due to their radiogenic values, potentially influenced by a number of factors (see results), the authors believe that a multifactorial approach, incorporating both the distribution of $^{87}Sr/^{86}Sr$ isotope data and the $^{87}Sr/^{86}Sr$ values for children (who are generally considered to be less mobile as in Knipper et al.[89]), provides the most accurate method currently available for assessing mobile vs. non-mobile status at Pithekoussai. Human sample distribution as a proxy for deriving the local baseline range is an accepted approach in cases where the baseline values are unreliable.[83,85] Furthermore, the complex and heterogeneous nature of Ischia Island's environment reinforces this methodological choice, as it is challenging to establish a consistent BASr baseline across the Island.

Furthermore, there is a potential issue concerning the equifinality of the $^{87}Sr/^{86}Sr$ isotope results, which is a widely discussed methodological problem in bioarchaeological and biogeochemical research.[104] According to this principle, $^{87}Sr/^{86}Sr$ isotope values from individuals identified as mobile could present an isotope ratio that matches $^{87}Sr/^{86}Sr$ values measured and modeled over wide areas in the Italian Peninsula and across Europe.[105–107] Hence, it cannot be ruled out that people originating from areas with similar $^{87}Sr/^{86}Sr$ signature to Pithekoussai might not be isotopically visible and, thus, identified as non-mobile.

Finally, the authors judged it unsuitable to apply the isotope-based geographical assignment[108] to this study for three main reasons as follows. (1) The method itself tries to estimate a probability of geographic origin based on isoscape and, ideally, from a multi-isotope perspective (e.g., oxygen, sulfur, and strontium). This study employed the analysis of a single isotope (strontium)—for the reasons mentioned previously—thus resulting in a less reliable mean to spot origins of the mobile individuals. Nonetheless, the use of a single isotope has successfully been applied in other studies.[83] Yet, the present study suffers from further limitations as follows. (2) The location of Pithekoussai itself made it difficult to produce a probability density plot that shows the likely distance of movements of the mobile individuals from a hypothetical location of origin to reach Pithekoussai. (3) From phase B, more heterogeneous isotope values are reported among the mobile individuals, suggesting—as discussed—possibly different places of origin for the outliers. The variability of $^{87}Sr/^{86}Sr$ values for the single chronological phases makes it intrinsically impossible to apply the joint probability method for the provenance of the mobile individuals.

Conclusions

The ancient site of Pithekoussai played a key role in the so-called eighth-century Greek colonization of the western Mediterranean. The rich archaeological record has revealed the features of an open community, in which material culture and funerary rituals suggest a heterogeneous society characterized by the coexistence of indigenous individuals, Phoenician traders and Italic peoples alongside the Greek settlers.

This work has further contributed to the understanding of the interconnectedness of Mediterranean societies during the Iron Age providing a deeper and more nuanced view of these biocultural interactions at Pithekoussai.

Despite the challenges posed by the burial volcanic environment, the combination of archaeology, human osteology and isotope data have shed new light on the pattern of human mobility at the site through time and in relation to different mortuary practices and burial goods.

Finally, this research has underlined the challenges and limitations of applying stable isotope analysis to archaeological samples, while encouraging the employment of $^{87}Sr/^{86}Sr$ isotope analysis on human mineralized samples for provenance, even in the case of taphonomic alteration of the human remains.

RESOURCE AVAILABILITY

Lead contact

Further information for resources should be directed to and will be fulfilled by the lead contact, Melania Gigante (melania.gigante@unipd.it).

Materials availability

This study did not generate new unique reagents.

All data produced in this study can be found in Tables S2 and S3, as well as in the main text of this article. The osteological remains discovered at Pithekoussai are currently housed at the Bioarchaeological Service of the Museum of Civilisations (Ministero della Cultura) in Rome, Italy.

The Soprintendenza Archeologia, Belle Arti e Paesaggio per l'area metropolitana di Napoli, Italy (Italian Ministry of Culture), which holds the legal responsibility for the entire osteological collection from the Pithekoussai necropolis, has authorized the study.

Data and code availability

$^{87}Sr/^{86}Sr$ isotope ratios from Pithekoussai's environmental samples are available from Table S2 of this article. $^{87}Sr/^{86}Sr$ isotope ratios from Pithekoussai's human samples are available from Table S3.

Osteological data from Pithekoussai's human odontoskeletal collections and archaeological data from Pithekoussai's necropolis are provided by Gigante et al.,[37,80,81] Buchner and Ridgway[30] and Cinquantaquattro,[34–36] respectively. Any additional information is available from the lead contact upon request.

The identification codes of the samples analyzed in this article (i.e., tomb ID; individuals ID; sample ID) are provided in Tables S2 and S3.

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AUTHOR CONTRIBUTIONS

Conceptualization, M.G., L.B., and W.M.; methodology, W.M. and L.B.; software, L.B. and F.L.; validation, W.M., L.B., and A.N.; formal analysis, M.G., C.E., L.B., and W.M.; investigation, M.G., C.E., and W.M.; resources, W.M. and A.N.; data curation, M.G., C.E., L.B., and W.M.; writing – original draft, M.G. and C.E.; writing – review & editing, all the authors have participated to the review and editing of the manuscript; visualization, M.G., C.E., L.B., F.L., and W.M.; project administration, M.G., L.B., and W.M.; funding acquisition, W.M. and A.N.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
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- METHOD DETAILS
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- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Chemicals		
Eichrom Sr-spec resin	Eichrom Technologies Inc	SR-B50-A
Nitric acid, 65% Suprapur®	Merck	CAS 7697-37-2
Ultrapure H_2O	Millipore system	N/A
Deposited data		
Osteological data of Pithekoussai's human dental and skeletal collection	Gigante et al.[80]; Gigante et al.[81]	Table S3
Archaeological data of Pithekoussai's necropolis	Buchner and Ridgway[30]; Cinquantaquattro[36]	Table S1 and in the main text
Raw and analyzed data	This study	Tables S2, S3
Software and algorithms		
R language and environment for statistical computing (ver. 4.4.1)	R Core team 2024	https://www.r-project.org/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Archaeological human and faunal samples

This study included human tooth and bone samples of n= 71 individuals from the Pithekoussai odonto-skeletal collection investigated so far. Previous morphological and histological studies of human remains provided biological information of the individuals (e.g., age-at-death and sex), as well as taphonomic information on the minimum number of individuals (MNI) for each tomb and the presence of faunal remains. These data characterized the funerary practices and reconstructed the demographic profiles of Pithekoussai community through time. Age-at-death and sex estimations (*see* Gigante et al.[37,80,81]) constituted the biological baseline for the interpretation of the results obtained from $^{87}Sr/^{86}Sr$ isotope analysis here discussed.

The $^{87}Sr/^{86}Sr$ isotope ratio analysis was performed on both primary inhumations and secondary cremations. The sampling dataset for humans included n = 45 permanent molars (from inhumations) and n = 26 petrous bones (from cremations). The most targeted tooth types for inhumations are the permanent first molar (M1; n = 35) or permanent second molar (M2; n = 9) and, more rarely, the third molar (M3; n = 1). The first lower M1 crown mineralization generally starts to around birth, until about 3 years of age.[109] The M2 tooth crown begins to form at 3 to 4 until 7 to 8 years of age.[109] M3 formation vary significantly among individuals and can start between 6 and 12 years of age.[109] Overall, these teeth came from both maxillary and mandibular dentition. As the upper and lower dentitions show similar rates of growth and mineralization, the $^{87}Sr/^{86}Sr$ values do not differ from the upper and lower teeth.[109] As for secondary cremations, wherever the tooth enamel was not suitable for sampling, this study used the otic capsule of the inner ear in the petrous bone of the temporal bone (e.g.,[110,111]). Its formation begins *in utero* (~16th-18th gestational week) and ossifies at birth.[112] Furthermore, it does not remodel after two years of age.[113,114] The use of petrous bone in $^{87}Sr/^{86}Sr$ isotope analysis as an analog to tooth enamel is possible because crystallized bone tissue, resulting from a cremation process, preserves *in vivo* strontium signatures rather well, as it is far more resistant to diagenesis compared to unburned bones.[115]

In the case of secondary cremations containing the remains of two individuals (i.e., male and female), the selection of *pars petrosa* samples was conducted in accordance with specific sampling criteria, with the objective of ensuring the accuracy and reliability of the extracted isotope data. In particular, the *pars petrosa* was only sampled in double cremations when it was still attached to the mastoid portion of the temporal bone, which was considered to be morphologically diagnostic for sex determination (*see* Gigante et al.[80,81]). This approach ensured the reliability of the attribution of isotope data to the individuals from the same cremation, thereby guaranteeing control over the $^{87}Sr/^{86}Sr$ results even in the case of commingled remains.

Archaeological and modern faunal and modern environmental samples

Eleven samples of archaeological and modern tooth enamel from small mammals, modern vegetation, and burial soil were collected up to ~10 km from the Pithekoussai necropolis. GPS coordinates were recorded for each sample site and provided in Table S2.

The tooth enamel sample from the small modern mammals (i.e., BASR_PTH/01) and vegetation samples (i.e., BASR_PTH/02 - BASR_PTH/09) were collected at distances of up to approximately 10 km from the Pithekoussai necropolis. The geographical positions of each sample site were recorded and are provided in Table S2.

In general, both the small-rooted plants and the modern faunal sample were obtained from forested and/or low anthropogenically impacted areas, with the aim of reducing the contamination of fertilizers and pesticides that could introduce anthropogenic strontium.[87,116] Tooth enamel from the wild rabbit specimen (BASR_PTH/01) was obtained from a skeletonized animal discovered in the forested region of Monte Epomeo (for further details, *see* Table S2). The burial sediment (i.e., BASR_PTH/10 and BASR_PTH/11) was retrieved from the micro-excavation of soil blocks containing human remains from the Pithekoussai necropolis (Buchner's excavation 1965–1967). The micro-excavation of the soil blocks and the subsequent dry cleaning of the dental and skeletal remains[80,81] was conducted at the Bioarchaeological Service of the Museum of Civilisations (Italian Ministry of Culture) in Rome, along with the recovery of the burial sediment samples.

Ethical statements and additional information

This research study was carried out in compliance with the relevant regulations for the treatment of human remains from archaeological contexts, as outlined in the Human Bones from Archaeological Sites (EH 2004) and the International Council of Archaeozoology (ICAZ) for the treatment and the destructive sampling of fauna specimens from archaeological horizons. The collection of modern faunal remains that were skeletonized adhered to the Berne Convention on the Conservation of European Wildlife and Natural Habits (Council Decision 82/72/EEC; OJ L 38, 10.2.1982).

METHOD DETAILS

$^{87}Sr/^{86}Sr$ isotope ratio analysis

Overall, the analytical research protocol follows Müller et al.[117] and Harving et al.[110] Sampling and chemical treatment as well as mass spectrometric analysis of environmental and human samples, both modern and archaeological ones, were carried out at the Department of Earth Sciences of the Royal Holloway, University of London (UK) and at the Frankfurt Isotope and Element Research Center (Frankfurt Isotope Element Research Center (FIERCE)) of the Institut für Geowissenschaften of Goethe Universität in Frankfurt (Germany). For laboratory procedures *see* Esposito et al.[83]

At the Frankfurt Isotope and Element Research Center (FIERCE) of the Institut für Geowissenschaften of Goethe Universität, $^{87}Sr/^{86}Sr$ ratios were measured with a NeptunePlus High-Resolution Multicollector ICPMS, overall following Müller and Anczkiewicz.[118]

The reproducibility of the standard NIST SRM987 during the analysis of samples is 0.000015 (2 SD, $n = 15$). Sr blank measurements were conducted using a dilute ^{84}Sr-enriched tracer solution ('spike') and found to be negligible relative to the relatively large Sr samples processed. At the Department of Earth Sciences, Royal Holloway University of London (UK), $^{87}Sr/^{86}Sr$ ratios were measured with a VG354 TIMS in multi-dynamic mode, following Alt and colleagues.[119]

δ^{13}CVPDB and δ^{15}NAIR isotope analysis

To assess the marine contribution to the dietary habit, which potentially influences the $^{87}Sr/^{86}Sr$ isotope ratio results, $n = 11$ dental roots were sampled from inhumed individuals and analyzed for $\delta^{13}C_{VPDB}$ and $\delta^{15}N_{AIR}$. Collagen was extracted from dentine samples by applying the protocol of ^{14}CHRONO Center (QUB), which is summarized as follows. The bone pre-treatment involves a simple AAA treatment followed by gelatinization[120] and ultrafiltration[121] using a Vivaspin filter cleaning method below introduced by Bronk Ramsey et al.[122]

Bone (0.5–1 g) is crushed until small fragments (ideally 1-3mm or smaller). Samples are treated with: (i) 10 mL 0.5M Hydrochloric Acid (3 or 4 rinses over ∼18 h) or until no further acid/carbonate reaction is seen; (ii) 10 mL 0.1M Sodium Hydroxide (15–30 min), and (iii) 10mL 0.5M Hydrochloric Acid (15–30 min). After the final HCL wash is rinsed, the crude collagen is gelatinized in pH2-pH3 solution at 70°C for 15 h. The resultant gelatin solution is then filtered using 'pre-baked' 7 μm and 12 μm glass fiber filters on a ceramic filter holder. The filtrate is transferred into a pre-cleaned ultrafilter (Vivaspin Turbo 15–30 kD MWCO) and centrifuged until 0.5–1.0 mL of the >30 kD gelatin fraction remains. This gelatin is then removed from the ultrafilter with borosilicate Pasteur pipettes and ultrapure water before being freeze-dried. The collagen yield is calculated from the ratio of the final weight to the starting weight of the bone.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses and figures were done with the R language and environment for statistical computing (ver. 4.4.1) R Core Team, 2024.