Journal of Archaeological Science: Reports 61 (2025) 104931

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

Echoes from the past: Bioarchaeological insights into the burial grounds of *Portus Romae*

Flavio De Angelis [a,b,c,*], Serena Vaccaro [d,e], Marco Romboni [f], Maria Rosa Di Cicco [g,h,**], Noemi Mantile [g,h], Simona Altieri [g,h], Antonio Mezzogiorno [a], Marina Lo Blundo [i], Olga Rickards [b], Carmine Lubritto [g,h], Paola Francesca Rossi [d]

[a] *Department of Mental, Physical Health and Preventive Medicine, University of Campania "Luigi Vanvitelli", Via L. Armanni 5, 80138 Naples, Italy*
[b] *Centre of Molecular Anthropology for Ancient DNA Studies, Department of Biology, University of Rome Tor Vergata. Via della Ricerca Scientifica 1, 00133 Rome, Italy*
[c] *Department of Biology, California State University Northridge, 18111 Nordhoff St, Northridge, CA 91330, USA*
[d] *Parco archeologico di Ostia antica, Servizo di Antropologia, Viale dei Romagnoli, 717, 00119 Ostia antica, Rome, Italy*
[e] *Doctorado en Patrimonio, Universidad de Huelva. Calle Dr. Cantero Cuadrado, 6, 21004 Huelva, Spain*
[f] *Department of Biology, University of Pisa, Via Luca Ghini 13, 56126 Pisa, Italy*
[g] *Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, University of Campania "Luigi Vanvitelli", Via Vivaldi 43, 81100 Caserta, Italy*
[h] *Mediterranean BioArchaeological Research Advances (MAReA Centre), Via Vivaldi, 43-81100, Caserta, Italy*
[i] *Parco Archeologico di Ostia antica, Area funzionale cura e gestione delle aree archeologiche e dei monumenti – Area archeologica dei porti imperiali di Claudio e di Traiano. Viale dei Romagnoli, 717, 00119 Ostia antica, Rome, Italy*

ARTICLE INFO

Keywords:
Portus Romae
Bioarchaology
Stable Isotopes Analyses
Ancient DNA
Genomics
Late Antiquity

ABSTRACT

Since its establishment, *Portus Romae* represented a hub for the trade of goods to and from Rome. Similarly, commercial activities should have pushed the intermingling of people and cultures. However, the political disruption following the starting decline of the Empire led to trade shrinkage, with the silting out of a portion of the basin in the 5th century CE and the building of defensive walls.

14 burials were discovered in the Antemurale area in the southwestern part of the port zone, around the Late Antique defensive structures. The bioarchaeological data from these burials herein presented contributes to broadening knowledge about the biological and cultural characteristics of people living at the chronological edge of the Roman Empire.

The osteological analysis showed that main part of the sample pertains to skeletally immature individuals, who were impacted by the harsh lifestyle experienced by the community, whose subsistence strategy was grounded on local and autarchic supply.

The isotopic characterization of the enamel and the individuals' genomic makeup suggest that people from Antemurale could be considered more similar to the Italian population of the Imperial Age and Late Antiquity than to the invading groups from Central Europe. Thus, the studied group of individuals were not biologically conditioned by the arrival of foreign armies to the outskirts of Rome in the previous centuries.

1. Introduction

Portus was the artificial maritime port of Rome at the estuarine landscape close to the mouth of the Tiber River. It was established under Emperor Claudius just a few kilometers away from Ostia in the mid-first century CE and further developed through time (Keay, 2012). Since its establishment, *Portus* represented a hub for the trade of different goods to and from the Mediterranean areas, which could reach Rome by the

---

* Corresponding author.
** Corresponding author.
E-mail addresses: flavio.deangelis@unicampania.it, flavio.deangelis@csun.edu (F. De Angelis), serenavaccaro86@gmail.com (S. Vaccaro), marco.romboni@phd.unipi.it (M. Romboni), mariarosa.dicicco@unicampania.it (M.R. Di Cicco), noemi.mantile@unicampania.it (N. Mantile), simona.altieri@unicampania.it (S. Altieri), antonio.mezzogiorno@unicampania.it (A. Mezzogiorno), marina.loblundo@cultura.gov.it (M. Lo Blundo), rickards@uniroma2.it (O. Rickards), carmine.lubritto@unicampania.it (C. Lubritto), paolafrancesca.rossi@cultura.gov.it (P.F. Rossi).

https://doi.org/10.1016/j.jasrep.2024.104931
Received 15 April 2024; Received in revised form 4 December 2024; Accepted 11 December 2024
Available online 28 December 2024
2352-409X/© 2024 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Via Campana/Portuensis, or the transfer of goods to Rome along the River Tiber in smaller riverboats. Similarly, commercial activities would have promoted the intermingling of people and cultures.

The *Portus* area activities spanned from the Imperial Age up to the Middle Age, even though its role in Late Antiquity, when a commercial downturn followed the barbarian invasions of the Roman Empire, is far from being understood comprehensively (Keay et al., 2005; O'Connell et al., 2019).

During this period, the imperial trading network experienced a significant decline due to a combination of internal and external challenges. The deterioration of Roman infrastructure, economic instability, and administrative inefficiencies weakened the Empire (Jones, 1955; Piganiol, 1950). At the same time, barbarian invasions further disrupted the economy and hampered trade, representing a pivotal factor in the Empire's decline, by reducing the security of roads and maritime routes, isolating parts of the domain, and severing long-standing trade connections with distant provinces and foreign regions (Moss, 1937).

Globally, these events caused severe damage to Rome's economic power, destabilizing the Empire and leaving its once-thriving trade network fragmented and vulnerable. Indeed, the series of incursions, culminating with the sack of Rome in 410 CE by the Visigoths and the Vandals' raid plundering the city in 455 CE, symbolized the vulnerability of the Empire (Salzman, 2021).

Locally, in the Antemurale area, political disruptions following the early fall of the Empire led to a shrinkage in trade, resulting in the silting of a portion of the basin in the 5th century CE and the construction of defensive walls (Keay, 2012).

Recently, a depiction of the biocultural characteristics of people buried in two administrative and commercial areas of the site has been published (O'Connell et al., 2019), suggesting their dietary habits. However, the local market activities would have caused a melting pot of people and cultures, and the reported data for those individuals cannot represent the complex human dynamics occurring in the area (O'Connell et al., 2019).

Accordingly, a multifaceted approach connecting the anthropological, isotopic, and genetic characteristics of the skeletal sample from the Antemurale area, would contribute to a more complete reconstruction of the biological characteristics of people buried in Portus (Fig. 1).

The Antemurale area is located in the southwestern part of the port zone, around the late antique defensive structures (Keay *et al.*, 2011).

Chronologically, it can be connected to the late stages of *Portus* activities, when defensive walls were already built, and a little cemetery was established in the embankments outside and inside the walls. This area was first archaeologically dated to the Late Antique/Early Medieval period (Paroli *et al.*, 2011), according to two archaeological sondages in 2004–2005, when 14 burials were discovered. The anthropological analysis of the recovered individuals was performed only in 2019–2020, under the supervision of the Anthropological Service of the Parco archeologico di Ostia antica and according to protocols and methodologies that later became national guidelines (Ministero Italiano Cultura, 2022). While the archaeological characteristics of the Antemurale area have been published previously (Paroli *et al.*, 2011; Paroli *et al.*, 2004), the bioarchaeological data herein presented will contribute to broadening the knowledge about the biological and cultural characteristics of people living in the area at the chronological edge of the Roman Empire.

The amount of bioarchaeological data concerning Romans and people living in the area of Rome and Ostia in Late Antiquity has continuously risen over the last years (Antonio et al., 2019, 2024; Baldoni et al., 2021; Catalano, 2015; De Angelis et al., 2015, 2021, 2022; De Angelis et al., 2020a; De Angelis et al., 2020b; Filograna et al., 2022; Gismondi et al., 2020; Killgrove, 2010; Killgrove & Montgomery, 2016; Killgrove & Tykot, 2013, 2018; Melchionda et al., 2022; O'Connell et al.,

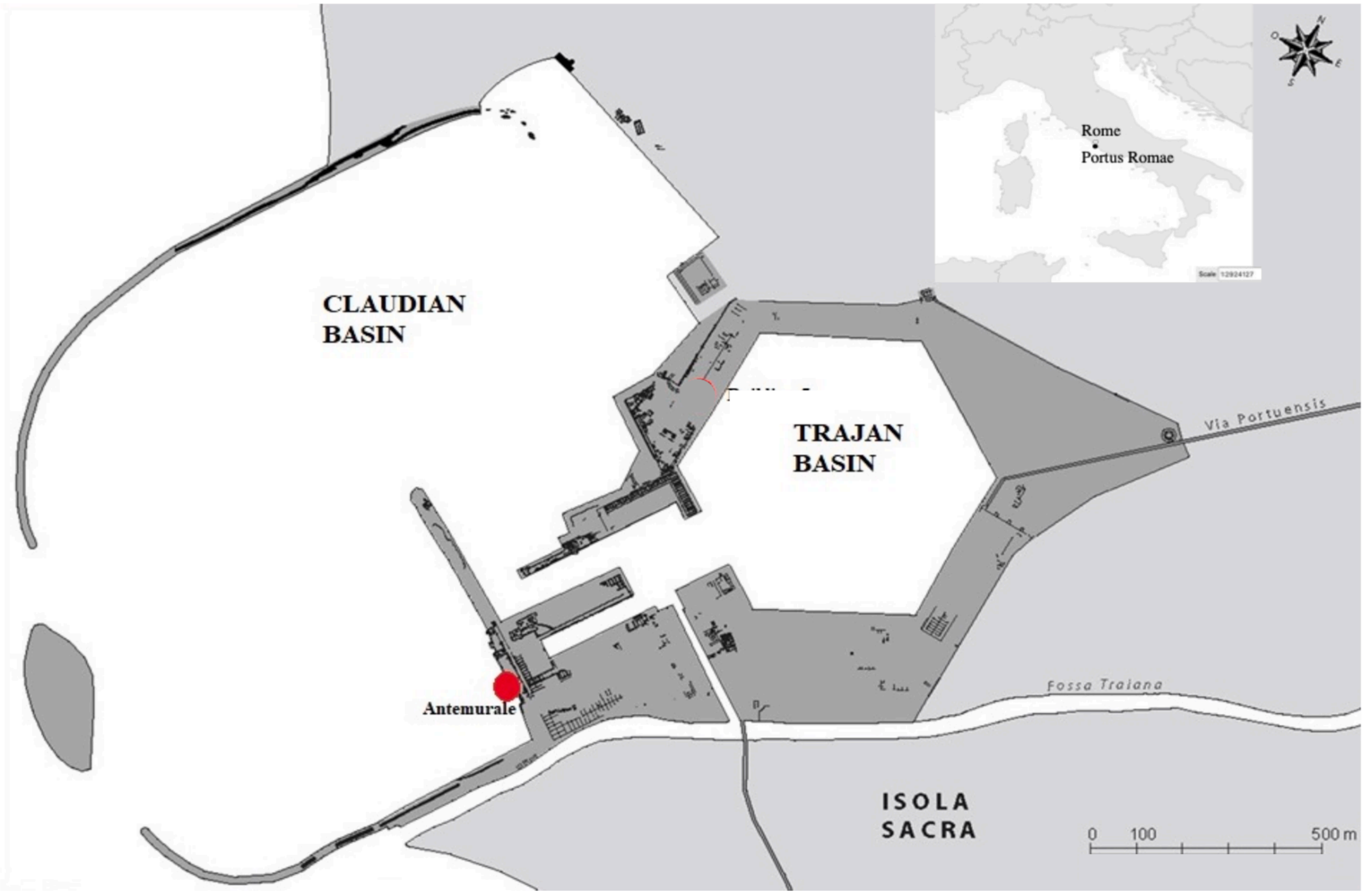

Fig. 1. Location of the Antemurale area. Modified from (Boetto et al., 2010).

2019; T. Prowse et al., 2004; T. L. Prowse et al., 2005; Varano et al., 2020), broadening knowledge about osteological characteristics, diet, mobility patterns, lifestyles, genomic makeup, and even phenotypic traits.

Accordingly, exploratory, multipronged research on the people buried in the Antemurale area of Portus would help further characterize the communities scattered throughout Rome's harbor area during the fall of the Empire, a period that had broadly impacted activities in the region.

Indeed, if the instability of the period disrupted the political and trade structures globally, it resulted in broader consequences involving either the social fragmentation and putative bio-cultural transformation through the blending of Roman and Barbarian cultures.

Specifically, we aimed to explore the biological characteristics of the Antemurale people through the osteological evaluation of the individuals, to be integrated with the exploration of the community's subsistence strategy through carbon and nitrogen stable isotope analysis of bone collagen to provide insight into human dependency on different types of food during an individual's lifetime (Ambrose, 1990; DeNiro, 1985; Hakenbeck, 2013; Katzenberg, 2007). Moreover, radiocarbon dating may confirm the exploitation period of the cemetery, which was obtained only by context (Keay et al., 2005).

Selected individuals were submitted to genomic analysis (Orlando et al., 2021) to provide information about their genetic characteristics and integrate with the few data on the genetic makeup of people living in the area in Late Antiquity. In that perspective, the data from the Antemurale area were compared with those from roughly coeval cemeteries to contribute to disentangling the complex dynamics occurring in Italian Late Antique communities during the decline of the Roman Empire. In order to study and identify mobility of the individuals themselves rather than the intergenerational mobility involving their ancestors, the information related to the genomic background was benchmarked comparing the $^{87}Sr/^{86}Sr$ signatures. Indeed, the comparison of the individual $^{87}Sr/^{86}Sr$ data with the recently developed map for both biological and geological $^{87}Sr/^{86}Sr$ values (Lugli et al., 2022) would be helpful in identifying the mobility pattern of the Antemurale individuals (Bentley, 2006), and it is widely used in archaeology to differentiate between local and non-local populations (Holt et al., 2021).

2. Materials and methods

2.1. Samples

The osteological sample from the Antemurale area consists of 14 skeletons, primarily from single burials. Still, two graves included two individuals: PTIX T12 was the burial of two children, and PTIX T13 hosted an adult individual and a child. One individual (PTIX T5) was selected for radiocarbon dating.

Diet was evaluated for all individuals, while the strontium isotopic signature was obtained for an exploratory sample consisting of 7 individuals (PTVIII T1, PTIX T3, PTIX T5, PTIX T10, PTIX T12A, PTIX T12B, and PTIX T13B), selected according to the best preservation of the tooth enamel.

The visual preservation of the teeth roots was the driving criterion for selecting four individuals (PT VIII T6, PT IX T12A, PTIX T12B, PTIX T13A) to be submitted for ancient DNA extraction and Whole Genome Sequencing.

The permit for the osteological and bioarchaeological evaluations was obtained by the Parco archeologico di Ostia antica, which granted access to the osteological collection and allowed for the study and sampling strategies by the suggestions provided by the Italian Ministry of Culture (Ministero Italiano Cultura, 2022) and international guidelines (Alpaslan-Roodenberg et al., 2021).

2.2. Osteological methods

Sex estimation was carried out only for adult individuals according to several methods, combining both morphological and metrical approaches. The morphological analysis of the hip-bone involved the examination proposed by established protocols (Bruzek, 2002; Haas et al., 1994; Phenice, 1969), which were already discussed in a recent evaluation (Nikita, 2017). The analysis of the skull and the mandible is essentially based on the indications from Haas (1994) also reported by Nikita (2017) and White et al. (2011).

Whenever the bone preservation allowed for a metrical approach, the hip-bone was evaluated by determining the ischio-pubic and the cotylo-sciatic index (Novotný, 1983; Sauter & Privat, 1954; Schultz & Schultz, 1930). In a few cases, at least 4 out of the suggested measurements on the hip-bone could be recorded for applying the method proposed by Brůžek et al. (2017). For the metrics of long bones, instead, reference was made to methods by Stewart (1979) and Pearson & Bell (1917).

Age-at-death estimation was performed according to the different methods available for young and adult individuals. For the juveniles, the level of dental (AlQahtani et al., 2010) and skeletal (Cunningham et al., 2000; Stloukal & Hakanova, 1978) growth were evaluated.

For the adults, we leveraged the combined method (Lovejoy et al., 1985a), supporting the estimates through information obtained by pubic symphysis morphology (Brooks & Suchey, 1990), dental wear (Lovejoy, 1985), morphology of the auricular surface (Lovejoy et al., 1985b), and degree of obliteration of the cranial sutures (Meindl & Lovejoy, 1985).

So far, the age classes (Haas et al., 1994) reported in Nikita & Karligkioti (2019) were considered, narrowing – whenever it was possible – the estimates according to the suggestions provided by the compared methods.

Stature was estimated for individuals who showed at least one tubular long bone fully preserved (Giannecchini & Moggi-Cecchi, 2008; Pearson, 1899; Trotter & Gleser, 1958).

Health status was evaluated through oral health indicators – caries (Temple, 2015), tooth loss (Nicklisch et al., 2022), enamel hypoplasia (Goodman & Rose, 1990), non-specific stress markers on the bones – porotic hyperostosis (Brickley, 2018), and the occurrence of trauma (Martin & Harrod, 2015).

2.3. Isotopic methods

To conduct both stable ($\delta^{13}C$ and $\delta^{15}N$) and radioactive (^{14}C) isotopic analysis, rib fragments were processed, isolating the organic phase of the bone (collagen) by adopting a modified procedure from the Longin method (Longin, 1971). A sample fragment of about 0.5–1 g was selected, and the bone surface abraded to remove superficial contaminants and pulverized.

The powder was then placed in demineralized polypropylene test tubes to carry out a sequence of acid attacks with hydrochloric acid (HCl 0.6 M); for this purpose, the tubes were stored in a cooler at 4 °C for several days. After each step, deionized water washes were carried out before the samples were dried. Lastly, the gelatinization protocol was applied.

The resulting material was weighed into tin capsules and measured at the iCONa lab of the University of Campania using a Delta V Advantage Isotope Ratio Mass Spectrometer coupled to a Flash EA 1112 Elemental Analyser via a ConFlo III interface (Thermo Fisher Scientific). Results were calibrated to the international standards VPDB for $\delta^{13}C$ and AIR for $\delta^{15}N$ using certified standard reference materials IAEA-CH6 ($\delta^{13}C = -10.45$ ‰ ± 0.03) for $\delta^{13}C$, IAEA-N2 ($\delta^{15}N = 20.3$ ‰ ± 0.2) for $\delta^{15}N$ and SIRFER yeast ($\delta^{13}C = -20.02$ ‰, $\delta^{15}N = -1.24$ ‰) for both elements. Typical analytical precision was 0.1 ‰ for $\delta^{13}C$ and 0.2 ‰ for $\delta^{15}N$, as calculated based on the repeated measurement of calibration standards (IAEA-CH6 for $\delta^{13}C$, IAEA-N2 for $\delta^{15}N$) every 24 samples (Szpak et al., 2017).

For collagen quality tests, C and N fractions of collagen dry mass (C% and N%) were measured via an elemental analyzer (CN Flash EA1112, Thermo Scientific); samples were retained for isotope analyses when the extracted collagen achieved a yield higher than 1 % and an atomic C:N ratio between 2.9 and 3.6 (DeNiro, 1985; Pate et al., 2016; van Klinken, 1999).

We developed a Bayesian mixed model through ReSources, an R application used to implement Bayesian mixing models for isotope-based dietary reconstruction upgrading the software FRUITS2 (Cocozza et al., 2023; Fernandes et al., 2014) to dissect the human diet, providing probabilistic quantification of dietary inputs. The average isotopic values of humans were used as consumer data, and all the estimated offset values were input into ReSources according to the details found in Supplementary File 1, following the directions provided by the literature (Fernandes et al., 2015). We used the data from local resources for the food categories (O'Connell et al., 2019). The carbon and nitrogen offset/weight ratios are taken from Fernandes et al. (2015). We calculated the source values in Italy and the amount of energy and proteins in each food group following previous studies (Cortese et al., 2022; Fernandes et al., 2015).

The selected sample for radiocarbon dating – PT IX T5 – underwent graphitization for accelerator mass spectrometry (AMS) radiocarbon dating, performed at the INFN-LABEC CHNet (Florence, Italy) (Fedi et al., 2014). Radiocarbon conventional dates were calibrated using the OxCal 4.4 (Ramsey & Lee, 2013) and the recommended calibration curve IntCal20 (Reimer et al., 2020).

For strontium isotopic measurements, dental enamel samples (40 mg) for PTVIII T1, PTIX T3, PTIX T5, PTIX T10, PTIX T12A, PTIX T12B, and PTIX T13B were sampled and treated in a dedicated and clean area.

Ultrapure HNO_3 obtained from a sub-boiling system (DuoPUR, Milestone, Bergamo, Italia) and ultrapure 18.2 MΩ water from a Milli-Q (Millipore, USA) system were used for the sample dissolution. HCl of hyperpure grade (Panreac, Barcelona, Spain) was used for sample treatment.

The solution was treated with selective chromatographic extraction resins for strontium (SR Resin-R, TrisKem Inter-national, Bruz, France) for separation and concentration of the analyte from other intrusive elements. The subsequent quadrupolar ICP-MS analysis (performed by 7500a, Agilent Technologies) of the solution demonstrated an excellent separation efficiency of the Sr from intrusive elements and an analyte recovery of about 90 %. The solution containing Sr was then evaporated and taken up with a volume of 1 % nitric acid (~ 500 μL) to ensure a concentration of Sr sufficient for analysis using a multi-collector mass spectrometer.

SRM-987 isotopic standard from the National Standards and Technology (NIST, Gaithersburg, MD, USA) was used for external precision measurement and method validation. Repeated measures of NBS987 yielded an $^{87}Sr/^{86}Sr$ value of 0.710144 ± 0.000010 (2 SD; $n = 12$). All values were normalized to an NBS987 accepted value of 0.710248 (McArthur et al., 2001). A Thermal Ionization Mass Spectrometer model MAT 262 VMC from Finnigan (Bremen, Germany), located at the Laboratory of Isotopic Mass Spectrometry (LIMS) of Laboratori Nazionali del Gran Sasso (LNGS) was used for isotope analysis. The double filament technique was adopted. The software Spectromat (Bremen, Germany) was used for data acquisition and analysis; mass calibration and gain calibration were performed daily (Wieser & Schwieters, 2005). Six blocks of ten replicates were acquired for each measurement reaching an associated average internal precision ≤ 0.003 %.

2.4. Genomic methods

The samples PTVIII T6, PTIX T12A, PTIX T12B, and PTIX T13A were selected for genomic evaluation and processed in a dedicated facility of the Centre of Molecular Anthropology for Ancient DNA Studies, University of Rome Tor Vergata (Italy). This clean lab is exclusively set for ancient DNA recovery and processing, as previously described (De Angelis et al., 2021, De Angelis et al., 2020a). Sterile surgical devices were used to remove soil from the samples effectively, and the specimens' surface was bleached with a clean wipe and UV-irradiated overnight at about 6 J/cm^2 at 254 nm. The powder for DNA extraction (0.08 to 0.1 g) was obtained from the cellular cementum of the teeth using a Dremel drill applying the lowest speed (Adler et al., 2011) and collected. The powder was incubated, rotating for 24 to 48 h at 37 °C in 1 mL of the extraction buffer (urea in EDTA 0.5 M and 10 μL of proteinase K (20 mg/mL) (Yang et al., 1998) and negative controls were set and maintained through the extraction process. The supernatant was collected and transferred to the Amicon Ultra-4 Centrifugal Filter Unit with Ultracel-30 from Millipore for spinning down to 100 mL. DNA was extracted and purified using MiniElute spin columns and Qiagen buffer and was stored at – 20 °C.

We applied a partial UDG treatment (Rohland et al., 2015).

An Illumina double-stranded library was built from 20 mL of extracted DNA for each specimen (Meyer & Kircher, 2010). The number of indexing cycles was gained using RT-PCR (ThermoFisher, Waltham, MA, USA). Indexing PCRs were set up in 25 mL with a final concentration of 1 × Gold Buffer (ThermoFisher, Waltham, MA, USA), 2.5 mM Magnesium Chloride, 250 mM dNTP (each), 3 mL of DNA library, 0.2 mM for each indexing primer, and 0.1 U/mL of AmpliTaq Gold (ThermoFisher, Waltham, MA, USA). The cycling conditions for library amplification were 5 min at 95 °C; followed by cycles of 30 s at 95 °C, 30 s at 60 °C, and 45 s at 72 °C; and a final extension of 5 min at 72 °C. Each library was six-fold amplified along with PCR blanks. PCR products were pooled and purified with Agencourt AMPureXP beads (Beckman Coulter, Indianapolis, IN, USA). The concentration and size profiles of the purified library were detected using a Bioanalyzer 2100 through a High Sensitivity DNA chip (Agilent, Santa Clara, CA, USA). Equimolar concentration pools were submitted to whole-genome sequencing on the Illumina HiSeqX (2 × 150 bp) at Macrogene (Seoul, Korea).

2.4.1. Data analysis for ancient DNA evaluation

Paired-end reads were trimmed for molecular barcodes and adapters using cutadapt v1.15 (M. Martin, 2011) and three bases to reduce the error rate due to deamination; and finally mapped to the human reference genome (GRCh37/hg19) as single-end reads using BWA mem algorithm v0.7.17 (Li & Durbin, 2009).

The alignments were merged through the MergeSamFiles option, available in picardtools (https://broadinstitute.github.io/picard/).

We removed duplicated sequences by identifying sets of reads with the exact external coordinates after alignment to GRCh37/hg19, executing Dedup (Peltzer et al., 2016).

The genetic sex was obtained by mapping the reads on the sex chromosomes through the Ry method (Skoglund et al., 2013). The authenticity and the quality of the suitable data were also set using ANGSD software (Korneliussen et al., 2014) to obtain a conservative estimate of contamination in the X-chromosome of males. Qualimap (Okonechnikov et al., 2016) and SAMtools (Danecek et al., 2021) flagstats command returned the basic descriptive statistics for each treated alignment. Samples' variants were filtered to those present in the 1240 K panel (release v54.1; 1,233,013 SNPs (Mallick et al., 2023) to optimize the comparison between them, ancient, and modern published references. Furthermore, filters of a minimum base and mapping quality 30 (–min-BQ and –min-MQ options) were used via samtools mpileup command. Pseudo haploid genotypes were called by pileupCaller (sequenceTools version 1.2.2: https://hackage.haskell.org/package/sequenceTools) to monitor the impact of reference bias on downstream analyses (Günther & Nettelblad, 2019). Principal component analysis (PCA) was performed using smartpca v0.13050 from EIGENSOFT package v1.6.4 (Patterson et al., 2006). The setting phase was planned through different strategies. First, a dataset comprising the Italian samples from the AADR v54.1 dataset from the Imperial period (1st-3rd cent. AD) and Late Antiquity (comprising the Longobards) (N = 125) were leveraged to detect putative genome-wide affinities in the

Italian setting. Then, the comparisons were extended to the coeval European context—323 individuals (Supplementary File 2).

In both approaches, we projected the Portus samples into the PC space (lsqproject option set to ON), due to the considerable amount of missing data in the ancient data from Portus individuals.

A supervised ADMIXTURE (Alexander & Lange, 2011) analysis was performed to reveal the genetic components related to both Imperial and Late Antique individuals in the dataset. The variant panel from the autosomes was previously pruned of rare variants and those in linkage disequilibrium through the PLINK 1.9 options –maf 0.05 and —-indep-pairwise 200 10 0.3. We applied the supervised mode to detect the components according to an *a priori* choice of the reference populations. We selected six reference populations: Italy (no Latium) Imperial Age, Italy (no Latium) Late Antiquity, Latium Imperial Age, Germany Late Antiquity, Lombards, and Slovenia Imperial Age. We exploited pong v1.4.9 (Behr et al., 2016), to visualize the admixture proportion inferences.

We calculated the outgroup f3 statistics to quantify the shared drift between two populations by measuring the length of the shared branch between them (i.e., shared genetic drift) from an outgroup. qp3Pop from ADMIXTOOLS v6.0 was used to consider the standard errors with a block jackknife. The outgroup f3 statistic was calculated in the form (Yoruba; X, Y) on the customized 1240 K panel.

Similarly, we tested for differences among comparative populations through D-statistics (Yoruba, Test; Pop1, Pop2).

Schmutzi (Renaud et al., 2015) was used to determine the consensus mitochondrial sequence and the contamination estimation. The mitogenome sequences were aligned against the revised Cambridge Reference Sequence (rCRS) (NC_012920.1) to assign the mitochondrial haplogroup through the Haplogrep build on the Phylotree 17 classification algorithm (Weissensteiner et al., 2016).

Samples identified as genetically male were submitted to the classification of the Y chromosome through Yleaf (Ralf et al., 2018).

3. Results and Discussion

Despite the restricted sample size available for the Antemurale Area in Portus, the osteological, isotopic, and genomic evaluations of skeletons buried therein could provide novel information and ultimately contribute to a better understanding of the resilience of the ancient communities against the historical events occurring just beyond the decline of the Roman Empire. Indeed, the radiocarbon dating performed on one of the samples from Antemurale returned a wide date of 551–706 CE (Fi4438-iCONa: 1400 + -58 BP) (Supplementary File 3).

The osteological characterization of the samples determined the basic demographic parameters, such as sex and age at death (Table 1) (Vaccaro et al., 2023).

Even though the preservation status impacted the reliable estimation of multiple osteological markers, we can score the presence of a single female and five male individuals. Remarkably, eight individuals were children, so identifying the sexually dimorphic osteological characteristics remains challenging (Buonasera et al., 2020).

Oral health was only slightly impacted by carious lesions, which are detectable only in six individuals, even though two were children. Three out of six adult individuals lost some teeth intra-vitam: the antemortem tooth loss (AMTL) was particularly striking for PT IX T5 and PT IX T10, who suffered from the loss of 9 and 13 teeth, respectively (Table 1). This seems to suggest their harsh living conditions (Walkup et al., 2023).

The localized hyperostosis on the skull – *Cribra orbitalia* – is detected in 50 % of the sample, while the linear enamel hypoplasia – a non-specific enamel defect due to stressful and unhealthy lifestyle (Minozzi et al., 2020) is detected in six individuals (Table 1). The harsh everyday life for the individuals buried in Antemurale was also testified by the co-occurrence of both these defects in five skeletally immature individuals (Table 1). However, the lifestyle of the people buried in Antemurale seems not to have exposed them to massive injuries, as the occurrence of trauma leaving signs on the skull is restricted to individual PT VIII T1, whose bones of the lower limbs were characterized by the partial fusion of the proximal Tibial and Fibular epiphyses due to traumatic events.

The overall picture gained from this sample shows a high mortality in children, who represent the most substantial part of this small sample and do not reach the age of ten. The significant presence and coexistence of non-specific stress markers indicate a disruption in metabolic rhythm during the growth period, which could have led to fatal outcomes. On the other hand, adults who have survived the most critical period—childhood—reach considerable ages.

The availability of three femurs allows for estimating the stature of only three adult individuals (Table 1) according to different methods. The results show statures slightly different from the average calculated in the Central Italian peninsula from the Roman period and Middle Ages (Giannecchini & Moggi-Cecchi, 2008): the two male individuals PT VIII T1 and PT IV T5 are taller than the average; conversely, the woman PT IV T10 was characterized by a shorter stature. Specifically, the results for PT VIII T1 is 2 SD higher than the reported average – from 164.4 to 166.9 cm for males (Danubio et al., 2017; Giannecchini & Moggi-Cecchi, 2008) and could come with the putative influence from taller northern populations. Similarly, the estimation for PT IV T10 is 2 SD lower than the mean stature in Medieval Central Italian population (154.5 cm for females (Giannecchini & Moggi-Cecchi, 2008)), suggesting that the short stature of the female individual could be consistent with the demanding lifestyle she experienced (Quade & Gowland, 2021), as testified by the conjoined massive AMTL, porotic hyperostosis (*cribra cranii*), and linear enamel hypoplasia.

Thirteen out of 14 individuals submitted to the diet reconstruction through the carbon and nitrogen stable isotope analysis returned a collagen yield good enough for the spectrometric evaluation, even though PT IX 13A was characterized by a C/N ratio falling outside the range suggested for obtaining suitable spectrometric data (van Klinken, 1999). Accordingly, even considering the δ^{13}C and δ^{15}N consistent with the overall distribution, we retain the data for 12 individuals (Table 1).

The isotopic values show heterogeneity in terms of δ^{13}C and δ^{15}N values. Indeed, the δ^{13}C ranges from −20.5 to −18.5 ‰ (median = -19.2 ‰), while the δ^{15}N values span from 5.6 to 11.1 ‰ (median 8.3 ‰).

Unfortunately, no faunal remains were analyzed from Antemurale, but the ecological background could be detailed by leveraging the data available for the Portus area through centuries (O'Connell et al., 2019).

Two out of 14 individuals from Antemurale died as toddlers (PTVIII T2 and PTIX T9), and their high δ^{15}N values mirror the well-known breastfeeding effect (Fuller et al., 2006) rather than the genuine protidic fraction of the individual's diet.

Remarkably, PTVIII T6 shows one of the lowest δ^{15}N fingerprints: even though the age of weaning cannot be determined precisely, the age-at-death of 2–2.5 paves the way to consider this individual as just weaned, when fast growth and weaning of the children may cause a drop in the δ^{15}N (Chinique de Armas et al., 2022; De Angelis et al., 2020a; Tsutaya & Yoneda, 2015). From that perspective, we can detect that in Antemurale, the children were considered adults, at least from a dietary perspective, at 2–3, and were in perfect agreement with the estimations for the previous Imperial period (De Angelis et al., 2020b; Killgrove & Tykot, 2013; Prowse et al., 2005).

Despite the proximity to the coastline, people from Antemurale did not ground their dietary preferences on marine resources. Instead, the exploitation of terrestrial resources seems somewhat consistent. So far, the comparison between Antemurale and people buried in Building 5 (Portus 5th-6th cent AD (O'Connell et al., 2019) underlines a slight difference in their resource exploitation. Indeed, there was an overall change in the protidic consumption in Antemurale with respect to Building 5, which is detectable through the Bayesian reconstructions (Fernandes et al., 2014) (Fig. 2, Supplementary File 1) leveraging the herbivore and C3 plants isotopic signals (O'Connell et al., 2019).

The evaluation of the human signals shows that people from the

Table 1

Summary Table for osteological and isotopic data. M: Male; F: Female; Ch: Child (undetermined sex). X.presence.

Sample	Sex	Age at death	Teeth	Teeth with cavities	Antemortem Lost Teeth	Diffuse Calculus	Stature Trotter & Gleser cm	Stature Pearson cm	Teeth with LEH	Cribra orbitalia	Cribra cranii	Trauma	δ13C (‰) vs. VPDB	δ15N (‰) vs. Air	%N	%C	C/N	87/86Sr
PT VIII T1	M	45–55	28	3	3	–	174 ± 3	173 ± 2	–	–	–	Lower limb	−18.5	8.5	1.3	3.8	3.6	0.70987 ± 0.00001
PT VIII T2	Ch	0.5 – 1.5	9	–	–	–	–	–	2	X	–	–	−18.7	11.1	9.4	25.8	3.2	–
PT VIII T4	Ch	5.5 – 6.5	13	–	–	–	–	–	1	X	–	–	−19.0	9.6	6.8	19.8	3.4	–
PT VIII T6	Ch	2.5—3.5	23	1	–	–	–	–	–	X	–	–	−19.8	7.6	9.8	27.6	3.3	–
PT IX T3	M	35–40	32	1	–	X			–	–	–	–	−18.6	11.0	5.7	16.6	3.4	0.70854 ± 0.00003
PT IX T5	M	50+	20	3	9	–	167 ± 3	168 ± 2	–	X	X	–	–	–	–	–	–	0.70959 ± 0.00005
PT IX T7	Ch	9–10	24	–	–	–	–	–	4	–	–	–	−20.5	5.6	7.8	21.8	3.3	–
PT IX T9	Ch	1.5	5	–	–	–	–	–	–	–	–	–	−19.0	10.6	14.6	40.7	3.2	–
PT IX T10	F	30–40	13	2	18	X	147 ± 3	147 ± 2	1	X	–	–	−19.9	7.9	2.7	8.2	3.6	0.71011 ± 0.00004
PT IX T11	M	Adult	–	–	–	–	–	–	–	–	–	–	−20.2	6.3	2.1	6.5	3.6	–
PT IX T12 A	Ch	5–6	14	–	–	–	–	–	–	–	–	–	−19.0	8.7	1.5	4.8	3.6	0.70980 ± 0.00007
PT IX T12 B	Ch	6–7	14	2	–	–	–	–	3	X	–	–	18.7	8.8	1.8	5.2	3.4	0.70982 ± 0.00002
PT IX T13 A	Ch	9–10	9	–	–	–	–	–	7	X	–	–	−17.8	8.8	0.6	3.7	6.8	–
PT IX T13 B	M	40–45	15	–	–	–	–	–	–	–	–	–	−19.4	6.9	1.0	3.1	3.6	0.70932 ± 0.00001

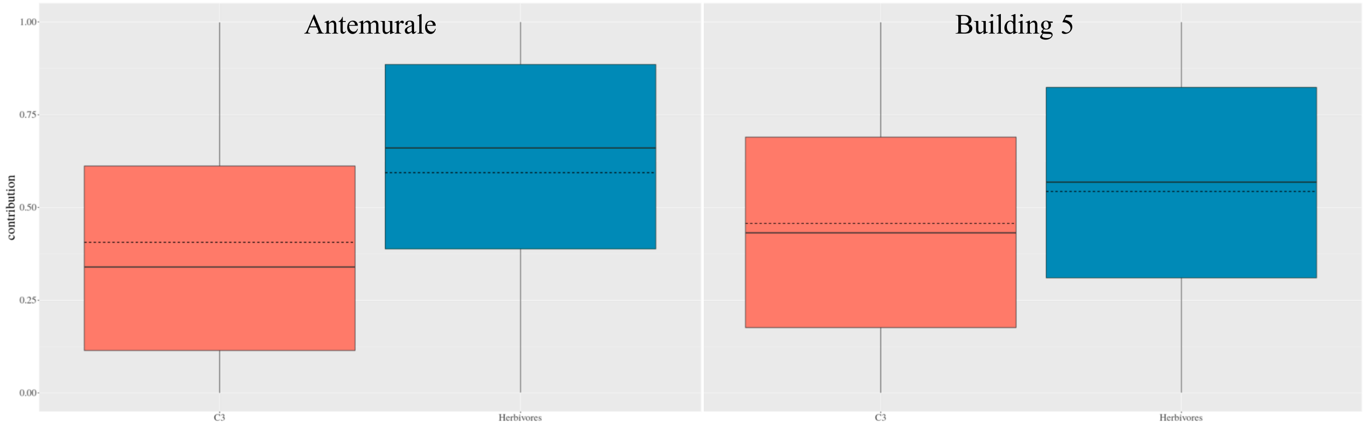

Fig. 2. Bayesian reconstruction of the differential exploitation of C3 plants and animal (herbivore) proteins in Antemurale (left) vs Building 5 (right) communities of Portus.

previous centuries experienced different dietary habits than the Antemurale people. Indeed, the two communities are different in their $\delta^{15}N$ ($T = 4.25$; $p = 7E\text{-}04$), while the difference at $\delta^{13}C$ is negligible ($T = 1.56$; $p = 0.064$).

This evidence agrees with the speculations about the differential dietary habits in Portus through time already proposed for the area (O'Connell et al., 2019), underlining the cultural variation of people who adapted their lifestyle to the socio-economic and environmental conditions of the society where they lived.

Indeed, the collapse of the centralized rule of the Western Roman Empire following Barbarian raids culminating in the Sack of Rome (410 CE) triggered the development of changing lifestyles across the Roman territories. Thus, the crisis of the centralized economy and the simultaneous closure of several trade routes resulted in the overall development of an autarchic economic system (Elliott, 2020). The Gothic War (461–476 CE) dramatically impacted the population size of Rome and surrounding areas, pushing people to relocate to small settlements (Kelly, 2023). Accordingly, the Antemurale individuals could match one of these small communities, whose daily life was characterized by self-procurement of foodstuffs rather than getting them through the market economy. Indeed, starting from the middle of the 5th century CE the harbor area was active, but the volume of trade that passed through contracted dramatically (Keay et al., 2005). Accordingly, terrestrial resources such as grains and vegetables, as well as secondary products such as milk and dairy products, should be the staple of their dietary habits for such dwellings. Indeed, the isotopic evidence in early medieval Rome (Varano et al., 2020) supports the exploitation of these resources, also confirmed in roughly coeval sites in Northern and Central Italy (O'Connell et al., 2019; Riccomi et al., 2020; Tafuri et al., 2018; Temkina, 2021).

The comparison with roughly coeval communities for which the isotopic data are available (Riccomi et al., 2020; Tafuri et al., 2018) shows a similar $\delta^{15}N$ signature in Selvicciola ($T = -0.81$; $p = 0.211$), a burial ground established in northern Latium between 4th and 8th

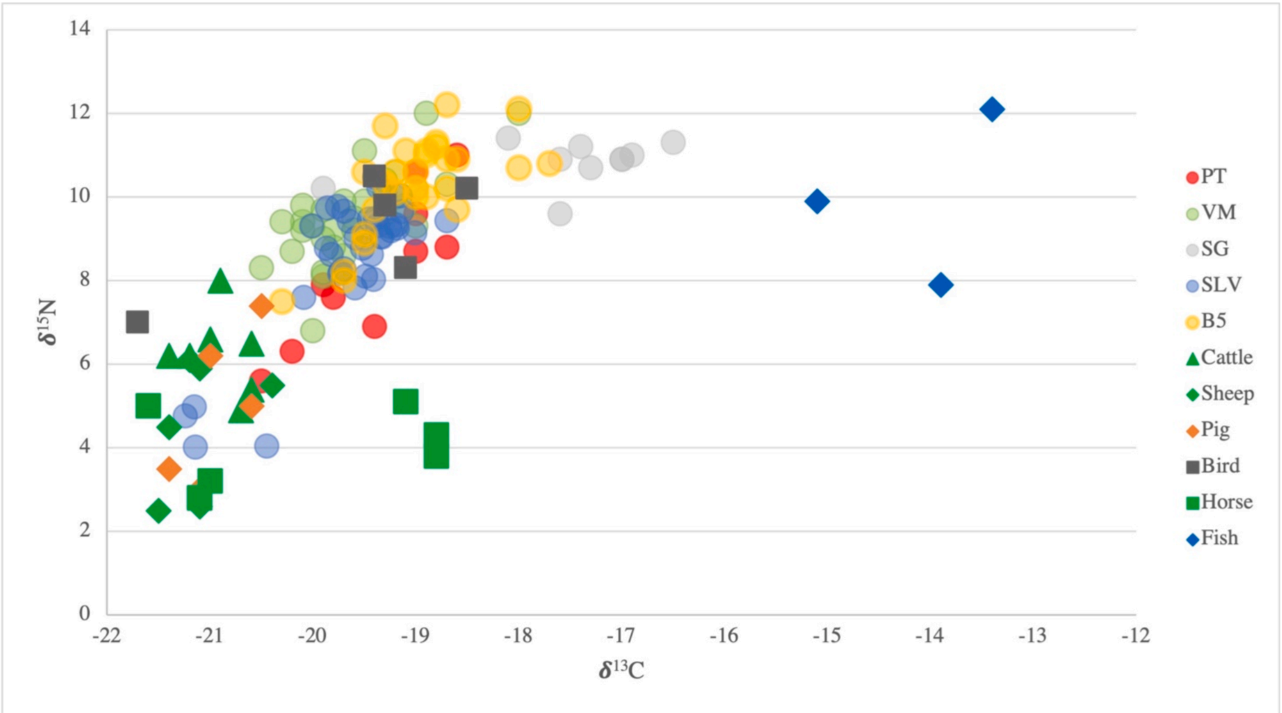

Fig. 3. Isotope data dispersion for faunal remains and humans. PT: Antemurale; B5: Building 5; SG: Wallari/Borgo San Genesio; VM: Via Marche; SLV: Selvicciola.

century CE, while two slightly diachronic communities in Tuscany show a different pattern (Via Marche, 3rd–5th centuries AD; T = -3.42; p = 7.16E-4; and Wallari/Borgo San Genesio, 6th–13th centuries AD; T = -4.77; p = 6.6E-4) (Fig. 3). Accordingly, our data are consistent with the hypothesis suggesting that the local environment, along with the 'collapse' and depopulation of much of the Italian urban networks following the fall of the Western Roman Empire, represented a critical factor in driving the lifestyles at a community level (Chavarría Arnau, 2011).

Indeed, the socio-political events in Late Antique Italy could have represented multiple tipping points for developing distinctive biocultural characteristics (Rose, 2021).

The arrival of Germanic armies up to Rome in the previous centuries, followed by sieges and multiple attacks, greatly increased the chance of introducing cultural phenomena, social habits, and even genes in the forthcoming generations (Amorim et al., 2018; Jones, 2021).

Recently published evidence has highlighted that roughly 10 % of Roman population in the Imperial period did not originate from the area where they were buried. This result, in turn, explains how trade routes and the movements of people fueled diversity in the Roman Empire (Antonio et al., 2024), which was further tuned in the following periods due to the forced migration and admixture occurring across communities.

We generated whole genome data for four individuals from Antemurale to explore the putative traces of allochthonous people in the cultural and biological characteristics of the individuals from Portus. Despite the restricted sample size, to the best of our knowledge, this is one of the first pilot studies about the genomic characteristics of people from the area in Late Antiquity – 5 individuals from San Ercolano, Ostia, were already characterized (Antonio et al., 2019) –, thus representing a helpful further step for future in-depth analyses.

The endogenous DNA ranges between 0.67 % and 7.05 %, with a maximum coverage of 0.053x (std. dev. 0.789), suggesting that the DNA preservation was greatly affected by the chemical-physical processes of the burial environment (Zhu et al., 2022) (Supplementary Table 1).

Three of four Antemurale samples (PTVIII T6, PTIX T12A, PTIX T12B) returned at least 40,000 reads and were compared to the variability across roughly coeval and Imperial period Italian populations. Fig. 4 shows that Antemurale people fall in the variability of the selected populations, even though their affinities with the Imperial period individuals cannot be denied. Indeed, the broad impact of the Roman Empire in the relocation of thousands of people from different geographical areas towards the center of the Empire resulted in a heterogeneous genetic makeup of these individuals (Antonio et al., 2019, 2024; De Angelis et al., 2021, De Angelis et al., 2020a), which could make the identification of differences across people from both Imperial and Late Antique periods challenging.

However, to detect the putative allochthonous genetic components in the sample, we broadened our evaluation, including European populations, that could be introduced in the Italian peninsula through the barbarian invasions of the 4th century CE (Halsall, 2005).

The first genetic component marks the overall differentiation between Central European and Mediterranean populations (Fig. 5). Antemurale individuals show a remarkable difference in the first genetic component. PT VIII T6 and PT IX T12A appear similar to the Imperial period Italians – even though PT IX T12A falls apart in the second

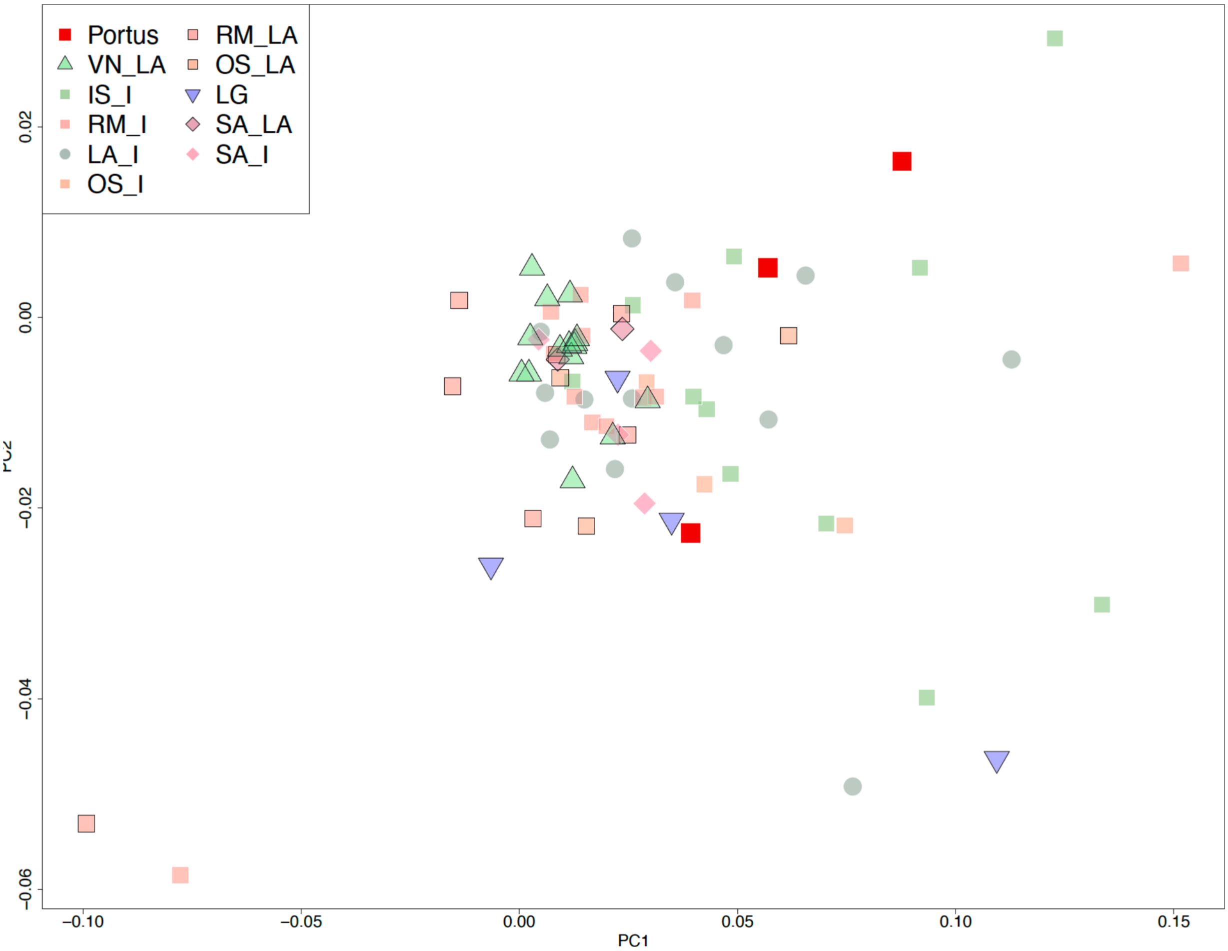

Fig. 4. PCA plot for the relationship of Portus individuals with roughly coeval Italian populations (Supplementary File 2). LG: Lombards; SA: Sardinia; OS: Ostia; RM: Rome; LA: Latium; IS: Isola Sacra; VN: Venosa._I: Imperial Time;_LA: Late Antiquity.

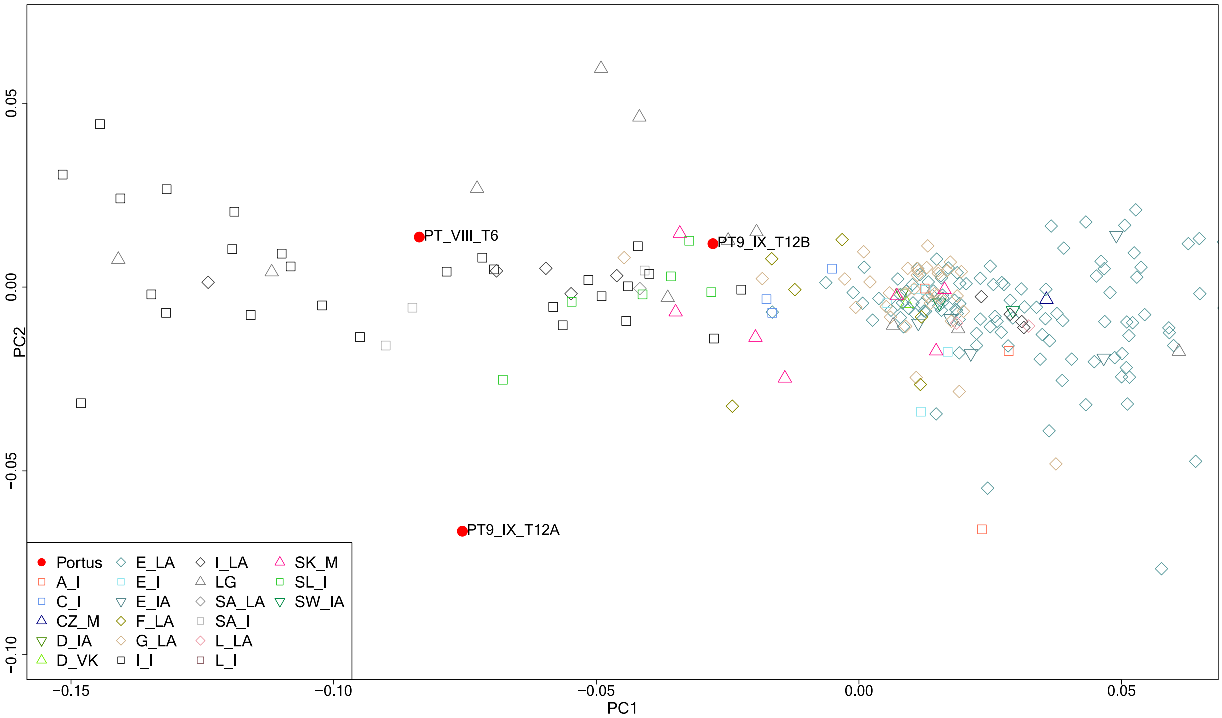

Fig. 5. PCA plot for the relationship of Portus individuals with roughly coeval Western European populations (Supplementary File 2). A: Austria; C: Croatia; CZ: Czech Republic; D: Denmark; E: England; F: France; G: Germany; I: Italy; LG: Lombards; SA: Sardinia; L: Lithuania; SK: Slovakia; SL: Slovenia; SW: Sweden._I: Imperial Age;_M: Medieval;_IA: Iron Age;_VK: Viking Age;_LA. Late Antiquity.

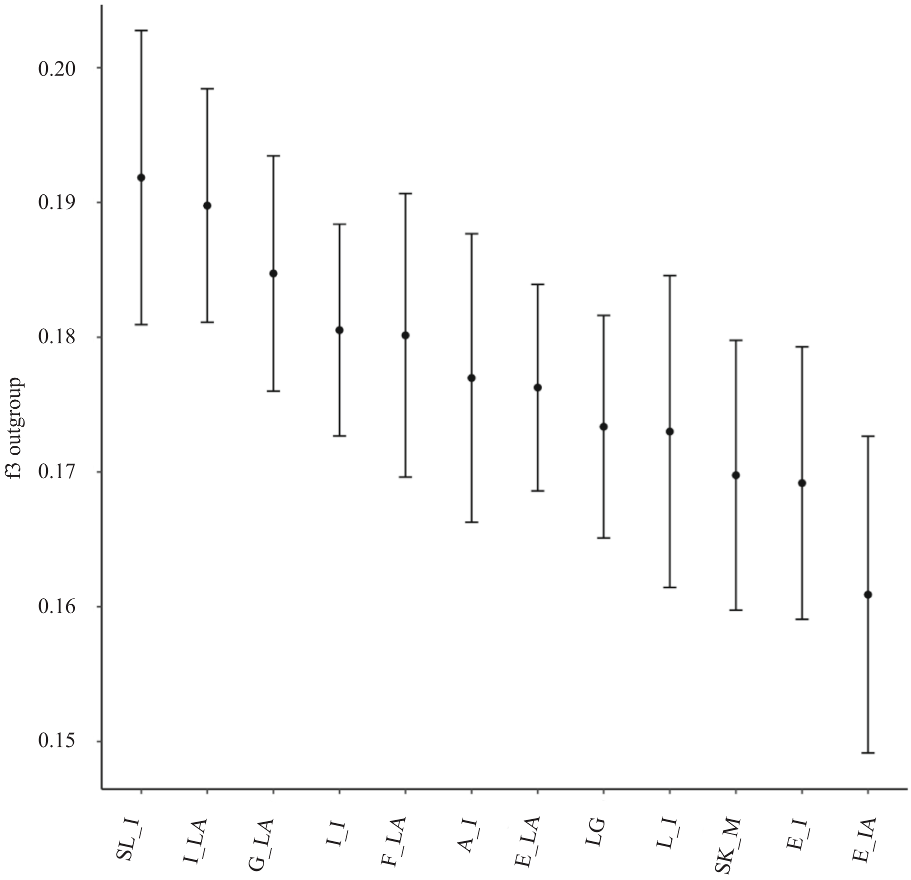

Fig. 6. f3 outgroup (Yoruba; Portus, popX). Codes for the populations (popX) are reported in Fig. 5.

component, probably because of the deficient number of useful SNPs – while PT IX T12B is between the Italians and the Continental Europeans, supporting the heterogeneity characterizing the Central Italian Late Antique population.

To further explore the genetic affinities of Antemurale, we leveraged the f3 outgroup statistic in the form (Yoruba; Portus, popX).

This analysis pointed out the magnitude of the impact of both Imperial and Late Antique continental populations' genetics in the Antemurale samples, even though we should consider the tiny difference in the magnitude of the statistic (Fig. 6) as well as the effect of the low sample size for the test sample, which makes this result to be considered with extreme caution (Mughal & DeGiorgio, 2022).

The D-statistic (Fig. 7) was also determined as an additional parameter to underline correlations of allele frequency differences by evaluating a test population's similarity for two references and the outgroup population (Yoruba, Antemurale; popX, popY).

Both the analyses showed that Antemurale people show evidence of introgression from Italian Late Antique groups and Slovenians from Imperial Age (Antonio et al., 2024), suggesting a putative gene flow between people coming from the northern fringe of the Balkan countries and Central Italian communities. This evidence could match the historical events in the 5th century CE when the Goths moved massively to Italy (Boin, 2020). However, the restricted sample size could bias that overall interpretation.

Indeed, the supervised ADMIXTURE analyses considering the Imperial Age people from Latium and all the Italian Peninsula, as well as from Slovenia and Late Antique people from Germany, Italy, and Lombards as reference populations, show that the three individuals from Portus share a consistent Italian genomic background (both from the Imperial Age and Late Antiquity), with only one sample returning a slight central European genetic component from the Imperial Age (Fig. 8).

So far, the genomic information concurs in defining the three samples from Antemurale as more similar to local and the Imperial Age groups than to people that belonged to incoming groups of invaders from Central Europe.

The mtDNA haplogroups for the three individuals were characterized by subsetting the reads aligning the mitogenome (coverage ranging from 0.94x to 4.45x): all the haplogroups pertain to the H lineages, supporting the European genetic origin of their maternal lineages (Roostalu et al., 2007), but not further specified.

The molecular sex determination was unambiguously possible for PT9_T12B, which returned a male assignment. His Y chromosome belongs to the T-L162*, which derive from T-M70, a lineage which is found at variable frequencies across West Asia, Africa, and Europe (Mendez et al., 2011).

As already stated, the radiocarbon dating performed on one of the samples from Antemurale returned a wide date of 542–716 CE, suggesting that the Antemurale people could represent the heirs of individuals who already experienced the gene flow from both the local and arriving populations.

That speculation is also supported by the Sr isotope ratios obtained in our study, which pointed out a local origin for the Antemurale individuals, also comparing those individuals with the restricted samples from previous studies attempting to determine a local range for those indicators (Killgrove & Montgomery, 2016; Killgrove & Tykot, 2018).

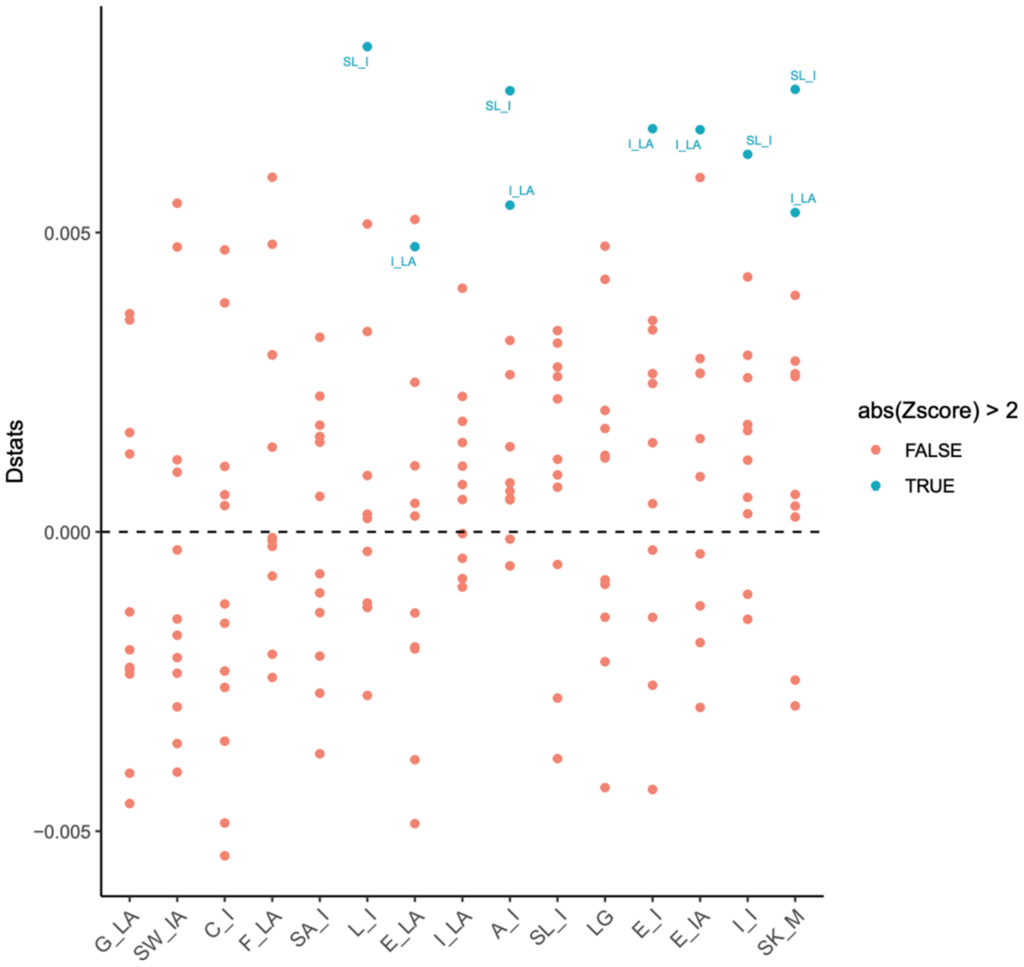

Fig. 7. D-statistics representation in the form (Yoruba, Antemurale; popX, popY). Codes for the populations are reported in Fig. 5.

Fig. 8. Supervised Admixture plot for K = 6. Codes for the populations are reported in Fig. 5.

Indeed, strontium isotope data for all the individuals from Antemurale are between 0.70854 and 0.71011, consistent with the geology of the Colli Albani and the recently developed local isoscape for the Italian peninsula (Lugli et al., 2022). Specifically, three out of four genomically characterized samples returned a narrow range of $^{87}Sr/^{86}Sr$ values from 0.70932 to 0.70982, which falls in the range defined for human and animal teeth in the area around Rome (Lugli et al., 2022).

Unfortunately, the strontium characterization of PT VIII T6 did not return enough strontium to be compared with the genomic information.

Overall, the archaeological speculations and the bioarchaeological survey herein are consistent in reasonably considering the individuals from Antemurale as a single community of local origin characterized by similar biocultural characteristics related to health and lifestyle. To the best of the knowledge gained through our analyses, we hypothesize that people buried there could be heirs of people inhabiting central Italy in the Imperial Age, which were only slightly impacted genetically by the arrival of allochthonous people from northern areas.

Certainly, despite the significant frequency of migration in the area, there is minimal indication of population homogenization, as already proposed in a wider perspective (Antonio et al., 2024). Compared to expectations, the relatively subdued impact of migration likely stems from decreased mobility following the decline of the Empire and the potential for a more intricate assimilation of migrating individuals into the societal framework of local populations.

4. Conclusions

The recent development of an integrated approach made possible the analyses we performed on different aspects of the biocultural characteristics of people living in the Antemurale area of Portus.

The osteological evaluation showed that most of the sample pertains to skeletally immature individuals. They were prone to be impacted by the harsh lifestyle of the local community. Indeed, the non-specific stress markers detectable on the adults' bone suggest they were part of a low-income community, where oral pathologies and stressful conditions undermined the overall health status.

The consumption of terrestrial resources was a staple for this community, whose subsistence was based on local and autarchic supply. Indeed, the isotopic characterization of the enamel supports the local development of the community, which exploited local plants for their subsistence. Accordingly, the individuals should be considered local in terms of their geographic origin. However, their genetic heritage is local as well. Indeed, the genomic characterization of a subset, though massively impacted by the deleterious diagenetic factors, showed that people from Antemurale could be considered more similar to the Italian people of the Imperial Age and Late Antiquity than the invading groups from Central Europe. In that perspective, to the best of our knowledge, we can conclude that people in the Portus area were not massively conditioned by the arrival of foreign armies on the outskirts of Rome in the previous centuries.

We are conscious that the data generated in the analyses of the 14 tombs from the Late Antique Antemurale area could represent the starting point for the systematic and comprehensive evaluation of the osteological material recovered in the Portus area, still underrepresented in the bioarchaeological assessment of the complex dynamics occurring in the area between Rome and Ostia in Late Antiquity. Indeed, the widely replication of our multipronged approach on other roughly contemporary funerary areas, as well as the evaluation of additional isotope systems on both humans and faunal/plant remains, will shed light on the bio-cultural impact of incoming people in the Italian peninsula at the end of the Roman Empire.

CRediT authorship contribution statement

Flavio De Angelis: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Serena Vaccaro:** Formal analysis, Data curation. **Marco Romboni:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Maria Rosa Di Cicco:** Writing – review & editing, Formal analysis, Data curation. **Noemi Mantile:** Writing – review & editing, Formal analysis, Data curation. **Simona Altieri:** Writing – review & editing, Formal analysis, Data curation. **Antonio Mezzogiorno:** Formal analysis, Methodology, Writing – review & editing. **Marina Lo Blundo:** Writing – review & editing, Resources. **Olga Rickards:** Writing – review & editing, Resources, Funding acquisition. **Carmine Lubritto:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Paola Francesca Rossi:** Writing – review & editing, Supervision, Resources, Formal analysis, Conceptualization.

Acknowledgments

We would thank the Director of the Parco archeologico di Ostia antica, Alessandro D'Alessio.

FDA was supported by the project: MNESYS—a multiscale integrated approach to the study of the nervous system in health and disease (PNRR).

This work was partially supported by the Italian Ministero dell'Università e della Ricerca (PRIN 2017 action ID 20177PJ9XF allotted to OR).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2024.104931.

Data availability

Data will be made available on request.

References

Adler, C.J., Haak, W., Donlon, D., Cooper, A., 2011. Survival and recovery of DNA from ancient teeth and bones. J. Archaeol. Sci. 38 (5), 956–964. https://doi.org/10.1016/j.jas.2010.11.010.

Alexander, D.H., Lange, K., 2011. Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. BMC Bioinf. 12 (1), 246. https://doi.org/10.1186/1471-2105-12-246.

Alpaslan-Roodenberg, S., Anthony, D., Babiker, H., Bánffy, E., Booth, T., Capone, P., Deshpande-Mukherjee, A., Eisenmann, S., Fehren-Schmitz, L., Frachetti, M., Fujita, R., Frieman, C.J., Fu, Q., Gibbon, V., Haak, W., Hajdinjak, M., Hofmann, K.P., Holguin, B., Inomata, T., Zahir, M., 2021. Ethics of DNA research on human remains: five globally applicable guidelines. Nature 599 (7883), 7883. https://doi.org/10.1038/s41586-021-04008-x.

AlQahtani, S.J., Hector, M.P., Liversidge, H.M., 2010. Brief communication: The London atlas of human tooth development and eruption. Am. J. Phys. Anthropol. 142 (3), 481–490. https://doi.org/10.1002/ajpa.21258.

Ambrose, S.H., 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. J. Archaeol. Sci. 17 (4), 431–451. https://doi.org/10.1016/0305-4403(90)90007-R.

Amorim, C.E.G., Vai, S., Posth, C., Modi, A., Koncz, I., Hakenbeck, S., La Rocca, M.C., Mende, B., Bobo, D., Pohl, W., Baricco, L.P., Bedini, E., Francalacci, P., Giostra, C., Vida, T., Winger, D., von Freeden, U., Ghirotto, S., Lari, M., Veeramah, K.R., 2018. Understanding 6th-century barbarian social organization and migration through paleogenomics. Nat. Commun. 9 (1), 1. https://doi.org/10.1038/s41467-018-06024-4.

Antonio, M.L., Gao, Z., Moots, H.M., Lucci, M., Candilio, F., Sawyer, S., Oberreiter, V., Calderon, D., Devitofranceschi, K., Aikens, R.C., Aneli, S., Bartoli, F., Bedini, A., Cheronet, O., Cotter, D.J., Fernandes, D.M., Gasperetti, G., Grifoni, R., Guidi, A., Pritchard, J.K., 2019. Ancient Rome: a genetic crossroads of Europe and the Mediterranean. Science 366 (6466), 708–714. https://doi.org/10.1126/science.aay6826.

Antonio, M.L., Weiß, C.L., Gao, Z., Sawyer, S., Oberreiter, V., Moots, H.M., Spence, J.P., Cheronet, O., Zagorc, B., Praxmarer, E., Özdoğan, K.T., Demetz, L., Gelabert, P., Fernandes, D., Lucci, M., Alihodžić, T., Amrani, S., Avetisyan, P., Baillif-Ducros, C., Pritchard, J.K., 2024. stable population structure in europe since the iron age, despite high mobility. eLife 13, e79714. https://doi.org/10.7554/eLife.79714.

Baldoni, M., Nardi, A., De Angelis, F., Rickards, O., Martínez-Labarga, C., 2021. How does diet influence our lives? evaluating the relationship between isotopic signatures and mortality patterns in italian roman imperial and medieval periods. Molecules (Basel, Switzerland) 26 (13), 3895. https://doi.org/10.3390/molecules26133895.

Behr, A.A., Liu, K.Z., Liu-Fang, G., Nakka, P., Ramachandran, S., 2016. pong: fast analysis and visualization of latent clusters in population genetic data. Bioinformatics (Oxford, England) 32 (18), 2817–2823. https://doi.org/10.1093/bioinformatics/btw327.

Boetto, G., Bukowiecki, É., Monteix, N., & Rousse, C. (2010). Portus. Les entrepôts de Trajan. Mélanges de l'École française de Rome - Antiquité, 122–1, Article 122–1. doi: 10.4000/mefra.469.

Boin, D., 2020. Alaric the Goth: An Outsider's History of the Fall of Rome. Norton & Company, W. W.

Brickley, M.B., 2018. Cribra orbitalia and porotic hyperostosis: A biological approach to diagnosis. Am. J. Phys. Anthropol. 167 (4), 896–902. https://doi.org/10.1002/ajpa.23701.

Brooks, S., Suchey, J.M., 1990. Skeletal age determination based on the os pubis: A comparison of the Acsádi-Nemeskéri and Suchey-Brooks methods. Hum. Evol. 5 (3), 227–238. https://doi.org/10.1007/BF02437238.

Bruzek, J., 2002. A method for visual determination of sex, using the human hip bone. Am. J. Phys. Anthropol. 117 (2), 157–168. https://doi.org/10.1002/ajpa.10012.

Brůžek, J., Santos, F., Dutailly, B., Murail, P., Cunha, E., 2017. Validation and reliability of the sex estimation of the human os coxae using freely available DSP2 software for bioarchaeology and forensic anthropology. Am. J. Phys. Anthropol. 164 (2), 440–449. https://doi.org/10.1002/ajpa.23282.

Buonasera, T., Eerkens, J., de Flamingh, A., Engbring, L., Yip, J., Li, H., Haas, R., DiGiuseppe, D., Grant, D., Salemi, M., Nijmeh, C., Arellano, M., Leventhal, A., Phinney, B., Byrd, B.F., Malhi, R.S., Parker, G., 2020. A comparison of proteomic, genomic, and osteological methods of archaeological sex estimation. Sci. Rep. 10 (1), 1. https://doi.org/10.1038/s41598-020-68550-w.

Catalano, P., 2015. What skeletons tell us. Med. Secoli 27 (3), 773–785.

Chavarría Arnau, A., 2011. In: Changes in Scale in the Italian Countryside from Late Antiquity to the Early Middle Ages. Brepols Publishers, pp. 121–132. https://doi.org/10.1484/M.TMC-EB.3.4770.

Chinique de Armas, Y., Mavridou, A.-M., Garcell Domínguez, J., Hanson, K., Laffoon, J., 2022. Tracking breastfeeding and weaning practices in ancient populations by combining carbon, nitrogen and oxygen stable isotopes from multiple non-adult tissues. PLoS One 17 (2), e0262435. https://doi.org/10.1371/journal.pone.0262435.

Cocozza, C., Teegen, W.-R., Vigliarolo, I., Favia, P., Giuliani, R., Muntoni, I.M., Oione, D., Clemens, L., Groß, M., Roberts, P., Lubritto, C., Fernandes, R., 2023. A Bayesian multi-proxy contribution to the socioeconomic, political, and cultural history of late medieval Capitanata (southern Italy). Sci. Rep. 13 (1), 1. https://doi.org/10.1038/s41598-023-30706-9.

Cortese, F., Angelis, F. D., Achino, K. F., Bontempo, L., Cicco, M. R. D., Gatta, M., Lubritto, C., Salari, L., Silvestri, L., Rickards, O., & Rolfo, M. F. (2022). Isotopic reconstruction of the subsistence strategy for a Central Italian Bronze Age community (Pastena cave, 2nd millennium BCE) (p. 2022.04.21.488758). bioRxiv. doi: 10.1101/2022.04.21.488758.

Ministero Italiano Cultura, M. C. I. (2022). I resti scheletrici umani: Dallo scavo al laboratorio al museo - Ministero della Cultura ICCD -Istituto Centrale per il Catalogo e la Documentazione ICA - Istituto Centrale per l'Archeologia.

Cunningham, C., Scheuer, L., Black, S., 2000. Developmental Juvenile Osteology. Elsevier.

Danecek, P., Bonfield, J.K., Liddle, J., Marshall, J., Ohan, V., Pollard, M.O., Whitwham, A., Keane, T., McCarthy, S.A., Davies, R.M., Li, H., 2021. Twelve years of SAMtools and BCFtools. GigaScience 10 (2), giab008. https://doi.org/10.1093/gigascience/giab008.

Danubio, E., Martella Sanna, M., 2017. Changes in stature from the Upper Paleolithic to the Medieval period in Western Europe. J. Anthropological Sciences = Rivista Di Antropologia : JASS 95. https://doi.org/10.4436/JASS.95015.

De Angelis, F., Pantano, W., Battistini, A., 2015. Paleodemographic Analysis. Med. Secoli 27 (3), 805–872.

De Angelis, F., Varano, S., Battistini, A., Di Giannantonio, S., Ricci, P., Lubritto, C., Facchin, G., Brancazi, L., Santangeli-Valenzani, R., Catalano, P., Gazzaniga, V., Rickards, O., Martínez-Labarga, C., 2020a. Food at the heart of the Empire: dietary reconstruction for Imperial Rome inhabitants. Archaeol. Anthropol. Sci. 12 (10), 244. https://doi.org/10.1007/s12520-020-01194-z.

De Angelis, F., Veltre, V., Varano, S., Romboni, M., Renzi, S., Zingale, S., Ricci, P., Caldarini, C., Giannantonio, S.D., Lubritto, C., Catalano, P., Rickards, O., Martínez-Labarga, C., 2020b. Dietary and weaning habits of the roman community of quarto cappello del prete (Rome, 1st-3 rd Century CE). Environ. Archaeol. 1–15. https://doi.org/10.1080/14614103.2020.1829297.

De Angelis, F., Veltre, V., Romboni, M., Di Corcia, T., Scano, G., Martínez-Labarga, C., Catalano, P., Rickards, O., 2021. Ancient genomes from a rural site in Imperial Rome (1st-3rd cent. CE): A genetic junction in the Roman Empire. Ann. Hum. Biol. 48 (3), 234–246. https://doi.org/10.1080/03014460.2021.1944313.

De Angelis, F., Romboni, M., Veltre, V., Catalano, P., Martínez-Labarga, C., Gazzaniga, V., Rickards, O., 2022. First glimpse into the genomic characterization of people from the imperial roman community of casal bertone (Rome, First–Third Centuries AD). Genes 13 (1), 1. https://doi.org/10.3390/genes13010136.

DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. Nature 317 (6040). https://doi.org/10.1038/317806a0.

Elliott, C.P., 2020. In: On Writing Roman Economic History. In Economic Theory and the Roman Monetary Economy. Cambridge University Press, pp. 1–19. https://doi.org/10.1017/9781108290531.002.

Fedi, M.E., Caforio, L., Liccioli, L., Mandò, P.A., Salvini, A., Taccetti, F., 2014. A simple and effective removal procedure of synthetic resins to obtain accurate radiocarbon dates of restored artworks. Radiocarbon 56 (3), 969–979. https://doi.org/10.2458/56.16930.

Fernandes, R., Millard, A.R., Brabec, M., Nadeau, M.-J., Grootes, P., 2014. Food Reconstruction Using Isotopic Transferred Signals (FRUITS): A Bayesian Model for Diet Reconstruction. PLoS One 9 (2), e87436. https://doi.org/10.1371/journal.pone.0087436.

Fernandes, R., Grootes, P., Nadeau, M.-J., Nehlich, O., 2015. Quantitative diet reconstruction of a Neolithic population using a Bayesian mixing model (FRUITS): The case study of Ostorf (Germany). Am. J. Phys. Anthropol. 158 (2), 325–340. https://doi.org/10.1002/ajpa.22788.

Filograna, L., Manenti, G., Mecchia, D., Tatulli, D., Pasqualetto, M., Perlangeli, V., Rossi, P.F., De Angelis, F., Floris, R., 2022. Investigation of human remains from the archaeological areas of "Parco archeologico di Ostia antica": The role of CT imaging. Forensic Imaging 31, 200521. https://doi.org/10.1016/j.fri.2022.200521.

Fuller, B.T., Fuller, J.L., Harris, D.A., Hedges, R.E.M., 2006. Detection of breastfeeding and weaning in modern human infants with carbon and nitrogen stable isotope ratios. Am. J. Phys. Anthropol. 129 (2), 279–293. https://doi.org/10.1002/ajpa.20249.

Giannecchini, M., Moggi-Cecchi, J., 2008. Stature in archeological samples from central Italy: Methodological issues and diachronic changes. Am. J. Phys. Anthropol. 135 (3), 284–292. https://doi.org/10.1002/ajpa.20742.

Gismondi, A., D'Agostino, A., Di Marco, G., Scuderi, F., De Angelis, F., Rickards, O., Catalano, P., Canini, A., 2020. Archaeobotanical record from dental calculus of a Roman individual affected by bilateral temporo-mandibular joint ankylosis. Quat. Int. https://doi.org/10.1016/j.quaint.2020.11.017.

Goodman, A.H., Rose, J.C., 1990. Assessment of systemic physiological perturbations from dental enamel hypoplasias and associated histological structures. Am. J. Phys. Anthropol. 33 (S11), 59–110. https://doi.org/10.1002/ajpa.1330330506.

Günther, T., Nettelblad, C., 2019. The presence and impact of reference bias on population genomic studies of prehistoric human populations. PLoS Genet. 15 (7), e1008302. https://doi.org/10.1371/journal.pgen.1008302.

Haas, J., Buikstra, J. E., Ubelaker, D. H., Aftandilian, D., & Field Museum of Natural History. (1994). Standards for data collection from human skeletal remains: Proceedings of a seminar at the Field Museum of Natural History, organized by Jonathan Haas / volume editors, Jane E. Buikstra and Douglas H. Ubelaker, assistant editor, David Aftandilian ; contributions by D. Aftandilian [and others].

Hakenbeck, S., 2013. Potential and limitations of isotope analysis in early medieval archaeology. Postclassical Archaeologies 3, 109–125.

Halsall, G., 2005. The Barbarian invasions. In: Fouracre, P. (Ed.), The New Cambridge Medieval History: Volume 1: C.500–c.700. Cambridge University Press, pp. 35–55. https://doi.org/10.1017/CHOL9780521362917.004.

Holt, E., Evans, J.A., Madgwick, R., 2021. Strontium (87Sr/86Sr) mapping: A critical review of methods and approaches. Earth Sci. Rev. 216, 103593. https://doi.org/10.1016/j.earscirev.2021.103593.

Jones, 1955. The Decline and Fall of the Roman Empire. History 40 (140), 209–226.

Jones, D., 2021. Barbarigenesis and the collapse of complex societies: Rome and after. PLoS One 16 (9). https://doi.org/10.1371/journal.pone.0254240.

Katzenberg, M. A. (2007). Stable isotope analysis: A tool for studying past diet, demography, and life history. In Biological Anthropology of the Human Skeleton, Second Edition (M. Anne Katzenberg Ph.D.,Shelley R. Saunders Ph.D.).

Keay, S., Millett, M., Paroli, L., & Strutt, K. (with Keay, S., Millett, M., Paroli, L., & Strutt, K.). (2005). Portus: An Archaeological Survey of the Port of Imperial Rome. British School at Rome. http://www.oxbowbooks.com/bookinfo.cfm/ID/45858//Location/Oxbow.

Keay. (2012). Rome, Portus and the Mediterranean. The British School at Rome.

Kelly, M. J. (n.d.). [Review of Review of: Rome's Gothic Wars: From the Third Century to Alaric, by M. Kulikowski]. Bryn Mawr Classical Review. Retrieved May 13, 2023, from https://bmcr.brynmawr.edu/2007/2007.05.40/.

Killgrove, K., Montgomery, J., 2016. All Roads Lead to Rome: Exploring Human Migration to the Eternal City through Biochemistry of Skeletons from Two Imperial-

Era Cemeteries (1st-3rd c AD). PLoS One 11 (2), e0147585. https://doi.org/10.1371/journal.pone.0147585.

Killgrove, K., Tykot, R.H., 2013. Food for Rome: A stable isotope investigation of diet in the Imperial period (1st–3rd centuries AD). J. Anthropol. Archaeol. 32 (1), 28–38. https://doi.org/10.1016/j.jaa.2012.08.002.

Killgrove, K., Tykot, R.H., 2018. Diet and collapse: A stable isotope study of Imperial-era Gabii (1st–3rd centuries AD). J. Archaeol. Sci. Rep. 19, 1041–1049. https://doi.org/10.1016/j.jasrep.2017.05.054.

Killgrove, K. (2010). Migration and mobility in imperial Rome [PhD dissertation, University of North Carolina,]. https://cdr.lib.unc.edu/record/uuid:84c02de7-2153-40f4-82f6-c9b54b19264a.

Korneliussen, T.S., Albrechtsen, A., Nielsen, R., 2014. ANGSD: analysis of next generation sequencing data. BMC Bioinf. 15 (1), 356. https://doi.org/10.1186/s12859-014-0356-4.

Li, H., Durbin, R., 2009. Fast and accurate short read alignment with Burrows–Wheeler transform. Bioinformatics 25 (14), 1754–1760. https://doi.org/10.1093/bioinformatics/btp324.

Longin, R., 1971. New method of collagen extraction for radiocarbon dating. Nature 230 (5291), 241–242. https://doi.org/10.1038/230241a0.

Lovejoy, C.O., 1985. Dental wear in the Libben population: Its functional pattern and role in the determination of adult skeletal age at death. Am. J. Phys. Anthropol. 68 (1), 47–56. https://doi.org/10.1002/ajpa.1330680105.

Lovejoy, C.O., Meindl, R.S., Mensforth, R.P., Barton, T.J., 1985a. Multifactorial determination of skeletal age at death: a method and blind tests of its accuracy. Am. J. Phys. Anthropol. 68 (1), 1–14. https://doi.org/10.1002/ajpa.1330680102.

Lovejoy, C.O., Meindl, R.S., Pryzbeck, T.R., Mensforth, R.P., 1985b. Chronological metamorphosis of the auricular surface of the ilium: a new method for the determination of adult skeletal age at death. Am. J. Phys. Anthropol. 68 (1), 15–28. https://doi.org/10.1002/ajpa.1330680103.

Lugli, F., Cipriani, A., Bruno, L., Ronchetti, F., Cavazzuti, C., Benazzi, S., 2022. A strontium isoscape of Italy for provenance studies. Chem. Geol. 587, 120624. https://doi.org/10.1016/j.chemgeo.2021.120624.

Mallick, S., Micco, A., Mah, M., Ringbauer, H., Lazaridis, I., Olalde, I., Patterson, N., & Reich, D. (2023). The Allen Ancient DNA Resource (AADR): A curated compendium of ancient human genomes. bioRxiv: The Preprint Server for Biology, 2023.04.06.535797. doi: 10.1101/2023.04.06.535797.

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. Embnet. J. 17 (1), 1. https://doi.org/10.14806/ej.17.1.200.

Martin, D.L., Harrod, R.P., 2015. Bioarchaeological contributions to the study of violence. Am. J. Phys. Anthropol. 156 (S59), 116–145. https://doi.org/10.1002/ajpa.22662.

McArthur, J.M., Howarth, R.J., Bailey, T.R., 2001. Strontium isotope stratigraphy: LOWESS version 3: Best fit to the marine Sr-isotope curve for 0-509 Ma and accompanying look-up table for deriving numerical age. J. Geol. 109 (2), 155–170. https://doi.org/10.1086/319243.

Meindl, R.S., Lovejoy, C.O., 1985. Ectocranial suture closure: A revised method for the determination of skeletal age at death based on the lateral-anterior sutures. Am. J. Phys. Anthropol. 68 (1), 57–66. https://doi.org/10.1002/ajpa.1330680106.

Melchionda, F., Silvestrini, B., Robino, C., Bini, C., Fattorini, P., Martinez-Labarga, C., De Angelis, F., Tagliabracci, A., Turchi, C., 2022. Development and validation of MPS-based system for human appearance prediction in challenging forensic samples. Genes 13 (10), 1688. https://doi.org/10.3390/genes13101688.

Mendez, F.L., Karafet, T.M., Krahn, T., Ostrer, H., Soodyall, H., Hammer, M.F., 2011. Increased resolution of Y chromosome haplogroup T defines relationships among populations of the Near East, Europe, and Africa. Hum. Biol. 83 (1), 39–53. https://doi.org/10.3378/027.083.0103.

Meyer, M., Kircher, M., 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. Cold Spring Harb Protoc 2010 (6), pdb.prot5448. https://doi.org/10.1101/pdb.prot5448.

Minozzi, S., Caldarini, C., Pantano, W., di Giannantonio, S., Catalano, P., Giuffra, V., 2020. Enamel hypoplasia and health conditions through social status in the Roman Imperial Age (First to third centuries, Rome, Italy). Int. J. Osteoarchaeol. 30 (1), 53–64. https://doi.org/10.1002/oa.2830.

Moss, H.S., B, L., 1937. Revisions in Economic History: VI. The Economic Consequences of the Barbarian Invasions. Econ. Hist. Rev. 7 (2), 209–216. https://doi.org/10.2307/2590151.

Mughal, M.R., DeGiorgio, M., 2022. Properties and unbiased estimation of F- and D-statistics in samples containing related and inbred individuals. Genetics 220 (1), iyab090. https://doi.org/10.1093/genetics/iyab090.

Nicklisch, N., Oelze, V.M., Schierz, O., Meller, H., Alt, K.W., 2022. A healthier smile in the past? dental caries and diet in early neolithic farming communities from central Germany. Nutrients 14 (9). https://doi.org/10.3390/nu14091831.

Nikita, E., 2017. Chapter 3—Sex and Ancestry Assessment. In: Nikita, E. (Ed.), Osteoarchaeology. Academic Press, pp. 105–134. https://doi.org/10.1016/B978-0-12-804021-8.00003-6.

Nikita, E., & Karligkioti, A. (2019). BASIC GUIDELINES FOR THE EXCAVATION AND STUDY OF HUMAN SKELETAL REMAINS.

Novotný, V. (1983). Sex Differences of Pelvis and Sex Determination in Paleoanthropology. Anthropologie (1962-), 21(1), 65–72.

O'Connell, T.C., Ballantyne, R.M., Hamilton-Dyer, S., Margaritis, E., Oxford, S., Pantano, W., Millett, M., Keay, S.J., 2019. Living and dying at the Portus Romae. Antiquity 93 (369), 719–734. https://doi.org/10.15184/aqy.2019.64.

Okonechnikov, K., Conesa, A., García-Alcalde, F., 2016. Qualimap 2: Advanced multi-sample quality control for high-throughput sequencing data. Bioinformatics (oxford, England) 32 (2), 292–294. https://doi.org/10.1093/bioinformatics/btv566.

Orlando, L., Allaby, R., Skoglund, P., Der Sarkissian, C., Stockhammer, P.W., Ávila-Arcos, M.C., Fu, Q., Krause, J., Willerslev, E., Stone, A.C., Warinner, C., 2021. Ancient DNA analysis. Nat. Rev. Methods Primers 1 (1), 1. https://doi.org/10.1038/s43586-020-00011-0.

Pate, F.D., Henneberg, R.J., Henneberg, M., 2016. Stable carbon and nitrogen isotope evidence for dietary variability at ancient Pompeii. Italy. Mediterranean Archaeology and Archaeometry 16 (1), 127–133. https://doi.org/10.5281/zenodo.35526.

Patterson, N., Price, A.L., Reich, D., 2006. Population Structure and Eigenanalysis. PLOS Genet. 2 (12), e190.

Pearson, K., Bell, J., 1917. A Study of the Long Bones of the English Skeleton. Cambridge University Press.

Pearson, K. (1899). Mathematical Contributions to the Theory of Evolution. V. On the Reconstruction of the Stature of Prehistoric Races. Royal Society of London. http://archive.org/details/philtrans06400427.

Peltzer, A., Jäger, G., Herbig, A., Seitz, A., Kniep, C., Krause, J., Nieselt, K., 2016. EAGER: Efficient ancient genome reconstruction. Genome Biol. 17 (1), 60. https://doi.org/10.1186/s13059-016-0918-z.

Phenice, T.W., 1969. A newly developed visual method of sexing the os pubis. Am. J. Phys. Anthropol. 30 (2), 297–301. https://doi.org/10.1002/ajpa.1330300214.

Piganiol, A., 1950. The causes of the fall of the Roman Empire. J. Gen. Educ. 5 (1), 62–69.

Prowse, T., Schwarcz, H.P., Saunders, S., Macchiarelli, R., Bondioli, L., 2004. Isotopic paleodiet studies of skeletons from the Imperial Roman-age cemetery of Isola Sacra, Rome. Italy. J. Archaeol. Sci. 31 (3), 259–272. https://doi.org/10.1016/j.jas.2003.08.008.

Prowse, T.L., Schwarcz, H.P., Saunders, S.R., Macchiarelli, R., Bondioli, L., 2005. Isotopic evidence for age-related variation in diet from Isola Sacra. Italy. Am. J. Phys. Anthropol. 128 (1), 2–13. https://doi.org/10.1002/ajpa.20094.

Quade, L., Gowland, R., 2021. Height and health in Roman and Post-Roman Gaul, a life course approach. Int. J. Paleopathol. 35, 49–60. https://doi.org/10.1016/j.ijpp.2021.10.001.

Ralf, A., Montiel González, D., Zhong, K., Kayser, M., 2018. Yleaf: Software for Human Y-Chromosomal Haplogroup Inference from Next-Generation Sequencing Data. Mol. Biol. Evol. 35 (5), 1291–1294. https://doi.org/10.1093/molbev/msy032.

Ramsey, C.B., Lee, S., 2013. Recent and planned developments of the program OxCal. Radiocarbon 55 (2), 720–730. https://doi.org/10.1017/S0033822200057878.

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Ramsey, C.B., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Talamo, S., 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). Radiocarbon 62 (4), 725–757. https://doi.org/10.1017/RDC.2020.41.

Renaud, G., Slon, V., Duggan, A.T., Kelso, J., 2015. Schmutzi: Estimation of contamination and endogenous mitochondrial consensus calling for ancient DNA. Genome Biol. 16 (1), 224. https://doi.org/10.1186/s13059-015-0776-0.

Riccomi, G., Minozzi, S., Zech, J., Cantini, F., Giuffra, V., Roberts, P., 2020. Stable isotopic reconstruction of dietary changes across Late Antiquity and the Middle Ages in Tuscany. J. Archaeol. Sci. Rep. 33, 102546. https://doi.org/10.1016/j.jasrep.2020.102546.

Rohland, N., Harney, E., Mallick, S., Nordenfelt, S., Reich, D., 2015. Partial uracil–DNA–glycosylase treatment for screening of ancient DNA. Philos. Trans. R. Soc., B 370 (1660), 20130624. https://doi.org/10.1098/rstb.2013.0624.

Roostalu, U., Kutuev, I., Loogväli, E.-L., Metspalu, E., Tambets, K., Reidla, M., Khusnutdinova, E.K., Usanga, E., Kivisild, T., Villems, R., 2007. Origin and expansion of haplogroup H, the dominant human mitochondrial DNA lineage in West Eurasia: The Near Eastern and Caucasian perspective. Mol. Biol. Evol. 24 (2), 436–448. https://doi.org/10.1093/molbev/msl173.

Rose, E., 2021. Citizenship discourses in late antiquity and the early middle ages. Frühmittelalterliche Studien 55 (1), 1–21. https://doi.org/10.1515/fmst-2021-0001.

Salzman, M.R., 2021. In: The FALLS of Rome: Crises, Resilience, and Resurgence in Late Antiquity. Cambridge University Press. https://doi.org/10.1017/9781316275924.

Sauter, M. R., & Privat, F. (1954). Sur un nouveau procédé métrique de détermination sexuelle du bassin osseux / par Marc-Rodolphe Sauter. s.n.. S.l. https://patrimoine.mediatheques-grandpoitiers.fr/PATRIMOINE/doc/SYRACUSE/1124716/sur-un-nouveau-procede-metrique-de-determination-sexuelle-du-bassin-osseux-par-marc-rodolphe-sauter.

Schultz, A.H., Schultz, A.H., 1930. The skeleton of the trunk and limbs of higher primates. Hum. Biol. 2 (3), 3. https://doi.org/10.2307/41447039.

Skoglund, P., Storå, J., Götherström, A., Jakobsson, M., 2013. Accurate sex identification of ancient human remains using DNA shotgun sequencing. J. Archaeol. Sci. 40 (12), 4477–4482. https://doi.org/10.1016/j.jas.2013.07.004.

Stewart, T. D. (1979). Essentials of forensic anthropology, especially as developed in the United States. Thomas. https://search.ebscohost.com/login.aspx?direct=true&scope=site&db=nlebk&db=nlabk&AN=631742.

Stloukal & Hakanova, 1978. Die Langr Der Langsknochen Atlslawisscher Bevolkerungen Unter Besonderer Berucksichting Ung Von Wachstumsfragen. Homo 29, 53–69.

Szpak, P., Metcalfe, J.Z., Macdonald, R.A., 2017. Best practices for calibrating and reporting stable isotope measurements in archaeology. J. Archaeol. Sci. Rep. 13, 609–616. https://doi.org/10.1016/j.jasrep.2017.05.007.

Tafuri, M.A., Goude, G., Manzi, G., 2018. Isotopic evidence of diet variation at the transition between classical and post-classical times in Central Italy. J. Archaeol. Sci. Rep. 21, 496–503. https://doi.org/10.1016/j.jasrep.2018.08.034.

Temkina, A., 2021. The Early Medieval Transition: Diet Reconstruction, Mobility, and Culture Contact in the Ravenna Countryside, Northern Italy. USF Tampa Graduate Theses and Dissertations. https://digitalcommons.usf.edu/etd/9241.

Temple, D.H., 2015. In: Caries. In A Companion to Dental Anthropology. John Wiley & Sons, Ltd., pp. 433–449. https://doi.org/10.1002/9781118845486.ch26

Trotter, M., Gleser, G.C., 1958. A re-evaluation of estimation of stature based on measurements of stature taken during life and of long bones after death. Am. J. Phys. Anthropol. 16 (1), 79–123. https://doi.org/10.1002/ajpa.1330160106.

Tsutaya, T., Yoneda, M., 2015. Reconstruction of breastfeeding and weaning practices using stable isotope and trace element analyses: A review. Am. J. Phys. Anthropol. 156 (S59), 2–21. https://doi.org/10.1002/ajpa.22657.

Vaccaro, S., Fiore, I., Blundo, M.L., Rossi, P.F., 2023. Archivi biologici e archivi di carta: I dati antropologici degli inumati dell'antemurale di Portus e il sistema di gestione dei resti umani antichi al Parco Archeologico di Ostia antica. Bollettino Di Archeologia on-Line XIV (3–4), 21–62.

van Klinken, G.J., 1999. Bone collagen quality indicators for palaeodietary and radiocarbon measurements. J. Archaeol. Sci. 26 (6), 687–695. https://doi.org/10.1006/jasc.1998.0385.

Varano, S., De Angelis, F., Battistini, A., Brancazi, L., Pantano, W., Ricci, P., Romboni, M., Catalano, P., Gazzaniga, V., Lubritto, C., Santangeli Valenzani, R., Martínez-Labarga, C., Rickards, O., 2020. The edge of the Empire: Diet characterization of medieval Rome through stable isotope analysis. Archaeol. Anthropol. Sci. 12 (8), 196. https://doi.org/10.1007/s12520-020-01158-3.

Walkup, T.N., Winburn, A.P., Stock, M., 2023. Antemortem tooth loss as a biomarker of poverty: Dental evidence of "weathering" in a contemporary U.S. skeletal sample. Forensic Sci. Int.: Synergy 6. https://doi.org/10.1016/j.fsisyn.2023.100333.

Weissensteiner, H., Pacher, D., Kloss-Brandstätter, A., Forer, L., Specht, G., Bandelt, H.-J., Kronenberg, F., Salas, A., Schönherr, S., 2016. HaploGrep 2: Mitochondrial haplogroup classification in the era of high-throughput sequencing. Nucleic Acids Res. 44 (W1), W58–W63. https://doi.org/10.1093/nar/gkw233.

White, T.D., Black, M.T., Folkens, P.A., 2011. Human Osteology. Academic Press.

Wieser, M.E., Schwieters, J.B., 2005. The development of multiple collector mass spectrometry for isotope ratio measurements. Int. J. Mass Spectrom. 242 (2), 97–115. https://doi.org/10.1016/j.ijms.2004.11.029.

Yang, D.Y., Eng, B., Waye, J.S., Dudar, J.C., Saunders, S.R., 1998. Technical note: Improved DNA extraction from ancient bones using silica-based spin columns. Am. J. Phys. Anthropol. 105 (4), 539–543. https://doi.org/10.1002/(SICI)1096-8644(199804)105:4<539::AID-AJPA10>3.0.CO;2-1.

Zhu, L., Fang, Q., Li, T., 2022. Distribution and diversity of organisms in tomb soil excavated in the laboratory: a case study of tomb m88 from sujialong cultural property. China. Heritage Sci. 10 (1), 166. https://doi.org/10.1186/s40494-022-00803-5.

Further reading

Elkamel, S., Marques, S.L., Alvarez, L., Gomes, V., Boussetta, S., Mourali-Chebil, S., Khodjet-El-Khil, H., Cherni, L., Benammar-Elgaaied, A., Prata, M.J., 2021. Insights into the Middle Eastern paternal genetic pool in Tunisia: High prevalence of T-M70 haplogroup in an Arab population. Sci. Rep. 11 (1). https://doi.org/10.1038/s41598-021-95144-x.