



New scientific evidence for the history and occupants of Tomb I (“Tomb of Persephone”) in the Great Tumulus at Vergina

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ABSTRACT

The Great Tumulus of Vergina (Aegae) is considered to be the royal burial complex of the Macedonian kings. Beneath it four tombs were discovered, labeled Tomb I, II, III and IV. Several hypotheses have been proposed for the identities of the occupants of the “royal tombs”, but without scientific backing. We present new data from Tomb I (“The Tomb of Persephone”), which contained inhumed (unburnt), in situ and commingled adult skeletal remains, as well as commingled nonadult and animal bones. We applied a range of scientific techniques, including radiocarbon dating, ancient DNA (aDNA), strontium and stable carbon and nitrogen isotope analysis, supported by osteological and odontological observations on the adult and nonadult bones found in Tomb I to provide concrete evidence for the date of burials, sex, age at death and origin of the individuals interred in this tomb. Our results show that, with the exception of four bones that were identified as female, all the adult bones are male according to the aDNA and osteological results, and they belonged to a man aged 25–35 years with a stature of approximately 167 cm. Radiocarbon dating places this burial in the first half of the 4th century calBC, specifically between 400 and 367 calBC, and by applying a potential collagen offset correction this is slightly shifted to 388–356 calBC at the latest. The female bones date to the same period. However, all the nonadults and animal bones, date to the Roman period from 150 calBC, the earliest to 130 calAD the latest. Therefore, these are not related to the primary adult burials. The male occupant was most likely an important Macedonian royal of the Argead/Temenid house who died in the period 388–356 calBC and was probably honored or worshipped in the shrine above and entombed likely together with a female. Previous suggestions that the skeletal remains belong to Philip II, his wife Cleopatra and newborn child are not scientifically sustainable.

1. Introduction

Vergina, a modern village in Central Macedonia, Greece, gained fame in 1977 when Professor Manolis Andronikos and his team from the Aristotle University of Thessaloniki excavated the Great Tumulus of Vergina (an artificial mound of 100 m in diameter and 12 m in height),

which is considered to be the royal burial complex of the Macedonian kings (Andronikos, 1984; Hammond, 1982). This, together with the palace and the theatre where Philip II, father of Alexander the Great, was assassinated, was deemed the most sensational and unique archaeological discovery of the 20th century in Greece and led to the widely accepted scholarly view that Vergina is linked to ancient Aegae, the first

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capital of the ancient Macedonian Kingdom and original seat of the Temenid (Argead) dynasty.

Four subterranean tombs, labeled Tomb I, II, III and IV, and an above-ground heroon (hero shrine) above and adjacent to Tomb I, were found beneath the Great Tumulus (Fig. 1A and B). Tomb IV and the heroon were almost completely destroyed, while Tomb I was plundered. Tombs II and III remained intact, providing invaluable information and drawing scholarly and public interest due to the high status of the individuals buried there (Andronikos, 1980; Borza and Palagia, 2007; Drougou, 2005; Drougou et al., 1994; Grant, 2019; Hammond, 1982; Hatzopoulos, 2008; Kottaridi, 2020a; Palagia, 2017; Saatsoglou-Paliadeli, 1996).

Tomb II, known as the “Tomb of Philip II”, is a double-chamber vaulted tomb that was untouched by grave robbers. Its main chamber contained the cremated remains of a male in a golden larnax, and the antechamber contained cremated remains of a female, also in a golden larnax. Based on the finds, Andronikos concluded that this tomb belonged to Philip II, who died in 336 BC, and one of his wives (Andronikos, 1984; Hammond, 1982), and so it was commonly referred to as the “Tomb of Philip II”. Alternative identities for the deceased have also been proposed (see Supplement, section S1).

Tomb III, referred to as the “Tomb of the Prince”, was also discovered untouched. Inside it, a silver hydria contained the cremated and fragmented remains of a youth (Andronikos, 1984). Osteological examinations indicated that it was an adolescent, most likely male, who died at the age of 13–15. The tomb was dated to the end of the 4th century BC. Most suggestions for the identity point to Alexander IV (323–310/309 BC), the son of Alexander the Great by his Bactrian (or perhaps Sogdian) wife Roxane (see Supplement, section S1).

Tomb I, also known as the “Tomb of Persephone”, is the only monument from the Great Tumulus to have received an archaeological scholarly publication (Andronikos, 1994). It is a cist-type (rectangular stone-box-like structure) tomb, with internal dimensions of 3.50 × 2.09 m and a height of 3 m, and is orientated roughly east to west (Fig. 1). It is a unique monument and considered as one of the most important cist graves in Macedonia as it preserves incomparable wall paintings in its interior (Fig. 2) (Andronikos, 1984, 1994; Kottaridi, 2007; Saatsoglou-Paliadeli, 1995). This tomb is also distinct for bearing a decoration with a mythological representation, which is probably the earliest known in Macedonia (Baferou, 2018). A fresco of superb artistic quality, representing the Abduction of Persephone by Pluto on the north wall (Fig. 2B), gave the tomb its name (Andronikos, 1994; Kottaridi, 2007). As has been stated by Andronikos and Saatsoglou-Paliadeli, “The artist without paying attention to its preliminary sketch, using a thin brush and with a fluent movement shaped his figures with restricted parallel hatching to stress their corporeality” (Andronikos, 1994; Saatsoglou-Paliadeli, 2002). The paintings, executed in an impressionistic style and technique, are unique for Macedonia and indicate the presence of an artist from Athens, who was invited to fulfill a special commission (Palagia, 2016). This unique decoration is attributed to Nikomachos of Thebes, a great master of the Classical period (Andronikos, 1994; Kottaridi, 2007; Lindner, 1984; Oakley, 1986) and manifests the eclectic character of the art of Macedonia (Palagia, 2016). Additional frescoes show a seated figure of the Goddess Demeter on the east wall (Fig. 2A) and three female figures, likely representing the Three Fates (*Moirae*) on the south wall (Andronikos, 1994; Kottaridi, 2007). The technical and stylistic features detected in the wall paintings indicate a quick execution (restricting painting procedures to the absolutely necessary for the completion of the artwork, a fact that reinforces the attribution to Nikomachos praised by Pliny (Plinius, Hist. Nat. XXXV, 108–109) for his rapid work (Andronikos, 1994; Saatsoglou-Paliadeli, 1995, 2002, and several other references there in). There are only a few other alternative suggestions for the identity of the artist (Brecoulaki, 2006; Thomas, 1989).

Apart from the stunning wall paintings, the removal of almost all the noticeable grave goods by the tomb's looters made the excavator (Andronikos, 1984) suggest that most of the objects must have been of

gold, silver and bronze, and hence the tomb probably belonged to a very wealthy person.

Based on the pottery fragments, the wall paintings and other elements, found inside the tomb, a date was suggested close to the end of the first half of the 4th century BC (≥ 350 BC) (Andronikos, 1994; Drougou, 2005; Hammond, 1982; Kottaridi, 2007).

It is generally accepted that the plundering took place in 274/3 BC by Gallic Celt mercenaries aiding Pyrrhus, king of Epirus, during his invasion of Macedonia, who, after conquering Aegae, left a Galatian “garrison” in the city. This event is recorded by ancient writers (Plutarch, *Life of Pyrrhus* 26.6 and Diodorus, *Library of World History* 22.12). According to Plutarch, the Galatae grabbed the valuable goods and the bones they ‘insolently cast to the winds’ (*τα δε οστά προς ὕβριν διέρριψαν*) in a deliberate insulting and arrogant action (Andronikos, 1994). Similarly, Diodorus writes, “the Galatae dug up all the Royal tombs, they grabbed the valuable goods and scattered the bones around”.

The excavators of Tomb I found numerous inhumed human bones inside, several still in situ, along with animal bones. The few non-osseous finds left by the looters included small ceramic vessels, intact and fragments, gilded clay beads and fruit imitations (probably from a wreath), a marble shell, tiny pieces of gold and copper, small fragments of silver and glass vessels, iron foils, an ivory pin head, and iron nails with wood fragments (Drougou, 2005). Similar objects were also found in the soil outside the tomb at the level of its roof, most likely dropped by the robbers (Andronikos, 1994).

There have been several suggestions for the identities of the occupant(s) of Tomb I, ranging from Amyntas III, the father of Philip II, an influential king who ruled for many years and died in 370/368 BC (Andronikos, 1984; Hammond, 1991), to Philip II himself, his wife Cleopatra and their newborn (Bartsiokas et al., 2015, 2023; Bartsiokas and Carney, 2008; Borza, 1987; Borza and Palagia, 2007). However, systematic scientific dating, aDNA and other analyses were never conducted on the osseous remains from Tomb I, or any of the tombs under the Great Tumulus to support the above hypotheses, which were solely based on macroscopic bone observations and/or archaeological interpretations of the finds.

To provide concrete evidence for the history of Tomb I, which remains a unique funeral monument under the Great Tumulus, and to establish scientific data to contribute to the possible identities of the important individuals interred there, we analyzed the skeletal remains found inside the tomb. We used a combination of scientific techniques, including radiocarbon dating, ancient DNA, strontium and stable carbon and nitrogen isotope analyses, supplemented by osteological and odontological observations. The results obtained for Tomb I may also lead to inferences about the other important tombs under the Great Tumulus and their occupants.

2. Archaeological context-the history of the bones

It is important here to provide an account of the excavation details in the tomb to elucidate which bones were found and where they were located, as well as their history after excavation.

The Galatian tomb robbers who reportedly plundered the tomb in 274/3 BC, removed a limestone block from the west wall (Fig. 3) and also broke one of the covering blocks on the top of the tomb (Fig. 4), creating two openings through which soil and other debris progressively accumulated in the tomb at different times. Archaeologist Stella Drougou, under the instruction of M. Andronikos, excavated the tomb's interior in 1977, removing the fill down to the bottom layer. According to her excavation logbook¹, the fill was highest near the west wall

¹ From the archives of the Aristotle University of Thessaloniki Excavations at Vergina, with the permission of the Heads of the University Excavations Prof. Ch. Saatsoglou-Paliadeli and consequently Assistant Prof. A. Kyriakou.

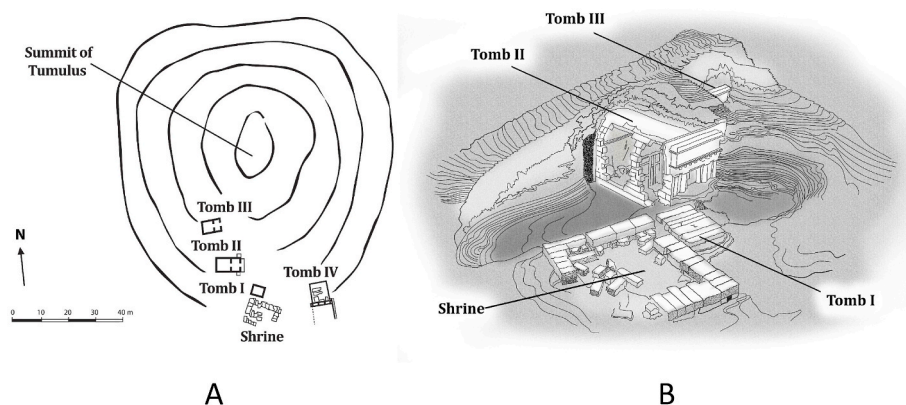


Fig. 1. A: Diagram of the Great Tumulus of Vergina with the 4 graves and the Heroon (Shrine). Tomb I, a cist tomb, is situated next to the foundations of Heroon. B: Representation of the Tombs in the Great Tumulus; the destroyed Heroon, above and adjacent to Tomb I, the two-chamber vaulted Tomb II and further away Tomb III. (From the book by Grant-2019, with the permission of the author).



Fig. 2. A view of the interior of Tomb I. A: On the upper part left (north wall) the abduction of Persephone fresco, on the east wall (center of picture) a seated figure of Demeter, and on the right (south wall) the three fates (not seen fully in this picture). B: The north wall with the famous Abduction of Persephone fresco. Photos adapted from Andronikos (1994), with the permission of the editor prof. Ch. Saatsoglou-Paliadeli.



Fig. 3. The hole opened by the tomb robbers on the west wall. A: As it was found during the excavation with the hole deliberately filled with large and small stones at an unknown time. B: The hole on the west wall from the inside after the excavation. Photos adapted from Andronikos (1994), with the permission of the editor prof. Ch. Saatsoglou-Paliadeli.

(estimated up to 1.10–1.20 m), where the biggest opening was located, reaching up to and just below the top of the red-painted wall surface (Fig. 2). According to Andronikos (1994), the looters probably encountered an obstacle from the inside; there is evidence of a construction (case, cabinet, other) on the west wall consisting of two parallel shelves, traces of which (square holes and evidence of beam marks along the east and north walls), can be seen in Fig. 3B, that probably

prevented their entry. For this reason, they broke the second opening in one of the covering stone blocks on the roof (Andronikos, 1994). The fill gradually decreased towards the east wall, barely covering the lower painted wall zone near the floor. The upper part of the fill contained gravel, soil, broken porous limestone pieces, marble chips (*λατύπη?*), plaster fragments with red paint, ceramic sherds and just a few scattered bone fragments.



Fig. 4. The top of Tomb I during the excavation. A: As it was found with the robbers' opening deliberately covered with a pile of stones at an unknown time. B: After the removal of the pile of stones showing the hole opened by the robbers in the 4th cover block. Photo taken from the east side. Photos adapted from Andronikos (1994), with the permission of the editor prof. Ch. Saatsoglou-Paliadeli

Along the west wall and in the middle of the fill, at the level of 50–60 cm from the floor, some large limestone slabs (one of them more compact), the biggest having dimensions of $70 \times 40 \times 42$ cm, were found. According to Drougou's notes, these limestone slabs probably fell from the structure on the west wall described above. The sizes of the slabs correspond to the beams and square hole cuttings on the wall (Fig. 3B). The fill below these slabs (last 50–60 cm from the floor) was hard and contained brown soil with fragments of limestone (some with red paint on them), and other rough stones, imprints of wood and scattered human bones and probably animal bones. Near the floor (20–10 cm), the accumulation of human bones increased substantially. According to her excavation notes she collected several bone fragments from that layer, at least three cranium fragments, two of animals (but they could be of human perinates as well). This bottom layer of the fill, rich in bones, was soft and consisted of ash (from a pyre or other disintegrated organic substance) and soil with fine gravel. Human tibiae and foot bones were found in situ in a supine² position towards the middle of the south wall (Fig. 5). Among the bones were large stone fragments that seemed to have crushed the burial. The ends of the femora appeared beneath the fill near the southwest corner also in a supine position (Fig. 5). Drougou noted that the largest bones measured 43 cm and 38 cm in length, corresponding obviously to the femora and tibiae found in situ and in supine, anatomical positions, as shown in the excavation photo (Fig. 5).

The body orientation was parallel to the long side of the tomb, roughly west to east with the head positioned to the west. According to archaeological evidence, this is the custom for male burials in Macedonia when the orientation of the tomb is east-west, while females were placed with their heads to the east (Kottaridi, 1997 and the references there in) and (Charalampidis, 2019; Duitsi, 2017).

The following year (1978), archaeologist Panagiotis Faklaris, under M. Andronikos' instruction, removed the bones lying on the lowest layer of the tomb floor. The assumption was that all those belonged to the primary burial. He noted in the excavation logbook³ that the burial was not in a single location, but separated into three clusters. Cluster A, in the southwest corner of the tomb, contained the femora, a jaw (mandible) and other bones. Cluster B, about the middle of the south wall, contained the lower leg and foot bones, and Cluster Gamma (Γ), near the northwest corner, contained part of a skull and other bones and teeth (Fig. 6). The bones, he notes, were not directly on the tomb floor but on a brownish soil layer with fine gravel about 12 cm thick. This is obviously the bottom layer, consisting of ash or other disintegrated

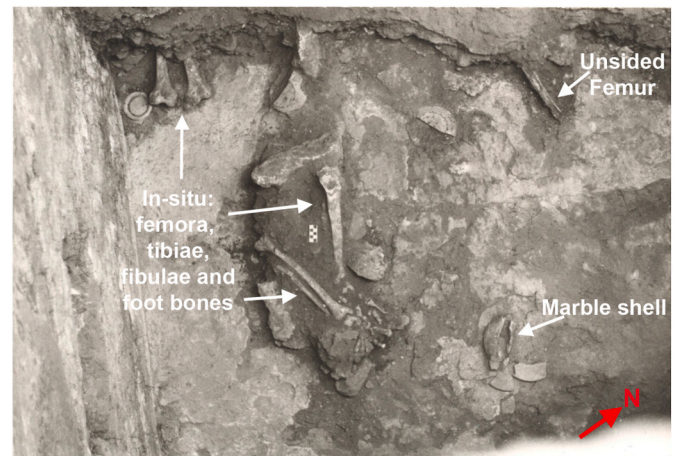


Fig. 5. Photo of the tomb's floor taken during the 1977 excavation showing the in-situ bones along the south wall and the southwest corner. (Photo adapted from Andronikos (1994), with the permission of the book editor prof. Ch. Saatsoglou-Paliadeli).

organic substances and soil described by S. Drougou the previous year.

As seen in Fig. 5, a large stone had fallen on the proximal end of the left tibia, of the in-situ leg bones (Cluster B), breaking it and causing it to jump and land upside down on top of the stone. This stone most likely fell when the tomb robbers broke the fourth cover block to create an entrance (Fig. 4B). The hole's position on the roof is approximately (calculated from photos and dimensions) above the tibiae. The femora in Cluster A, visible in Fig. 5, are also in anatomical and supine positions about 40 cm from the tibiae towards the southwest corner of the tomb. Cluster Γ (Fig. 6) contains a random accumulation of bones and bone fragments. A diaphysis fragment of a third unsided femur was also found isolated on the bottom layer (Fig. 5) and because it is a duplicate femur, it indicates a different individual. Its approximate location on the floor has been indicated in the original bone drawing of 1978 (Fig. 6).

The fact that the in-situ leg (femora/tibiae/fibulae) and foot bones, found in a supine position, typical for a primary inhumed burial, were located in the last 10–15 cm from the floor within a layer of soil, ash and fine gravel indicates that the deceased was likely laid originally on a perishable organic material (e.g. a wooden bed, a special rug, or other). This disintegrated over time, especially after the tomb was opened by the grave robbers, allowing soil to mix with it.

The in-situ bones as well as the commingled bone fragments found in the three Clusters (A, B, Γ), all nearly on the floor (Figs. 5 and 6), will be conventionally called hereafter the bones “on the floor” (see a full list in Table S3.1). These were transferred to the Archaeological Museum of

² Supine position is where the individual is lying on their back, with their face and body facing upwards, which is the normal position a body is placed for burial.

³ Ibid 1.

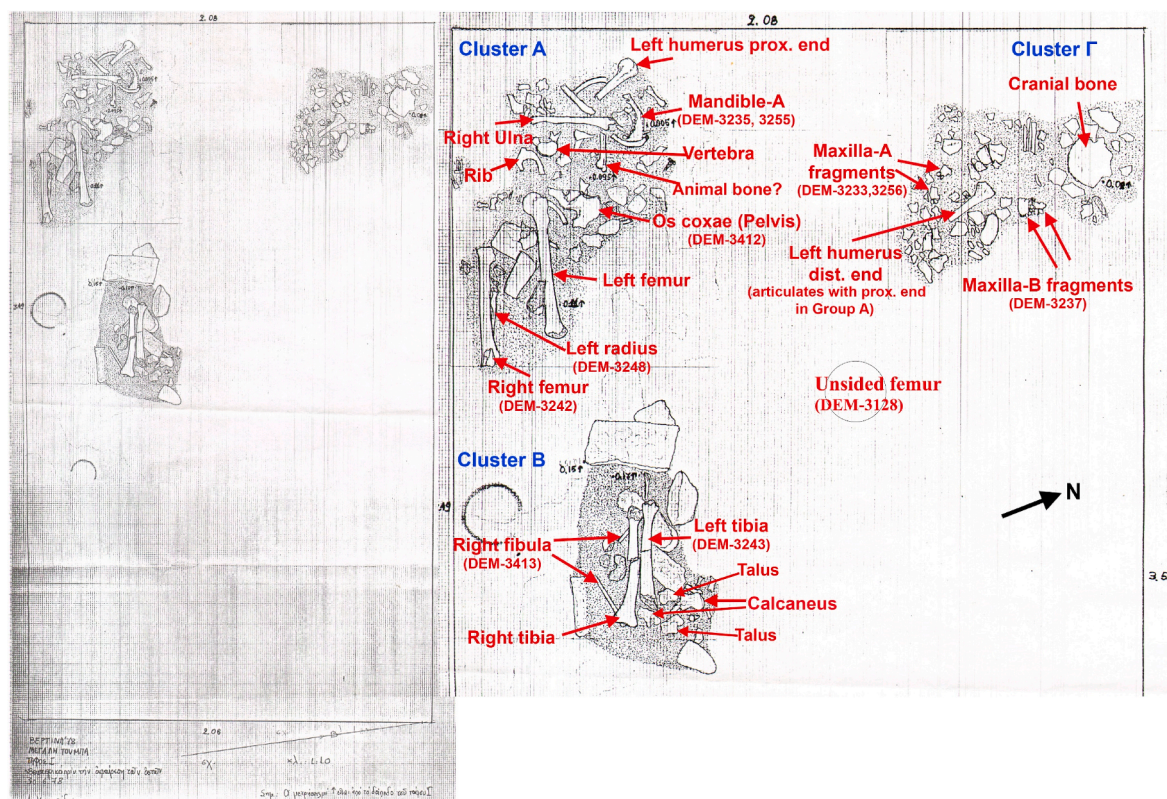


Fig. 6. Left: The original drawing of the floor bones made and signed by A. Kottaridi and included in the 1978 excavation logbook. Right: Enlargement of the part with the bones on the floor accumulated in three Clusters A, B, Γ in the west half of the tomb. Bones that can be identified are labeled by L. Wynn-Antikas. Note that the bones were put back in their "approximate" original positions for the drawing, as some had moved slightly during the excavation. Thus, their positions do not exactly match the excavation photo (Fig. 5). The estimated approximate position of the unsided femur is indicated with a circle. (Original drawing from the Archives of the Aristotle University of Thessaloniki, with the permission of the former Director prof. Ch. Saatsoglou-Paliadeli).

Thessaloniki (AMTh) in the 1980's, where the anthropologist Professor Jonathan Musgrave of Bristol University, briefly examined them (Musgrave, 1984, 1985, 1991) and provisionally suggested the presence of a male, a female and a full-term fetus/neonate. The human (adult and nonadult) and animal bones collected by Drougou in the 1977 excavation from the last 60–50 cm of the fill, (although most of them must have been found close to the floor as judged from the excavation notes and Andronikos (1994)), will be conventionally called hereafter the bones "in the fill" (see list in Table S3.2). These remained at Vergina and were never moved to Thessaloniki or elsewhere, so they never featured in these initial studies and were never factored into the Tomb I identity conclusions.

In 2014, the bones found "in the fill" and stored at Vergina since the original excavation, were given a preliminary anthropological examination by Th. Antikas and L. Wynn-Antikas for the purpose of selecting suitable samples for aDNA, radiocarbon dating, and other analyses. That examination, which was extended and updated for this publication, identified over 45 fragments of human and animal bones (Table S3.1). These included: adult human bone fragments such as a right radius, left ulna, left scapula, femur diaphysis, right temporal bone, ribs, vertebrae, and hand and foot bones. Also included were numerous nonadult bones, all identified as bones belonging to a minimum of five different fetus/perinate individuals.

The bones "on the floor" from the 1978 excavation (Table S3.1) that were transferred to AMTh, following Musgrave's initial examination, were further transferred in the late 1980s to the Anthropology Laboratory of the Democritus University of Thrace (DUTH) in Komotini by Professor N. Xirotiris for a detailed anthropological examination, which never occurred. In 2015, his successor, Prof. Antonis Bartsiokas, published a paper about these bones (Bartsiokas et al., 2015). At that time, a

new pair of bones, never seen or recorded previously, appeared for the first time as part of the Tomb I bone collection stored at DUTH since the late 1980s. This was a pair of unusually large leg bones (left femur and tibia) fused together at the knee at 79° of flexion with a hole in that area (Bartsiokas et al., 2015, Fig. 4). The authors of that paper claimed that this fused pair of bones belonged to Philip II, who was known historically to have suffered a leg injury, though not specifically in the knee, by a spear or lance (Justin 9.3.2),⁴ which allegedly also killed his horse. This injury occurred in a battle with the Triballi in the spring of 339 BC, three years before Phillip's assassination.

In 2017, the bones "on the floor" housed at DUTH were transferred to the Rhodopi Ephorate of Antiquities at Komotini and from there to Vergina, reuniting them with the rest of the bones "in the fill" stored there. Mrs. Angeliki Kottaridi, then Head of the Imathia Ephorate of Antiquities and who supervised the transfer, refused to accept the large fused femur and tibia. Based on her personal knowledge from participating in the Tomb I excavations of 1977 and 1978 and her drawings of the bones inside the tomb (Fig. 6A), she asserted that this pair did not belong to Tomb I.

Indeed, this idiomorphic pair of large fused leg bones (Fig. S3.13, Fig. S3.14) was never seen, photographed, described or recorded by any of the excavators of Tomb I, namely S. Drougou, P. Faklaris and A. Kottaridi, or by Andronikos, director of the excavations. It was also never observed or mentioned by the anthropologists Musgrave and Xirotiris (for an account of their observations and other details, see Supplementary section S3.4).

Sacrificial pyre: The 1977 excavation of the Great Tumulus, when the

⁴ For a full description of Philip's wounds see (Riginos, 1994, p.116).

soil was being removed from the upper layers downwards, revealed the remains of a circular pyre of about 1 m in diameter consisting of animal bone fragments and charcoal. We found together with the bone collection the remains of a pyre (Fig. S4.12), labeled, “North of Tomb I and east of Tomb II”. This must be one of the two pyres found above and between Tombs I and II on the red soil of the older smaller tumuli covering Tomb I and II which, according to Andronikos (Andronikos, 1984, p.64, 1980, p.161), may be attributable to sacrificial rites (*enagismos*) in honour of the prominent deceased buried below.

3. Materials and methods

For this study, the bones and teeth from Tomb I are categorized as follows:

Category 1: Bones “on the floor”, include adult and fetus/perinate bones found in situ and commingled in three clusters (A, B, Γ) on the lowest layer of the floor (Table S3.1), initially transferred to AMTh and then to DUTH in Komotini;

Category 2: Bones “in the fill”, include adult and fetus/perinate bones as well as animal bones, some showing butchery marks, found at different, unspecified levels in the last 50–60 cm above the floor in the fill, but mostly close to the floor (Table S3.2). Remained in storage at Vergina.

It was considered necessary to maintain a distinction in the following analyses and treatment between the above two groups as an initial precaution against the possibility that some bones in the fill may have been intrusions from the outside.

The adult bones “on the floor” include (apart from the in-situ bones), a maxilla and a mandible that most certainly belonged to the same individual since they articulate and have a similar morphology (size and tooth wear patterns) (Figs. 7 and 8), in agreement with Musgrave (1985) and Bartsiokas et al. (2015). These are referred to as maxilla-A and mandible-A. The bone collection also included a second maxilla now termed maxilla-B (Fig. 9) (Table S3.1). The nonadult (fetus/perinate) bones, include those found “on the floor” (Table S3.1, Fig. S4.10) and (Bartsiokas et al., 2015, p.35, photo S20) and those found at various levels in “the fill” (Table S3.2) and represent a minimum of six different individuals. Samples from the above categories and types of bones were



Fig. 8. Mandible-A (3235, 3255) (superior view), belonging to the same individual as maxilla-A (Fig. 7). (Photo by L. Wynn-Antikas).

analyzed. Additionally, the fused pair of leg bones presented for the first time by Bartsiokas et al. (2015) is included for comparison.

After receiving the permit from the Central Archaeological Council of Greece (KAS) in April 2016, sampling took place at the Vergina Laboratory at different times in 2017 and 2018, resulting in the selection of 40 representative and suitable bone/teeth samples from Tomb I for analyses. Samples from the fused (at the knee) pair of femur and tibia, which remained in the Archaeological Museum of Komotini, were also collected. The bone samples were small fragments (a few mm to 1 cm, depending on the size and significance of the bone). Special precautions were taken during sampling to avoid modern DNA contamination, including the use of face masks and gloves. Samples were wrapped in aluminum foil, placed in double plastic bags, and transferred to the Laboratory of Archaeometry at NCSR Demokritos in Athens (Lab Code:



Fig. 7. Maxilla-A (DEM-3233,3410) (inferior view) belonging to the same individual as mandible-A (Fig. 8). A group of three teeth (left molars 1,2,3) were found separate but articulates with the rest (Photo by L. Wynn-Antikas).

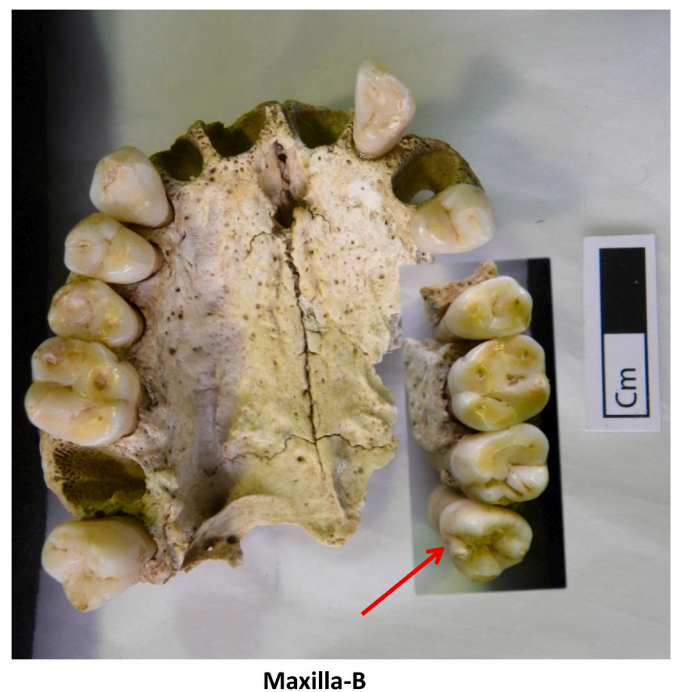


Fig. 9. Maxilla-B (DEM-3237) (inferior view) and the group of four teeth found separate from the rest of the maxilla but articulate with it. The arrow indicates left molar 3. The apical end of its roots are closed (Photo by L. Wynn-Antikas).

DEM). There, they were examined macroscopically and microscopically, removing soil deposits where necessary. The samples were photographed, archived, and divided into sub-samples for the various analyses. Table 1 provides descriptions of all the bones and teeth sampled, along with their locations in the tomb for those that could be identified by photos and drawings.

The techniques used included osteological and odontological macroscopic observations, aDNA analysis, radiocarbon dating, stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) analysis.

Osteological and odontological observations: Standard osteological and osteometric analyses of the human skeletal remains were conducted. Additionally, teeth were examined for dental attrition and articular surfaces for age-related degenerative changes. Joins of identifiable fragments of bones, wherever recognizable, are reported. The purpose of these osteological and odontological examinations was to: 1) determine the biological sex of the individuals for complementing, combining and extending the DNA molecular sexing, 2) estimate the age at death and stature, and 3) assign bones to individuals in combination with the other analyses results.

Ancient DNA analysis: We sequenced 23 samples from Tomb I, of all categories and bone types, to determine the genetic sex of the individuals, including three teeth, four petrous bones, and 16 post-cranial bone fragments. Additionally, we analyzed one sample from the fused femur/tibia pair. The samples were processed in clean lab facilities at the Manchester Institute of Biotechnology, University of Manchester, and the Globe Institute, University of Copenhagen, following established protocols for DNA extraction and library preparation. Briefly, DNA was extracted from 100 to 200 mg of bone/tooth powder using an EDTA-based buffer including a 10 min “pre-digestion” step (Damgaard et al., 2015). The DNA extracts were built into Illumina sequencing libraries using two different library preparation protocols (Carøe et al., 2018; Kapp et al., 2021). Negative controls were included throughout to monitor for contamination. The optimal number of PCR cycles was determined with qPCR. Sequencing data was processed using the nf-core/eager pipeline v2.4.3 (Fellows Yates et al., 2021). Ancient DNA damage patterns were assessed using DamageProfiler v1.1 (Neukamm et al., 2021). Contamination estimates were performed using hapCon (Huang and Ringbauer, 2022). Sex determination was carried out using three different methods including Ry_compute (Skoglund et al., 2013), SexDetErrmine (Lamnidis et al., 2018), and BeXY (Caduff et al., 2024). For more details of the methods see Supplementary section S2.

Radiocarbon dating: 35 bone samples were pretreated for radiocarbon dating. After initial screening, cleaning, and selection at NCSR Demokritos (Lab code: DEM), sample aliquots were sent to the AMS facility at the Curt-Engelhorn-Centre Archaeometry at Mannheim, Germany (Lab Code: MAMS), equipped with a Mini Carbon Dating System (MICADAS) accelerator. At Mannheim the collagen was extracted from bone and teeth samples using a modified Longin method (Brown et al., 1988; Longin, 1971), purified by ultrafiltration (>30 kDa) and freeze-dried. The collagen was then combusted to CO_2 in an Elemental Analyzer (EA) and catalytically converted to graphite. The ^{14}C ages were normalized to $\delta^{13}\text{C} = -25\text{‰}$ (Stuiver and Polach, 1977). A few samples failed to yield sufficient collagen for dating. Two of them, which were considered important (in-situ femur and tibia) and the sample size permitted, were sent to the Department of Human Evolution at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig. These samples underwent a detailed pretreatment as outlined in (Talamo et al., 2021; Talamo and Richards, 2011) (See Supplementary, Section S4.1 for details). The collagen extracted at the MPI-EVA was also dated by AMS at Mannheim. All radiocarbon dates were calibrated using IntCal20 (Reimer et al., 2020) in the OxCal v4.4.4 calibration program (Bronk Ramsey, 2021).

Stable isotope analyses (C and N): Collagen from samples yielding enough material for AMS dating and also additional bone samples were analyzed for isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) at Elementex Ltd at Callington,

Cornwall. Collagen was extracted by demineralizing bone samples in 0.5M HCl at 4 °C, solubilizing the organic material by heating at 60 °C in HCL (pH3) for 24 h, and ultra-filtering >30 kDa. The solution was freeze-dried to obtain collagen for analysis. All samples were analyzed on an ANCA SL elemental analyzer linked to a Sercon 2020 isotope ratio mass spectrometer with triplicate analysis for each sample.

Strontium (Sr) isotope analyses. A range of different types of samples were analyzed for strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) at the Department of Geosciences and Natural Resource Management, University of Copenhagen. These included: 1) Human remain samples from two adult individuals consisting of a few mg of enamel from three teeth belonging to two different individuals (two samples from premolar teeth from maxilla-A and mandible-A and one sample from a first molar from maxilla-B), as well as three petrous bones, analyzed for provenance investigation. Due to the scarcity of samples, the human femur and tibia samples from the in-situ bones “on the floor” were also analyzed, though mostly for the purpose of monitoring diagenetic alteration processes. 2) Pristine samples of soil, water, and plants were collected and analyzed from the archaeological sites of Vergina and Pella, to establish a somewhat preliminary baseline for these regions. Details for the methods of sample pre-treatment, Sr separation, and analysis are provided in Supplementary section S.6.

4. Results

The summarized results are reported in Table 2 (detailed results from each technique can be found in the Supplementary files). The samples are dealt with according to the categories and bone types discussed above.

- Bones “on the floor”:** Include: a) the adult in-situ and in anatomical position bones (Clusters A and B), b) the adult commingled bones (Clusters A and I) “on the floor”, c) the nonadult (fetus/perinate) commingled bones found on the floor and collected in the 1978 excavation (Table S3.1).
- Bones “in the fill”:** Include: a) the adult, b) the fetus/perinate bones and c) animal bones, found at different, unrecorded, levels in the lowest part of the fill, and collected in the 1977 excavation (Table S3.2).
- The fused femur and tibia:** The fused pair (femur and tibia) presented for the first time in Bartsiokas et al. (2015) and which remained in Komotini.

4.1. Ancient DNA analysis

We were able to recover ancient human DNA from 23 out of the 24 samples analyzed. We generated between 6 and 120 million reads per sample, while one of the samples (DEM-3133) failed to generate any reads. The DNA preservation was relatively poor with endogenous human DNA contents varying between 0 and 9.3 %. While the contamination estimates for some of the samples are relatively high, the damage patterns obtained are consistent with what would be expected for ancient DNA of that age. The detailed sexing results are reported in the Supplementary Excel Table S2.1 and the raw sequencing data are available for download via the European Nucleotide Archive (ENA) under Project Accession Number PRJEB87529. In total, we were able to assign sex to 21 of the 24 samples. Of those samples, 13 of the assignments were molecularly uncertain due to degradation, but combined with the osteological observations (section 4.2), we are confident that the sex determination results are correct. The molecular sexing results, together with all other examination and analyses results, are summarized in Table 2. The last column of this table indicates the individual whom each sample belongs to.

Most of the samples that could be confidently assigned a sex were male, while three were identified as female: maxilla-B (DEM-3237),

Table 1

Description of all the bones and teeth examined and sampled.

Lab code number	Sampling number	Bone, Dimensions (mm)	Archaeological context	Comments	Technique applied
Adult bones					
DEM-3125	C2q2	R-radius diaphysis (Fr) Preserved length L = 123.9	In the fill	(V)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3126	C2p	R-metacarpal-1 (In) L = 46.3	In the fill	(V)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3127	C20	L-scapula with coracoid process and glenoid cavity Preserved length L = 87.5	In the fill	(V)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3128	C21	Unsided femur diaphysis (Fr) Preserved length L = 205	In the fill	(V) Can be seen in the excavation photo (Fig. 5)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3133	A2g	Rib body (Fr) Preserved length L = 65.5	In the fill	(V)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3134	A2b	Prox. hand phalange- 5 (In) L = 32.4	In the fill	(V)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3233	RTL1a	Maxilla-A, R-molar 3 (In)	On the floor	(K) Seen in Cluster Γ (Figs. 6 and 7)	DNA
DEM-3235	RTL1c	Mandible-A, R-molar-2 (In)	On the floor	(K) Seen in Cluster A (Figs. 6 and 8)	DNA
DEM-3236	RTL1d	L-petrous portion (Fr) Preserved length L = 33.2, W = 24	On the floor	(K)	DNA, RCD, Sr-isotopes
DEM-3237	RTL2a	Maxilla-B, alveolus (Fr) with L-molar-1 (In)	On the floor	(K) Seen in Cluster Γ (Fig. 6, Fig. 9)	DNA, RCD, Sr-isotopes
DEM-3238	RTL2b	Prox. hand phalange-1 (In) L = 31, W = 16.5	On the floor	(K)	DNA, RCD
DEM-3239	RTL2c	R-humerus diaphysis (Fr) Preserved length L = 254.2 Intact L-humerus L = 320	On the floor	(K) (Figs. S3.1)	DNA, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3240	RTL2d	L-metacarpal-1 (In) L = 45.3	On the floor	(K)	DNA
DEM-3241	RTL2e	L-metacarpal-4 (In) L = 53.2	On the floor	(K)	DNA
DEM-3242	RTL2f	R-femur diaphysis (Fr) Preserved length L = 433.7 Intact L-femur L = 439	On the floor	(K) In-situ, Cluster A (Fig. 6, Fig. S3.3) L-femur (Fig. S3.3)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, Sr-isotopes
DEM-3243	RTL2g	L-tibia diaphysis (Fr) Preserved length L = 277.42 Intact R-tibia L = 357	On the floor	(K) In-situ, Cluster B (Fig. 6, Fig. S3.5) R-tibia, Cluster B (Fig. 6, Fig. S3.5)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, Sr-isotopes
DEM-3244	RTL2h	R-zygomatic (originally articulated to the right-orbit) (Fr) Preserved Size of both L = 83.2 x 50.1	On the floor	(K) (Fig. S3.7)	DNA, RCD
DEM-3246	RTL.U1	R-petrous portion (Fr) Preserved L = 41.4, W = 32.7	On the floor	(K)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, Sr-isotopes
DEM-3247	RTL.U2	L-petrous portion (Fr) Preserved L = 42.2, W = 23.2	On the floor	(K)	DNA, Sr-isotopes
DEM-3248	RTL.U3	L-radius diaphysis (In) L = 230	On the floor	(K) Seen in Cluster A, lying next to right femur (Fig. 6, Fig. S3.10)	DNA, RCD
DEM-3255	RTL1e	Mandible-A, L-premolar-1 (In)	On the floor	(K) Seen in Cluster A (Figs. 6 and 8)	RCD, Sr-isotopes
DEM-3256	RTL1f	Maxilla-A, L-premolar-2 (In) with bone (Fr)	On the floor	(K) Seen in Cluster Γ (Figs. 6 and 7)	Sr-isotopes
DEM-3274	RTL2I	Metatarsal-4 (Fr) Preserved L = 59.2	On the floor	(K)	RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3410	Ant-01	Maxilla-A (Fr), Bone	On the floor	(K) (Fig. 7)	RCD
DEM-3412	Ant-03	R-Innominate (Pelvis) Preserved dimensions: 79.4 x 56.4	On the floor	(K) Seen in Cluster A (Fig. 6, Fig. S3.11)	DNA, RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3413	Ant-04	R-Fibula (Fr), in two fragments Total Preserved L = 280	On the floor	(K) Seen in-situ (Fig. 5), Cluster B (Fig. 6, S3.5)	DNA, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
Fetus/Perinate bones					
DEM-3129	C1.11	Perinate, L-petrous bone (In) L = 39.2	In the fill	(V)	RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3130	C1.12	Fetus/perinate, L-petrous bone (In) L = 36.8	In the fill	(V)	RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3131	C1.13	Perinate, L-petrous bone (In) L = 39.2	In the fill	(V)	RCD
DEM-3132	C1.14	Fetus/perinate, L-petrous bone (Fr) Preserved L = 23.0	In the fill	(V)	RCD
DEM-3245	RTL3a	Fetus, L-petrous bone (In) L = 31.8	On the floor	(K) (Fig. S4.6)	DNA, RCD
DEM-3273	RTL3b	Fetus/perinate, sphenoid (In)	On the floor	(K)	RCD

(continued on next page)

Table 1 (continued)

Lab code number	Sampling number	Bone, Dimensions (mm)	Archaeological context	Comments	Technique applied
		L = 20		(Fig. S4.6)	
Animal bones					
DEM-3137	AA	Animal tibia/fibula (Fr) <i>capra/ovis</i> with butchery marks Preserved L = 60.8, W = 23	In the fill	(V)	RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3138	AC	Small animal humerus (In) L = 54.8	In the fill	(Fig. S4.7) (V)	RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3139	AD	Animal horn (Fr) <i>capra/ovis</i> with butchery marks Preserved L = 58.5	In the fill	(V)	RCD
DEM-3140	AE	Animal (dog?) tibia (Fr) Preserved L = 60.6	In the fill	(Fig. S4.7) (V)	RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3411	Ant-02	Animal metacarpal (Fr) <i>capra/ovis</i> Preserved L = 61.9	From a pyre above and between Tomb I and II	(K)	RCD, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$
DEM-3414	Ant-05	Animal metacarpal (Fr) <i>capra/ovis</i> Preserved L = 78.9	In the fill	(V)	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$
For Sr isotope baseline					
DEM-3257	RTL.C1	Animal maxillary teeth and bone (Fr) <i>capra/ovis</i>	In the fill	(V)	Sr-isotopes
DEM-3258	RTL.C2	Small animal bone diaphysis, <i>Leporidae</i> (hare/rabbit) (In) L = 69.0	In the fill	(V)	Sr-isotopes
Unknown origin fused adult bones					
DEM-3254	1969/15	L-femur (In) L = 492	Unknown (not from Tomb I)	Originally fused with tibia DEM-3276 (Figs. S3.13, S3.14) (remained in Komotini)	RCD, DNA
DEM-3276	1969/15	L-tibia (In) L = 438	Unknown (not from Tomb I)	Originally fused with femur DEM-3254 (Figs. S3.13, S3.14) (remained in Komotini)	RDC, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$

Notes.

In= Intact, Fr=Fragment, L = Length, W = width.

(V) = Remained in storage at the Vergina Museum.

(K) = Moved to the Archaeological Museum of Thessaloniki in the early 1980's and then to the Laboratory of Anthropology Democritus University of Thrace at Komotini in the late 1980's. Returned to Vergina in 2018.

Fetus = 8–39 weeks in utero.

Perinate = At or around the time of birth.

identified in Cluster Γ in the excavation drawing (Fig. 6), a right (DEM-3246), and a left (DEM-3247) petrous bone (Table 2). The in-situ leg bones, femur (DEM-3242), tibia (DEM-3243) and fibula (DEM-3413), along with maxilla-A and mandible-A (DEM-3233, 3235 and 3255), as well as the left radius (DEM-3248), left metacarpal-1 (DEM-3240), and the right humerus (DEM-3239), were all sexed confidently as male. Among the adult bones in “the fill”, DEM-3125, 3126, 3127 and 3134 were sexed male, albeit with lower confidence due to lower coverage. Three samples (DEM-3128, 3133 and 3244) could not be sexed due to insufficient coverage.

4.2. Osteological and odontological observations

The primary focus was on the bones found “on the floor”, both in-situ and commingled in clusters (Table S3.1), because they are most likely associated with the primary burial(s). Additionally, some of the adult bones from “in the fill” reported to be from the last layers of the fill (Table S3.2), were also included in the examination. All the bones and teeth examined are presented in Table 1 and discussed below. Further information and measurements are provided in Supplementary section S3.

4.2.1. In-situ bones “on the floor” (Clusters A and B)

1. *Right (DEM-3242) and left in-situ femur in anatomical position* (Figs. S3.3): These leg bones were found in their anatomical/supine positions in Cluster A which indicates they belong to the same individual (Fig. 5). DNA analysis confirmed they are male. The head and the greater and lesser trochanters of the intact left femur are fully fused. In males, this occurs by 21 years of age (Herrmann et al.,

1990). The left femur's (found complete, Fig. S3.3B) dimensions are within the male range (Suppl., Section S3), and a stature of 167.4 ± 3.94 cm was calculated (Trotter and Gleser, 1952). No age-related degenerative changes were observed. The left femur head retains an epiphyseal line (Fig. S3.4). From now on, this individual will be referred to as the “In-situ male (ISM)”.

2. *Right and left (DEM-3243) in-situ tibia in anatomical position* (Figs. S3.5): These tibiae, found in their anatomical/supine positions in Cluster B along with their fibulae (DEM-3414) and foot bones, tested confidently male with DNA (Fig. 5). The proximal and distal epiphyses of the right tibia are fused. In males, this occurs by 23 years of age for the proximal end and at age 20 for the distal (Johnston, 1962). Neither tibia show any age-related degenerative changes (Figs. S3.5), like the femora bones. The right tibia's dimensions are within the male range, consistent with the DNA analysis. A stature of 168.5 ± 3.37 cm was estimated, which is in agreement with the stature calculated from the left femur above. For more details and measurements see Suppl. Section S3. These bones clearly belong to the ISM.

4.2.2. Commingled bones “on the floor” (Clusters A and Γ)

3. *Right zygomatic/frontal bone (DEM-3244)*: This bone could not be sexed via DNA. The supra-orbital margin's thickness suggests it is male, as males have thicker, more rounded margins compared to those of females, which are thinner and sharper (White, 2000), (Fig. S3.7).

4. *Left temporal bone fragment with mastoid process* (not sampled) (Fig. S3.8): The long and prominent mastoid process indicates it belongs to an adult male (White, 2000).

Table 2
Radiocarbon, DNA and isotope results.

Laboratory Code	Type of Bone	Sex (Molecular)	Sex (Osteol.)	⁸⁷ Sr/ ⁸⁶ Sr	δ ¹⁵ N (‰)	δ ¹³ C (‰)	C/N	Radiocarbon date (BP)	Calibrated age cal (BC/AD)	Probabilities (overall = 95.4 %)	Individual
Floor bones: Adult in-situ (Clusters A and B)											
DEM – 3242 (R-EVA 3193; MAMS-43167)	In-situ, R-femur diaphysis	Male	Male	0.708959	10.03	−18.63	3.3	2320 ± 21	410–367 BC	(95.4 %)	ISM
DEM – 3243 (R-EVA 3194; MAMS-41863)	In situ, L-tibia diaphysis	Male (confidently)	Male	0.709285	10.25	−18.44	3.2	2315 ± 25	411–359 BC 276–261 BC 244–234 BC	(90.1 %) (3.3 %) (2.1 %)	ISM
DEM – 3413 (MAMS-46667)	In-situ, R-fibula	Male (confidently)	Male		10.38	−18.34	3.2	Not dated			ISM
Floor bones: Adult commingled (Clusters A and I')											
DEM – 3246 (MAMS-37120)	R-petrous bone	Female	?	0.708936	11.13	−19.25	3.2	2317 ± 22	410–363 BC 272–266 BC	(94.5 %) (0.9 %)	The Female
DEM – 3247	L-petrous bone	Female (consistent)	?	0.708570				No collagen for dating			The Female
DEM – 3255 (MAMS-37111)	Mandible-A, Left PM-1 (dentine and roots)	Male (as 3235)	Male	0.711353			3.2	2315 ± 22	410–362 BC 273–264 BC	(94.0 %) (1.5 %)	ISM
DEM – 3235	Mandible-A, Right M-2	Male (consistent)	Male					Not dated			ISM
DEM – 3233	Maxilla-A, Right M-3	Male	Male	–				Not dated			ISM
DEM – 3410 (MAMS-46664)	Maxilla-A, Bone	Male	Male					Not enough collagen			ISM
DEM – 3412 (MAMS-46666)	Innominate (Pelvis)-Right	Male (consistent)	Male		9.81	−19.11	3.3	2302 ± 21	405–359 BC 276–234 BC	(87.3 %) (8.1 %)	ISM
DEM – 3238 (MAMS-37663)	Proximal Hand phalange -1	Male (consistent)	?				3.2	2284 ± 19	400–356 BC 281–232 BC	(71.1 %) (24.3 %)	ISM
DEM – 3236 (MAMS-37113)	L-Petrous bone	Male (consistent)	?	0.709714			3.2	2275 ± 22	398–352 BC 286–211 BC	(57.0 %) (38.5 %)	ISM
DEM – 3237 (MAMS-37114)	Maxilla-B, alveolus and left M-1	Female	Female	0.709311			3.2	2269 ± 23	396–351 BC 292–209 BC	(48.8 %) (46.6 %)	The Female
DEM – 3128 (MAMS-31748)	Unsided femur diaphysis	n.a.	Female?		11.61	−18.56	3.1	2268 ± 24	396–351 BC 294–208 BC	(47.0 %) (48.5 %)	The Female
DEM – 3274 (MAMS-38627)	Metatarsal-4	n.t.	?		9.46	−19.30	2.9	2267 ± 24	396–351 BC 295–208 BC	(46.0 %) (49.4 %)	ISM?
DEM-3244 (MAMS-37118)	R-zygomatic	n.a.	Male				3.0	2258 ± 21	393–351 BC 295–208 BC	(40.2 %) (55.2 %)	ISM
DEM – 3248 (MAMS-37121)	L-radius diaphysis	Male	Male				3.2	2257 ± 22	392–351 BC 302–208 BC	(38.5 %) (56.9 %)	ISM
DEM – 3256	Maxilla-A, Left PM-2	Male (see 3235)	Male	0.711676				Not enough collagen			ISM
DEM – 3239	R-humerus diaphysis	Male	Male		10.34	−18.98	3.3	Not enough collagen			ISM
DEM – 3240	L-metacarpal-1	Male	?					Not dated			ISM
DEM – 3241	L-metacarpal-4	Male	?					Not dated			ISM
Floor bones: Fetus/Perinate commingled (Unknown location in the tomb)											
DEM – 3273 (MAMS-38626)	Sphenoid (Fetus/perinate)	n.t.	?				3.3	2040 ± 26	150–135 BC 114 BC – 60 AD	(1.7 %) (93.7 %)	
DEM – 3245 (MAMS-37119)	L-petrous bone (Fetus)	Male (consistent)	?				3.2	2027 ± 27	101–67 BC 60 BC – 68 AD	(7.5 %) (88.0 %)	
Bones “in the fill”: Adult											
DEM – 3134 (MAMS-31754)	Hand phalange	Male (consistent)	?		9.56	−19.13	3.2	2333 ± 22	450–446 BC 416–374 BC	(0.4 %) (95.1 %)	ISM
DEM – 3133 (MAMS-31753)	Rib body	n.a.	?		9.76	−18.87	3.2	2278 ± 23	400–352 BC 286–211 BC	(58.8 %) (36.6 %)	?
DEM – 3125 (MAMS-31745)	R-radius diaphysis	Male (consistent)	Male		10.26	−18.61	2.9	2237 ± 23	386–346 BC 316–204 BC	(23.8 %) (71.7 %)	ISM

(continued on next page)

Table 2 (continued)

Laboratory Code	Type of Bone	Sex (Molecular)	Sex (Osteol.)	$^{87}\text{Sr}/^{86}\text{Sr}$	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	C/N	Radiocarbon date (BP)	Calibrated age cal (BC/AD)	Probabilities (overall = 95.4 %)	Individual
DEM – 3126 (MAMS-31746)	R-Metacarpal-1	Male (consistent)	Male		9.96	−18.99	2.9	2233 ± 24	384–346 BC	(21.9 %)	ISM
DEM – 3127 (MAMS-31747)	L-scapula	Male (consistent)	Male		9.61	−19.03	2.9	2226 ± 23	383–342 BC	(19.4 %)	ISM
<i>Bones “in the fill”: Fetus/Perinates</i>											
DEM – 3130 (MAMS-31750)	L-petrous bone (fetus/perinate)	n.t.	?		9.61	−19.53	3.2	2038 ± 22	103 BC – 28 AD	(94.0 %)	
DEM – 3131 (MAMS-31751)	L-petrous bone (perinate)	n.t.	?				3.2	2014 ± 22	46 AD – 58 AD	(1.5 %)	
DEM – 3129 (MAMS-31749)	L-petrous bone (perinate)	n.t.	?		10.10	−19.50	3.0	1996 ± 23	51 BC – 66 AD	(95.4 %)	
DEM – 3132 (MAMS-31752)	L-petrous bone (fetus/perinate)	n.t.	?				3.3	1954 ± 25	45 BC – 79 AD	(93.7 %)	
<i>Bones “in the fill”: Animals</i>											
DEM – 3138 (MAMS-31756)	Small animal (<i>Felis?</i>) humerus	n.t.	–		4.90	−21.06	3.3	2022 ± 22	100–108 AD	(1.7 %)	
DEM – 3140 (MAMS-31758)	Tibia <i>canis</i> (Dog)	n.t.	–		7.65	−19.36	3.1	1963 ± 24	35–14 BC	(3.2 %)	
DEM – 3137 (MAMS-31755)	Tibia/fibula <i>capra/ovis</i> with butchery marks	n.t.	–		4.11	−19.99	2.9	1956 ± 24	5–128 AD	(92.2 %)	
DEM – 3139 (MAMS-31757)	<i>Capra/ovis</i> horn with butchery marks	n.t.	–				2.9	1950 ± 23	88–82 BC	(1.1 %)	
DEM – 3414	Metacarpal, <i>capra/ovis</i>	n.t.	–		3.96	−20.60	3.1	Not dated	54 BC – 62 AD	(94.4 %)	
DEM - 3257	Maxilla teeth and bone (Fr), <i>capra/ovis</i>	n.t.	–	0.709572, 0.709505				Not dated	33–16 BC	(4.5 %)	
DEM - 3258	Small animal bone diaphysis, <i>leporidae</i> (hare/rabbit)	n.t.	–	0.709350				Not dated	6–123 AD	(91.0 %)	
<i>Sacrificial Pyre between Tombs I & II: Animals and charcoal</i>											
DEM – 3411 (MAMS-46665)	Animal metacarpal, <i>capra/ovis</i>	n.t.	–		7.65	−16.02	3.1	2215 ± 19	32–16 BC	(2.7 %)	
DEM – 2719	Charcoal	n.t.	–					2209 ± 25	7–125 AD	(92.8 %)	
<i>The unknown origin fused femur/tibia</i>											
DEM – 3254 (MAMS-41864)	(1969/15) Femur from fused pair of unknown origin (Remains in Komotini)	Male	Male				3.2	2202 ± 25	32–16 BC	(1.5 %)	
DEM – 3276 (MAMS-38313)	(1969/15) Tibia from the same fused pair as DEM-3254 (Remains in Komotini)	Same as 3254	Male		10.63	−20.17	3.3	2178 ± 25	32–16 BC	(1.5 %)	
DEM – 3254/3276 Combined date	Femur & tibia							2190 ± 18	7–129 AD	(93.9 %)	
									370–340 BC	(14.8 %)	
									324–199 BC	(80.7 %)	
									372–196 BC	(94.6 %)	
									184–179 BC	(0.9 %)	
									365–176 BC	(95.4 %)	
									361–242 BC	(55.7 %)	
									236–152 BC	(39.7 %)	
									358–277 BC	(58.4 %)	
									260–235 BC	(3.7 %)	
									234–173 BC	(33.3 %)	

Notes: n.a. = not assigned, n.t. = not tested, ISM=In-situ male.

5. *Maxilla-A (DEM-3233, 3256) and Mandible A (samples DEM-3235, 3255) (Figs. 7 and 8)*: These bones and teeth were confirmed as male by DNA and all the evidence indicates they belong to the same individual (the ISM). This conclusion is in agreement with Musgrave (1985) and Bartsiokas et al. (2015). Mandible-A is located in Cluster A and maxilla-A fragments are in Cluster Γ (Fig. 6). The degree of dental attrition in molars 1, 2 and 3 on either side of the maxilla and mandible suggests an age of 25–35 years (Brothwell, 1981; Miles, 1962) in agreement with Musgrave's estimate (Musgrave, 1985). Details are provided in [Supplementary section S3](#)
 6. *Right humerus (DEM-3239) (Figs. S3.1 and S3.2)*: This bone, confidently sexed as male by DNA, is incomplete, missing the superior portion of the diaphysis and proximal end. The distal epiphysis (medial epicondyle) is completely fused, indicating this male individual was at least 20 years old (McKern and Stewart, 1957). No age-related degenerative changes were observed. Some dimensions of the distal end were recorded ([Supplementary section S3](#)).
 7. *Left humerus (not sampled) (Figs. S3.1 and S3.2)*: This was originally found in two pieces and in two different clusters (proximal end in Cluster A and distal end in Cluster Γ), (Fig. 6). The humeral head diameter (49 mm) is within the male range ([Suppl. Section S3](#)). The proximal epiphysis is completely fused, indicating the individual was at least 21 years old and the distal epiphysis (medial epicondyle) is completely fused, indicating an age of at least 20 years old (McKern and Stewart, 1957). No age-related degenerative changes were observed. We believe this left humerus also belongs to the ISM along with the right humerus and mandible-A, maxilla-A.
 8. *Left radius (DEM-3248) (Fig. S3.9)*: This bone was confidently sexed as male by DNA analysis. The proximal and distal epiphyses are fused, which occurs by age 19, and at 24–25 years of age in males, respectively (McKern and Stewart, 1957). No age-related degenerative changes were observed. This bone has also been assigned to the ISM.
 9. *Right ulna (not sampled) (Figs. S3.10)*: Found intact in Cluster A (Fig. 6), both its proximal and distal epiphyses are fused, which occurs by the age 19 and 23 respectively, in males (McKern and Stewart, 1957). No age-related degenerative changes were observed. This bone has also been assigned to the ISM.
 10. *Right pelvis fragment (DEM-3412)*: Located in Cluster A (Fig. 6). This fragment (Greater Sciatic Notch) was sampled for radiocarbon dating and DNA analysis (Fig. S3.11). Its narrow morphology indicates it is male consistent with the DNA results.
 11. *Maxilla-B (Fig. 9) (DEM-3237)*: This bone and teeth are seen in Cluster Γ on the excavation drawing (Fig. 6). It belonged to a **female** as confirmed by DNA analysis. An overall age range of 18–25 at death was determined through dental attrition of the extant molars, root closure timing and suture obliteration of the maxilla⁵ (Fig. S3.6) (see a full description in the [Suppl. S3](#)). From now on this individual will be referred to as “**The female**”.
- 4.2.3. *Bones “in the fill” above the floor*
12. *Left Scapula (DEM-3127)*: Found in two fragments, one piece includes the coracoid process, the proximal end of the glenoid cavity and part of the body. The other piece includes the middle and distal end of the glenoid cavity and the infraglenoid tubercle. The two pieces join at the glenoid cavity and so its length could be measured at 39 mm. The length of the glenoid cavity is used as a marker for sex determination. A cavity >37 mm indicates male (Bass, 1995), consistent with the DNA results. No age-related degenerative changes were observed around the articular surface of the glenoid cavity.
 13. *Right radius (DEM-3125)*: Found in three pieces (proximal end, diaphysis, and distal end) (Fig. S3.9A), these fragments join to form a complete bone. The diaphysis (DEM-3125) was sampled for radiocarbon dating and DNA. It was sexed most likely male. Its fully fused proximal and distal epiphyses indicate an age over 25 years at death. Its morphology matches the left radius found on the floor (DEM-3248). It most likely belonged to the ISM and was found near the floor, probably from Cluster A or Γ .
 14. *Left ulna (not sampled)*: This bone, was found in two pieces (incomplete diaphysis and proximal end) (Fig. S3.9). The fused proximal end's morphology matches the right ulna found on the floor (Fig. S3.10). Although not sampled for DNA, its morphology and lack of age-related degenerative changes make us believe it also belonged to the ISM, and most likely came from cluster A or Γ .
 15. *Unsided femur diaphysis (DEM-3128)*: This is a femur fragment found on the floor of the tomb (Fig. 5) and somehow separate from the three clusters (Fig. 6). Due to missing diagnostic elements, it was not possible to accurately side this bone and its sex could not be reliably assigned by DNA. However, its gracile morphology, along with its dimensions (see details in the [Supplementary section S3.3](#)), suggests it belongs to a female, and as such, we treat it together with the other female bones and teeth (maxilla-B and the right and left petrosas, DEM-3246, 3247). See radiocarbon date and combined testing ([Section 4.3](#)).
- 4.2.4. *Fetus/perinate bones*
- A minimum of six fetuses and perinates were identified through duplication of their left petrous bone. Some of these bones, including one left petrous, one sphenoid and other fragments (Bartsiokas et al., 2015) were collected in the 1978 excavation and included in the “on the floor” bones. Additional fetus/perinate bones (from at least five different individuals) were found “in the fill” at unknown levels and collected in the 1977 excavation ([Table S3.2](#)). Their ages at death were determined from the length of the petrous bone according to published data (Fazekas et al., 1978) ([Table 1](#), [Table 2](#), [Table S3.1](#), [Table S3.2](#)).
- The six different fetus/perinate bones and one sphenoid identified and analyzed are.
1. *Left petrous perinate bone (DEM-3129)*: Found in the fill at an unknown depth, collected in the 1977 excavation. Length = 39.2 mm, approx. age = 10 LM.
 2. *Left petrous fetus/perinate bone (DEM-3130)*: Found in the fill at an unknown depth, collected in the 1977 excavation. Length = 36.8 mm, approx. age = 8–10 LM.
 3. *Left petrous perinate bone (DEM-3131)*: Found in the fill at an unknown depth, collected in the 1977 excavation. Length = 39.2 mm, approx. age = 10 LM.
 4. *Left petrous fetus/perinate bone (fragment) (DEM-3132)*: Found in the fill at an unknown depth, collected in the 1977 excavation. Preserved length = 23.0 mm, approx. age = 6.5–10 LM.
 5. *Left petrous perinate bone (Table S3.1, code A9, not analyzed)*: Found in the fill at an unknown depth, collected in the 1977 excavation. Length = 37.5 mm, approx. age = 10LM.
 6. *Left petrous fetus bone (Fig. S4.10) (DEM-3245)*: Found most probably among the commingled adult bones “on the floor” and collected together in the 1978 excavation (Bartsiokas et al., 2015, p.35, S20). Length = 31.8 mm, age = 8–9 LM.
 7. *Fetus/perinate Sphenoid bone (Fig. S4.10) (DEM-3273)*: Found most probably among the commingled adult bones “on the floor” and collected together in the 1978 excavation (Bartsiokas et al., 2015, p.35, S20). Length = 20 mm.

⁵ Dr. Efthymia Nikita, Associate Professor in Bioarchaeology of The Cyprus Institute, was kind enough to examine the dentition and she fully agrees with this age estimate of 18–25.

Additional cranial and post-cranial fetus/perinate bones and fragments were found in the fill (Table S3.2) and also on the floor (Table S3.1) (Bartsiokas et al., 2015), but they were not useful for determining the minimum number of individuals.

4.2.5. Summary

The male bones: All the analyzed adult bones, whether found “on the floor” or slightly above “in the fill” are male either by aDNA or osteometric analysis or both. In particular, the in-situ leg bones (femora, tibiae, fibulae, foot bones) are male and belong to one individual. The arm bones (right/left humerus, right/left radius and right/left ulna) are also male and have a similar size, morphology and epiphyseal fusion timing, and none of them shows any age-related degenerative changes that might indicate they come from different individuals. The left scapula (DEM-3127) was also confidently sexed male by aDNA and osteometrics. The age range of 25–35 years was determined from the dentition and leg bones of the in-situ male.⁶ Therefore, the arm bones, the in-situ leg bones, along with the maxilla-A, mandible-A, the zygomatic, and the other male bones, comprise almost a complete skeleton with no duplicates, indicating they all belong to the same individual, namely the in-situ male (ISM) (Fig. S3.12).

The female bones: Maxilla-B and the right and left petrosas (DEM-3246, 3247) identified as female with aDNA (Table 2 and S1), together with the *unsided* femur fragment, are the only female bones amongst all the bones analyzed. Most likely they all belong to the same individual, namely “The female” (Fig. S3.12). More evidence for this is provided in the Radiocarbon section 4.3.

The fetus/perinate bones: They belong to at least six different individuals. Due to their number and age at death (fetus and perinates) they cannot be related to the initial primary adult burial(s) in the tomb. In any case, they all date within the Roman period (see radiocarbon section 4.3).

Animal bones: A number of animal bones were also found together with the fetus/perinate bones. Some species identified are: *Capra/ovis*, *canis*, *leporidae*, (*felis*?).

4.2.6. The fused leg bones (femur and tibia) with a hole

This pair (DEM-3254/3276) remained in Komotini as discussed previously. These bones, originally fused together, were broken at the joint at some unknown time (Figs. S3.13 and S3.14). They are unusually large with approximate lengths of 49.2 cm and 43.8 cm for the femur and tibia respectively, giving an approximate stature for this individual of about 180 cm, as also estimated by Bartsiokas et al. (2015, Fig. 4). During our detailed examination of this fused pair at the Archaeological Museum of Komotini, very important evidence came to light that excludes any connection of this pair of fused bones with the human remains excavated from Tomb I. We discovered the presence of a number written on the outer or cortical surface of the femur, about mid diaphysis. The number was written in red ink and partly eroded, but with the use of a digital optical microscope (*Dino-Lite premium*) the number 1969/15 was clearly legible (Fig. 10). This obviously denotes the year of excavation and the number of the find or burial, likely coming from a cemetery with many graves. Given the fact that the Vergina Great Tumulus excavation began in 1977, this pair of bones cannot be from Tomb I but instead originated from an unknown excavation somewhere else. It should be further noted that no bone numbering or cataloging system was ever applied to any of the skeletal material from the Vergina Great Tumulus excavations, until Th. Antikas and L. Wynn-Antikas catalogued the Tomb II bones between 2009 and 2015 (Antikas and Wynn-Antikas, 2016). Further details about this fused pair can be found in the Supplementary section S3.4.

⁶ Dr. Efthymia Nikita, Associate Professor in Bioarchaeology of The Cyprus Institute, was kind enough to look at the dentition and the other bones and she also agrees with this age estimate of 25–35.

4.3. Radiocarbon dating

Table 2 presents the radiocarbon dating results alongside other analyses. The calibrated age ranges are given with the highest probability ($2\sigma = 95.4\%$). Due to the wiggles in the calibration curve, some samples give split calibrated ages. These are given as sub-ranges with their individual probabilities within the overall 2σ range. The C/N ratio for all samples falls between 2.9 and 3.3, confirming collagen integrity for dating and isotope analysis (DeNiro, 1985; Sealy et al., 2014). The isotopic results indicate a terrestrial diet (Vika, 2011), negating the need for reservoir correction. Fig. 11, shows a multi-plot of calibrated ages for all dated bone samples (human and animal) ordered by radiocarbon date (BP) and grouped by location in the tomb.

As shown in Table 2 and Fig. 11, all human adult bones, male and female, whether found “on the floor” or “in the fill”, have calibrated ages in the range of 400–350 calBC. However, due to calibration curve wiggles, some samples produce a second range in the 3rd century calBC with varying probabilities.

An exception to this typical calibrated age probability distribution of the adult bones in the tomb is the fused femur/tibia with the hole. This bone has a combined radiocarbon date (femur and tibia) of 2190 ± 18 BP (Table 2), corresponding to a 2σ calibrated age 358–173 calBC. This differs from the adult bones in Tomb I (Fig. 11), suggesting a different time period.

All nonadult (fetus/perinate) bones analyzed, either found “on the floor” or “in the fill”, date more than two centuries later than the adult bones, as can be seen in Fig. 11. Their calibrated dates fall within the Roman period, more specifically within the extreme limits of 150 calBC the earliest and 130 calAD the latest, (95.4 % probability) (Table 2, Fig. 11).

Similarly, the animal bones analyzed (capra/ovis and others), some with butchery marks (Fig. S4.11), date also in the Roman period and in the same date range as the fetus/perinates, concentrating more towards the end part (0–130 calAD) of the overall nonadult age range (Table 2, Fig. 11).

4.3.1. Statistical treatment of all the adult bone dates

As seen from Fig. 11, all the adult bones, male and female, “on the floor” and “in the fill”, with the exception of the fused femur/tibia pair stored at Komotini, give similar dates. To test if the Tomb I bones could all belong to the same depositional phase and detect any outliers, we ran a Bayesian statistical analysis (excluding the fused pair) with a one-phase model, combined with a *general outlier model* (Bronk Ramsey, 2009) (see Suppl. S4). The output of this analysis is shown in Fig. 12. The overall agreement is excellent (Amodel: 146) and the individual agreement of all samples is above 71 %, with only one sample DEM-3127 (L-scapula) from “the fill”, having a somewhat lower agreement, 47 % (Fig. 12). The posterior probability of outliers for all samples is <5 %. This indicates that all the adult bones in Tomb I most likely belong to one depositional phase, that is, a single burial event. The Boundaries for this phase are:

START: 406–382 calBC (2σ range). Weighted mean = 395 ± 6 calBC (Fig. S4.2)

END: 388–354 calBC (2σ range). Weighted mean = 370 ± 15 calBC (Fig. S4.2)

Taking the outer limits, the overall date range for this burial phase is 406–354 calBC with 95.4 % probability.

4.3.2. Statistical treatment of the adult bones “on the floor” dates

For a more precise dating, we ran a new treatment using only the adult bones “on the floor” whose positions in the tomb were more securely recorded (Figs. 5 and 6). The bones included in this treatment are: The in-situ bones (Fig. 5), the commingled bones in Clusters A, B and Γ, drawn by A. Kottaridi in 1978 (Fig. 6), and the *unsided* femur fragment shown on the floor in the excavation photo (Fig. 5). In addition, the fused pair femur/tibia at Komotini was included for

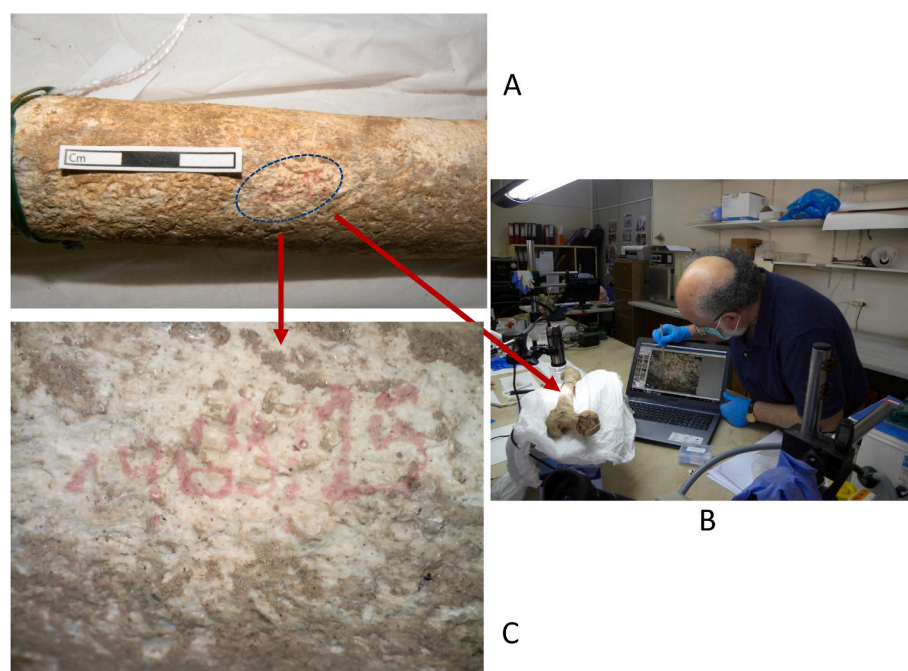


Fig. 10. A: The femur with the number in red located anteriorly about mid-diaphysis. B: examination under a digital microscope at the Archaeological Museum of Komotini. C: Image from the microscope showing clearly the number 1969/15 in red ink. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

comparison. The same Bayesian analysis model as above was used (Suppl S4). The analysis showed (Fig. S4.3) that the adult bones from “on the floor” of Tomb I (male and female), could belong to the same phase with individual sample agreements above 87 %, except for the fused pair, which had only 13 % agreement and a 62 % outlier probability. In contrast, all the other Tomb I bones had outlier probabilities below 2 %. Therefore, besides its complete absence from the archaeological records and the irrelevant excavation year written on it, the fused pair also cannot be related to the Tomb I bone assemblage by the radiocarbon evidence.

Then, removing the fused pair, we reran the phase analysis for the bones “on the floor” (male and female) (Fig. 13). The model’s overall agreement was excellent ($A = 183$), with individual sample agreements above 85 %. This confirms that all the recorded bones “on the floor”, both in-situ and commingled, belong to a single depositional event. This event’s time range is confined within the boundaries:

START: 405–382 calBC (2σ range), with a weighted mean = 393 ± 5 calBC (Fig. S4.5).

END: 391–360 calBC (2σ range), with a weighted mean = 378 ± 8 calBC (Fig. S4.5).

Thus, all the analyzed bones “on the floor” (male and female) date within an overall range of 404–362 calBC, with 95.4 % probability.

The in-situ male bones (femora, tibiae, fibulae and foot bones) alone, found in their anatomical positions (Fig. 5), are crucial, as they suffered the least disturbance and are clearly associated with the primary burial. DNA and osteometric analyses confirmed these bones belonged to the same male individual (ISM). Radiocarbon dating of the right femur (DEM-3242) and left tibia (DEM-3243) (Table 2), yielded dates of 2320 ± 21 BP and 2315 ± 25 BP, respectively, resulting in a combined calibrated age of 406–378 calBC with 95.4 % probability, consistent with the overall “on the floor” bones range.

It has been suggested that there might be a potential “collagen aging” effect in long bones, which may account for an apparent shift of the radiocarbon date to a slightly older date than the actual date of death of the individual (Hedges et al., 2007; Manolagas, 2000). For individuals aged 30–50, this offset is minor, around 10–15 years (Bayliss et al., 2013). Nevertheless, due to the historical importance of these finds,

taking this possibility into account was deemed scientifically necessary. Therefore, we applied a model to calculate the corrected age. Using the combined radiocarbon date of 2318 ± 17 BP and the range of 25–35 years at death, the corrected for collagen offset calibrated age is 395–368 calBC at a 95.4 % probability. For more details, refer to Supplementary section S4.

Extending the statistical analysis to all male bones “on the floor”, including the commingled bones, such as the mandible-A (DEM-3255), left radius (DEM-3248), pelvis (DEM-3412), left petrous (DEM-3236) and others sexed by aDNA, and osteometric analysis with high confidence, an R-Combine test was conducted. This test passed the chi-square test, indicating that all these bones could belong to the same male individual as the in-situ bones. The combined radiocarbon date for these male bones is 2295 ± 9 BP, which calibrates to 400–367 calBC with 95.4 % probability (Fig. S4.6).

Applying a collagen offset correction for this combined date for all male bones, using the same method as for the in-situ bones, results in a corrected calibrated date range of 388–356 calBC with 95.4 % probability (Fig. S4.7). Thus, the date of the male individual (ISM) burial in Tomb I, including all male bones “on the floor” (in-situ and commingled) with all corrections, is 388–356 calBC.

Regarding the four female bones identified, the left petrous (DEM-3247) did not produce enough collagen for dating. The radiocarbon dates of the remaining ones: maxilla-B (DEM-3237), right petrous bone (DEM-3246) and the unsided femur fragment (DEM-3128), align with the male “on the floor” bones as shown in the unmodelled dates of Fig. 11 and the modelling of all adult dated bones (Fig. 12), as well as the modeling of only the bones “on the floor” (Fig. 13). An R-Combine test indicates that they could belong to the same female, with a combined date of 2286 ± 14 BP, yielding calibrated age ranges: 399–359 calBC (83.8 %) and 276–234 calBC (11.6 %) (Fig. S4.8). The low probability for the younger range and the unlikelihood of a 3rd-century BC burial after the Gallic plundering, allows us to exclude the second range and accept the range 399–359 calBC as the most plausible.

Applying again a possible collagen offset correction model to the combined date of these female bones (although some of them may not exhibit a measurable collagen offset), results in calibrated age ranges of

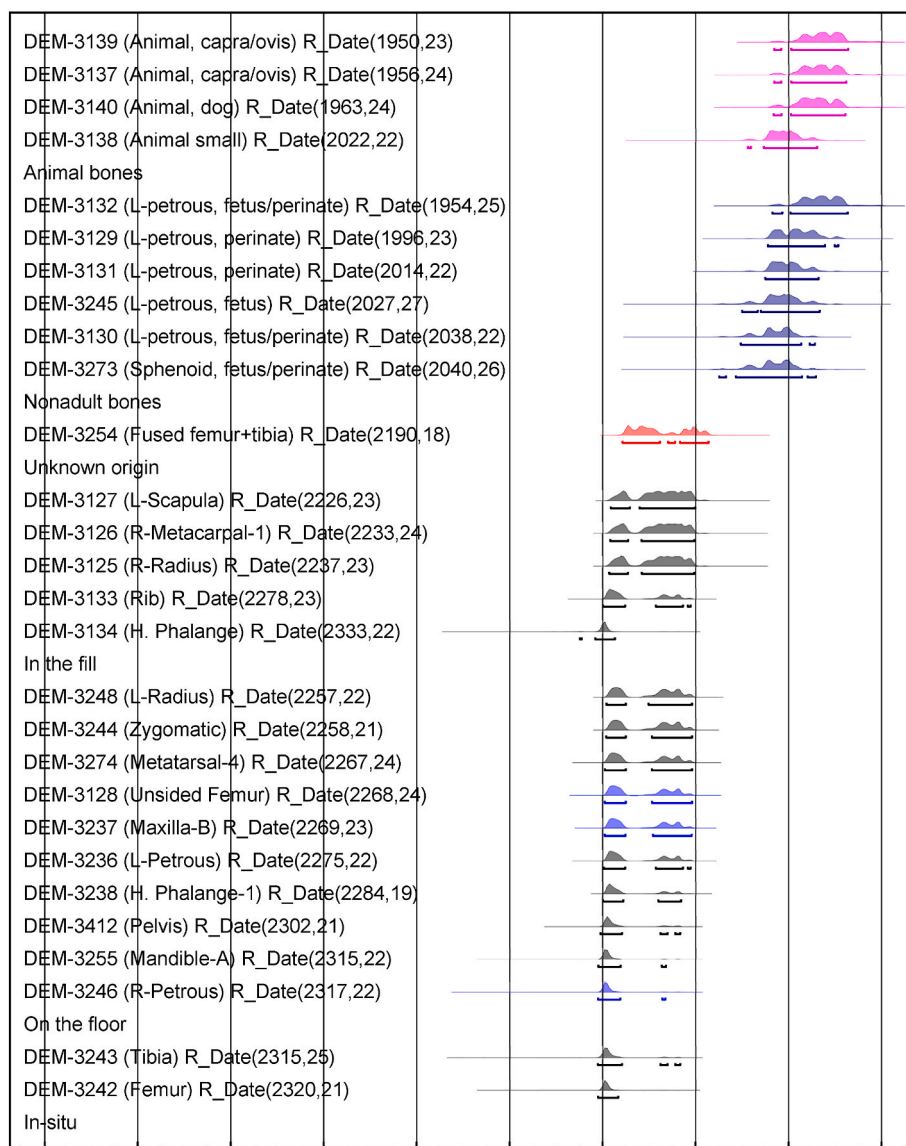


Fig. 11. Calibrated age distributions (unmodelled) of all dated samples, ordered by find location in the tomb and type. Color code: Black = adult male human bones, Blue = adult female bones, Navy = nonadults, Magenta = animals, Red = the unknown origin fused femur and tibia, presented by Bartsiokas et al. (2015). (Diagram produced by Y. Maniatis with the program OxCal v.4.4.4, Bronk Ramsey, 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

389-351 calBC (81.6 %) and 269-225 calBC (13.9 %) within an overall 95.4 % probability (Fig. S4.9). Ignoring again the 3rd-century range for the reasons explained above, the corrected date for “The female’s” death and burial is 389-351 calBC at the latest, which tightly correlates with the male’s (ISM) date.

4.3.3. The sacrificial pyre (enagismos) dates

Two samples from pyre debris found in the soil above and between Tomb I and Tomb II were radiocarbon dated: An animal bone fragment was dated with AMS (DEM-3411, MAMS-46665) and a sample from the charcoal pieces with GPC (DEM-2719) (Fig. S4.12). The radiocarbon ages are nearly identical (Table 2), but the AMS date has a smaller uncertainty, giving two calibrated age ranges, 370-340 calBC (14.8 %) and 324-199 calBC (80.7 %). The older range (370-340 calBC), broadly agrees with Andronikos dating of about 340 BC (Andronikos, 1984), based on the pottery found around it, and suggests that the pyre was in honor of the dead from Tomb I. However, the younger range (324-199 calBC) cannot be entirely excluded, but in this case the part of this range postdating the Galatian plundering must be excluded. This confines the

age range to 324-274/3 calBC, in which case it could represent a sacrificial rite that could have been performed in honor of the deceased from Tomb II.

4.4. Stable isotope dietary results

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses for samples with sufficient material and collagen, obtained by IRMS, are presented in Table 2 (and Suppl Table S5.1). The atomic C/N ratio, ranging from 2.9 to 3.3, and the carbon and nitrogen percentage yield are within the accepted standards for non-contaminated collagen (Ambrose, 1990; Cheung et al., 2012; DeNiro, 1985; Harbeck and Grupe, 2009). The samples include adult (male and female) bones “on the floor” and in “the fill” of Tomb I. In addition, four animals from the tomb and one from the sacrificial pyre above the tomb are also included for assessing the level of local fauna values. The fused femur/tibia pair (alien to Tomb I) has also been analyzed and its isotopic signature is provided for comparison.

The isotope results of the samples analyzed are plotted in Fig. 14, together with the published isotopic values of adults from the Pella

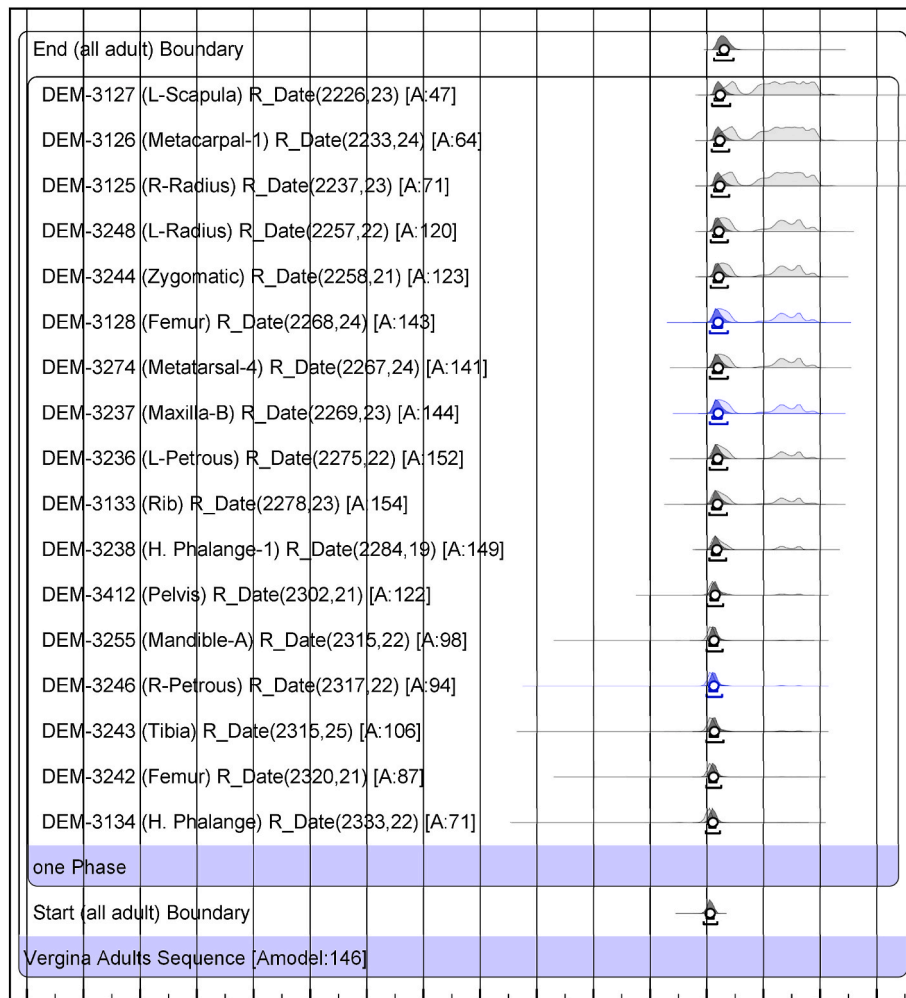


Fig. 12. All adult bones from Tomb I (male, female, “on the floor” and “in the fill”). Bayesian statistical analysis with one-phase model, combined with a general outlier model. Black = male, Blue = female. The dot indicates the weighted mean value. (Diagram produced with the program OxCal v.4.4.4, [Bronk Ramsey, 2021](#)). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

classical cemetery ([Maniatis et al., 2023](#)). In addition, the human isotope values from other sites of the Classical, Hellenistic and Roman periods are plotted in the form of ellipses covering the full range of values (the actual points have been omitted for simplicity of the graph).

As can be seen in the plot ([Fig. 14](#)), the values of the male bones from Tomb I (red circle) cluster in a very narrow range of values with $\delta^{13}\text{C}$ from -18.44 to -19.30 ‰, averaging at -18.87 ± 0.32 (1 σ) and $\delta^{15}\text{N}$ from 9.46 to 10.38 ‰, averaging at 9.95 ± 0.32 ‰ (1 σ). These values fall within the overall range of the Pella classical cemetery values obtained from different individuals; however, the Tomb I male values form a very tight group compared with the scattered values of the Pella cemetery. Similarly, the Tomb I male values also cluster in the center of the classical period values from Thebes (ellipse 1) ([Vika, 2011](#)), but again the scattering of the Thebes values is much greater. Additionally, the Hellenistic Thebes period values (ellipse 2), although the diet in that period has been deteriorated compared to the classical period in the same site ([Vika, 2011](#)), still show a much greater scattering than the Tomb I male values. Furthermore, the isotope values from the Roman period sites of Pondokomi-Vrysi (ellipse 3) and Nea Kerdylia-Strovolos (ellipse 4) in Macedonia ([Vergidou et al., 2023](#)) obtained from different individuals, show again a much bigger scattering than the tight cluster of the Tomb I male bones.

These all indicate that the tight clustering of the Tomb I male bones compared to data from other assemblages coming from different individuals indicates that they most likely all belong to the same

individual, re-enforcing the aDNA, osteological and radiocarbon results. These samples include both “on the floor” and “in the fill” male bones. In particular, from the in-situ bones “on the floor” the femur, tibia, fibula (DEM-3242, 3243, 3413) and the pelvis (DEM-3412). They also include commingled bones “on the floor” a metatarsal-4 (DEM-3274) and from the “in the fill”, the right radius (DEM-3125), the right metacarpal-1 (DEM-3126), the left scapula (DEM-3127), the hand phalange (DEM-3134) and a rib (DEM-3133). The slight variation between different bones of the same individual in the cluster most probably relates to the difference of collagen turnover and remodeling effect in different bones. For example, the long bones of the skeleton such as the femur, tibia and fibula (DEM-3242, 3243, 3413) together with the right radius (DEM-3125) show practically identical values ([Fig. 14](#)). Variation in isotopic values between different bones in the same skeleton, by 0.93 ‰ in $\delta^{13}\text{C}$ and up to 1.7 ‰ in $\delta^{15}\text{N}$, have been observed in the past ([Berg et al., 2022](#); [Dauven et al., 2017](#); [Fahy et al., 2017](#)). The Tomb I male bones variation of 0.86 ‰ in $\delta^{13}\text{C}$ and 0.92 ‰ in $\delta^{15}\text{N}$, is much below these values.

Therefore, there is corroborating evidence that the male bones “on the floor” and the male bones “in the fill” are complementary and constitute a single unified skeleton, the ISM individual ([Fig. S3.12](#)).

Regarding the two female bones analyzed for isotopes, the petrous bone (DEM-3246) and the unsided femur diaphysis (DEM-3128) both exhibit $\delta^{15}\text{N}$ values (11.13 ‰ and 11.61 ‰ respectively) which are statistically higher than the average value of the male bones and their

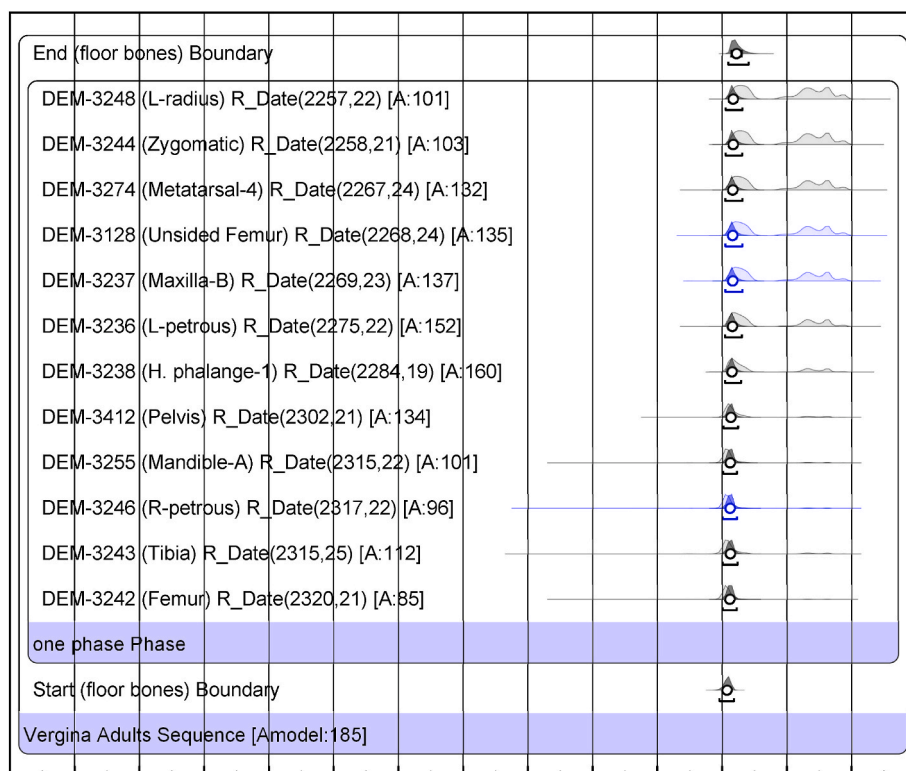


Fig. 13. Adult bones “on the floor” from Tomb I (male and female). Bayesian statistical analysis with one-phase model, combined with a general outlier model. Black = male, Blue = female. The dot indicates the weighted mean value. (Diagram produced with the program OxCal v.4.4.4, [Bronk Ramsey, 2021](#)). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

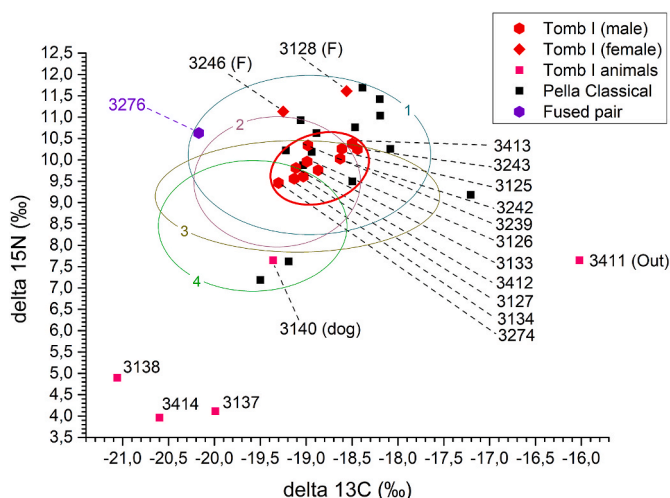


Fig. 14. Stable Isotope results of the adult bones from Tomb I plotted together with adult bones from the Pella Classical cemetery burials ([Maniatis et al., 2023](#)). The isotopic values of the Roman period animals (a dog-3140 and three herbivores, 3138-rabbit, 3137&3414-goat/sheep) also found in the tomb are shown as reference of the fauna values in the area. Sample 3411 is a goat/sheep sample from the sacrificial pyre found above and between Tomb I & II. In addition, the isotope signature of the fused femur/tibia pair value is plotted for comparison (Diagram produced by Y. Maniatis).

standard deviation (9.95 ± 0.32 ‰). This brings them clearly outside the cluster of the male bones belonging to the ISM ([Fig. 14](#)). The small difference in the $\delta^{15}\text{N}$ between these two bones (0.48 ‰) supports the assumption that these female bones (petrosa and femur), along with maxilla-B, likely belong to the same female individual (The Female), as

indicated by the R-combine test of their radiocarbon dates ([Fig. S4.8](#)). The difference in $\delta^{13}\text{C}$ (-0.69 ‰) between the petrous bone and femur may have resulted from the different mineralization periods, with the petrous bone reflecting an early childhood diet and the femur reflecting the last 10 years of life ([Paetz et al., 2017](#); [Berg et al., 2022](#); [Dauven et al., 2017](#); [Fahy et al., 2017](#)).

The higher $\delta^{15}\text{N}$ values of The Female buried in Tomb I suggest that she had a slightly richer diet in animal protein than the ISM. No difference is observed between male and female $\delta^{15}\text{N}$ values in the Pella Classical period cemetery ([Maniatis et al., 2023](#)), with the highest $\delta^{15}\text{N}$ values in males reaching 11.69 ‰ and in females 10.93 ‰. No difference between males and females was also observed in the Thebes classical period graves (11.6 ‰ and 11.3 ‰ respectively), possibly a slight difference, mostly in the $\delta^{13}\text{C}$ values, in the Hellenistic period ([Vika, 2011](#)). Finally, no differences between male and female were observed in the two Roman period sites in Macedonia ([Fig. 14](#)), where the $\delta^{15}\text{N}$ values of both male and female are all below 10.30 ‰ ([Vergidou et al., 2023](#)).

The fused femur/tibia pair at Komotini (DEM-3276) has an isotopic signature characterized by a very low $\delta^{13}\text{C}$ value, distinctly different from all the adult bones in Tomb I (male and female). Furthermore, this value is also outside the range of the Pella Classical cemetery samples and outside the range of the other sites plotted in [Fig. 14](#). Therefore, this individual to whom the fused pair of leg bones belonged had a very different diet than the male (ISM) and The Female buried in Tomb I. This diet, depleted in carbon but enriched in nitrogen, could imply either a large input of freshwater fish ([Dotsika et al., 2019](#); [Dufour et al., 1999](#); [Katzenberg and Weber, 1999](#)), or imply the person lived in a distinct environment different from the Vergina/Pella region.

The Roman period fauna samples include three herbivores (two *capra/ovis*, one *leporidae* (hare/rabbit) and a *canis* (dog) from inside Tomb I and one *capra/ovis* from the sacrificial pyre above the tomb ([Table 2](#), [Fig. 14](#)). The *capra/ovis* and *leporidae* (DEM-3137, 3138, 3414) exhibit typical free-ranging herbivore values while the values of the

sacrificial pyre *capra/ovis* (DEM-3411) indicate a domesticated animal fed with millet and perhaps also grazing in manured fields. Their average $\delta^{15}\text{N}$ content ($\sim 6\text{‰}$) aligns with similar fauna from prehistoric to classical periods in North Greece (Triantaphyllou, 2015) and Pre-historic, Classical and Hellenistic periods in Thebes (Vika, 2011). Assuming a diachronic $\delta^{15}\text{N}$ value of 6‰ for fauna, the ISM's diet is enriched in $\delta^{15}\text{N}$ by about 4‰ (i.e., from about 6‰ to about 10‰). Given the highest reasonable human collagen enrichment over diet is 5‰ (Hedges and Reynard, 2007), a 4‰ enrichment implies that at least 80% of the ISM's dietary protein came from animal sources (meat and milk), and likely higher for The Female, excluding significant freshwater fish consumption (Hedges and Reynard, 2007).

In summary, the analyzed male bones from Tomb I, both from "on the floor" and "in the fill", have similar isotopic concentrations forming a very tight cluster, indicating they most likely belong to the one and the same male individual, the ISM, in agreement with the radiocarbon, osteological and DNA results. This individual had a diet enriched in animal protein by about 80% .

The Female had a diet richer in animal protein than the ISM. This diet is not related to sex difference but to the different diet this particular female had compared to the male in Tomb I.

4.5. Strontium isotope results

The results of Sr-isotope analyses ($^{87}\text{Sr}/^{86}\text{Sr}$) of the adult human samples are presented in Table 2 with full details in Table S6.1, together with baseline samples of soil extracts, plants and water from Vergina and Pella, as well as bone and tooth enamel samples of animals from Tomb I. Samples from the cortical bone of the in-situ femur and tibia of the ISM individual were also analyzed, following a deep-pre-cleaning treatment (Sillen, 1986, 1989), mainly for the purpose of monitoring diagenetic alteration.

The human samples analyzed for provenance investigation purposes include premolar tooth enamel from the maxilla-A and mandible-A of the ISM individual and molar tooth enamel from maxilla-B of The Female individual. Additionally, three petrous bone samples (otic capsules) from the bones "on the floor" (DEM-3236-male, DEM-3246-female, and DEM-3247-female) were also included for this reason.

Several studies have indicated that strontium isotope analysis of the petrous portion of the temporal bone is a viable method for provenance studies of both inhumed and cremated human remains (Seghi et al., 2024; Snoeck et al., 2022; Veselka et al., 2021). The pivotal and original study by (Harvig et al., 2014) concluded that strontium isotope ratios in the otic capsule closely align with those in dental enamel from the same individuals, regardless of whether the remains were cremated or not. This finding underscores the petrous bone's reliability in tracing childhood origins. Additionally, a more recent study by Kootker and Laffoon (2022), which assessed the preservation of biogenic strontium isotope ratios in the otic capsule of unburnt petrous bones, supports Harvig et al.'s (2014) main conclusions. These studies collectively highlight the significance of the petrous bone in archaeological provenance investigations, particularly for inhumations and non-cremated remains, offering an additional source of information.

The ISM's tooth enamel samples (DEM-3255 and 3256) from mandible-A and maxilla-A exhibit $^{87}\text{Sr}/^{86}\text{Sr}$ isotope signatures of 0.711353 in the first premolar and 0.711676 in the second premolar (Fig. 15, Table S6.1). The calcification of the first molar starts around 1.5 years of age and its formation is complete around between the ages of 5–6 years (Schuurs, 2013). The ISM's left petrous bone (DEM-3236) returned a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.709714 . The petrous bone begins mineralizing before birth and continues to grow until about 2 years of age (Harvig et al., 2014; Paetz et al., 2017). Hence, the strontium isotope signature of the petrous bone reflects an earlier childhood period compared to that represented by the premolar samples.

The Female's tooth enamel sample from a left first molar (DEM-3237) yielded a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.709311 , while her right petrous

bone (DEM-3246) has a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.708936 . The left petrous bone, most likely also assumed female (DEM-3247), yielded a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.708570 . The tooth enamel of the first molars forms approximately between 0 and 3 years of age, creating an overlap in the strontium isotope signature time span with that of the petrous bone forming during the first two years. However, for the final year (age 2 to 3), only the first molar continues to form, completing its development around the age of 3. Therefore, we do not expect a complete overlap in Sr isotope signatures from these samples.

The plant and soil extract-based Vergina baseline samples yield homogenous Sr isotope signatures ranging from 0.70986 to 0.70992 (Fig. 15; Table S6.1). If one includes the fauna bone samples from *capra/ovis* (sheep/goat) and *leporidae* (rabbit/hare) found in Tomb 1, the local baseline range could potentially be broadened down to a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.70935 (Fig. 15). Similar $^{87}\text{Sr}/^{86}\text{Sr}$ values to the Vergina animal samples have been measured in Neolithic fauna from Revenia-Korinos, Paliambela-Kolindros and Makrygiolos-Pierias in Pieria County on Pliocene-Quaternary and Cenozoic sediments (Vaiglova et al., 2018; Whelton et al., 2018).

The ancient well water and soil extract-based Pella baseline samples yield rather homogenous Sr isotope signatures ranging from 0.7089 to 0.7091 (Fig. 15; Table S6.1). This range is somewhat lower than the range defined by the environmental Sr samples from Vergina (Fig. 15).

The interpretation of the strontium isotope analyses of the human remains with respect to provenance is a difficult task at this stage as regional coverage of baseline data is still rather limited. The following interpretations should therefore be considered preliminary. The ISM's left petrous bone (DEM-3236) returned a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.709714 while his tooth enamel samples (DEM-3255 and 3256) from mandible-A and maxilla-A exhibit isotope signatures of 0.711353 and 0.711676 respectively (Fig. 15, Table S6.1). While the strontium isotope signature measured in the petrous falls within the local baseline of Vergina, the $^{87}\text{Sr}/^{86}\text{Sr}$ signatures from the two premolars are significantly more radiogenic than the range of bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ values in the Vergina, Pella and the entire Pieria region. The slight difference between the two samples may be due to different mineralization periods represented by the premolars; PM-1 (mandible) mineralizes from 1.5 to 2.0 years with the enamel completing by age 5–6, while PM 2 (maxilla) mineralizes from 2 to 2.5 years with the enamel completing by age 6–7 (Logan and Kronfeld, 1933; Moorrees et al., 1963). Assuming that Sr isotope signature of the pars petrosa sample represents an original and true biosignature, the value measured suggests that the ISM individual could have originated from the local area of Vergina, but, as implied by the Sr isotope signatures of the PM 1 and PM 2 tooth enamel samples, he

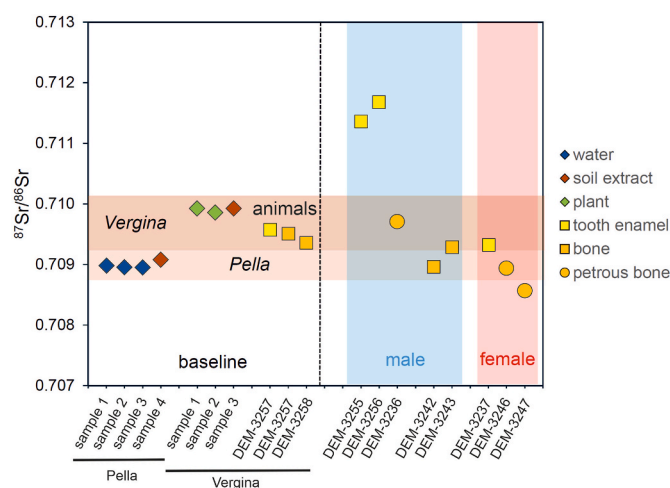


Fig. 15. Strontium isotope results of human samples from Tomb I compared against the baseline of Vergina and Pella and the Roman period animals found in Tomb I. (Diagram produced by R. Frei).

moved to another place during his early childhood and lived there at least up to the age of seven. Interestingly, the bioavailable Sr isotope values in Vergina, Pella, and surrounding regions seem not to exceed $^{87}\text{Sr}/^{86}\text{Sr}$ values of 0.711 as predicted by Whelton et al. (2018) and also shown by (Frank et al., 2021a; Hoogewerff et al., 2019; Nafplioti, 2011). This could support the view that this male might have lived somewhere else outside these areas.

To trace the region where the ISM spent some of his childhood is challenging. One human sample (PM enamel) from the Neolithic site of Stavroupoli (Grammenos and Kotsos, 2002) in northern Thessaloniki shows a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.71113, which is still lower than the signatures measured in the ISM male teeth. However (Whelton et al., 2018), suggest that higher values may be expected about 3 km northeast of Stavroupolis along the slopes of mount Chortiatis, where Cenozoic and Mesozoic metamorphic rocks are exposed, but no measurements are currently available. High $^{87}\text{Sr}/^{86}\text{Sr}$ values (0.71467 and 0.71285) were also found in PM enamel from two of eight individuals at the late Neolithic site of Kleitos in the Kozani region, West Macedonia (Whelton et al., 2018; Ziota et al., 2013). These values were considered foreign, but more recent baseline characterization for West Macedonia by Frank et al. (2021a) who reported a wide range of compositions ranging from about 0.703 to about 0.718 for this province might change this interpretation. High baseline samples ($^{87}\text{Sr}/^{86}\text{Sr} \approx 0.7119$) have been measured about 50 km north of Kozani in Northwest Greece, near Florina, and further north in ancient Upper Macedonia (Serbomacedonian Massif) (Hoogewerff et al., 2019).

Similarly, high baseline values have also been recorded in some areas in the Peloponnese, particularly in Laconia, including the Tripolis, Mani and Arna rock formations (Frank et al., 2021b).

Besides the above-mentioned samples, the in-situ femur and the tibia samples of the ISM, analyzed mostly for the purpose of monitoring the potential effects of diagenetic alteration, yield a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.708959 for the right femur (DEM-3242) and a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.709285 for the left tibia (DEM-3243) (Fig. 15, Table S6.1, Photos S3.4 and S3.5). What is interesting with these analyses is that both $^{87}\text{Sr}/^{86}\text{Sr}$ values are lower than the Vergina baseline range defined herein, particularly the signature of the immediate archaeological soil extract in the tomb (cf., Fig. 15) and that they are also lower than the animal enamel and bones from the same tomb (Fig. 15). This difference with respect to the animal bones, combined with the fact that the femur and tibia values are lower than the Vergina baseline, might suggest that these bones still contain, at least partially, some information of the original biosignature of the ISM. This discrepancy may imply that the original $^{87}\text{Sr}/^{86}\text{Sr}$ signatures were not completely masked by diagenetic alteration. If this is true, then one possible scenario would be that this pattern could indicate mobility of the ISM during the later years of his life from the high radiogenic region in his childhood to the Pella/Vergina region. It is important to remember that the femur and tibia do not record the exact same period in life, hence, a difference (as in our study) between their $^{87}\text{Sr}/^{86}\text{Sr}$ signatures is to be expected. Cortical bone reflects the environment of the last 10–20 years of life depending on the turnover rate (Bentley, 2006; Hedges and Reynard, 2007; Price et al., 2000).

The Female petrous bone $^{87}\text{Sr}/^{86}\text{Sr}$ values are difficult to interpret as there is a slight difference in $^{87}\text{Sr}/^{86}\text{Sr}$ composition between them. At this stage, we are unable to explain why the signatures are different. The left petrous bone (DEM-3247) is paired with the right female petrous bone (DEM-3246) due to its likely female DNA designation. The Female's tooth enamel sample from left Molar 1 (DEM-3237) is characterized by a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.709311, and with this signature it falls very close to the lower range of the baseline of Vergina and just above the baseline of Pella (Fig. 15). One of the two petrous bones (DEM-3246) is compatible with the Pella baseline range, whereas the other one (DEM-3247) plots below it (Table S6.1, Fig. 15). The female's tooth enamel signature, which is very similar to the ISM's tibia signature (DEM-3243; Table S6.1; Fig. 15), represents the biosignature attained

during the first three years of The Female's life. This, in combination with the signature measured in the petrous bone sample (DEM-3246), indicates The Female could have originated from within the greater Pella/Vergina region. But, other regions in Central Macedonia and Pieria cannot be excluded (Vaiglova et al., 2018; Whelton et al., 2018).

In conclusion, the $^{87}\text{Sr}/^{86}\text{Sr}$ values of the ISM petrous bone and tooth enamel samples suggest he moved in early childhood from a place with values that fall within the Vergina area to a place characterized by much more radiogenic bioavailable Sr isotope values, meaning a place outside the Pella/Vergina greater region. Tentative suggestions based on existing baseline information could be regions in Northwest Greece, Upper Macedonia, and Peloponnese, or other regions from which detailed baselines are currently lacking. Sr isotopes from his leg bones, if it is assumed that the bones have only partially been diagenetically altered, potentially indicate that he could have lived his last years of his life in an area with lower bioavailable strontium isotope values than that in and around Vergina. Based on the measured $^{87}\text{Sr}/^{86}\text{Sr}$ values it could well be within the area around Pella.

5. Discussion

The DNA and radiocarbon dating results indicate the in-situ bones and the other adult bones found in Tomb I are mostly male and date to the first half of the 4th c. BC. Therefore, there is indisputable evidence there was a male burial (ISM individual) with all his leg bones still in an in-situ/supine position. There was most probably also a female burial (The Female) represented by just three or four bones among those analyzed.

5.1. The in-situ male burial (ISM)

The vast majority of the adult bones found “on the floor”, either in-situ or commingled in three clusters, belong to a male. The adult bones “in the fill” are also male and as it appears from the osteological study, they are counterparts to the floor bones. Their radiocarbon dates all agree statistically in the first half of the 4th c. BC and their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values are very closely distributed. Also, there are no duplicate bones, and they all lack age-related degenerative changes. Therefore, they almost certainly all belong to the same male individual (ISM). The fact that some of the adult bones of the ISM were found “in the fill”, but apparently in the lowest part of the fill close to the floor, can be explained by soil entering inside the tomb from the covering soil above. This likely occurred when the robbers made the openings and before they started scattering the bones around in their attempt to search for valuables.

Concentrating only on the in-situ male leg bones (femora and tibiae) found “on the floor”, as identified in the excavation photo (Fig. 5) and drawing (Fig. 6), the radiocarbon results give a combined calibrated date in the period 406–378 calBC. And if a correction for collagen offset (Suppl. section S4.3) is applied, the in-situ femora and tibiae bones date from 395 to 368 calBC. Furthermore, all the male bones “on the floor” together date from 400 to 367 calBC and if a correction for collagen offset is applied, this becomes 388–356 calBC (Fig. S4.7). This is the latest possible date, taking into account that the collagen offset in bones other than the femora and tibiae may be negligible.

Andronikos, based on the wall frescoes and pottery, estimated a date for Tomb I around the middle of the 4th c. BC (Andronikos, 1984, 1994). He attributed the Abduction of Persephone fresco to the famous painter Nikomachos and says that this painter was known and active from 360–350 BC (Andronikos, 1994). Furthermore, Drougou (2005), who made a more detailed study of the pottery in Tomb I, estimated a date of around 350 calBC or earlier (Drougou personal communication⁷).

⁷ In a personal communication Prof. Drougou agreed that a higher than 350 BC date would be compatible with the pottery.

Hammond dates Tomb I to 370-360 BC (Hammond, 1991). Palagia (2017) states that underground cist tombs with a small shrine on top, as with the Vergina Tomb I and heroon above, date from the 5th c. BC (Tomb D, at Aiane, near Kozani in Macedonia) to the early 4th c. BC (Tomb A at Aiane), (Karamitrou-Mentessidi, 2008). Similarly, the large cist tomb in Katerini is dated to 381-369 BC (Despini, 1980; Schmidt-Dounas, 2017). These dates are very much in agreement with the radiocarbon results from the bones found in Tomb I.

The in-situ leg bones provide the most important evidence for the original or primary burial in Tomb I, because they were found in their respective anatomical supine positions and in the expected orientation of the body (aligned east-west along the long side of the tomb, with the head placed to the west) as was accustomed for male burials in that period.⁸ The other upper body bones, including the cranial bones, were found fragmented and scattered, most likely by the robbers in an effort to remove precious objects generally placed around the head, neck and upper part of the body. The tibiae/fibulae and foot bones were found articulated, except the left tibia, which was broken and overturned by a stone that fell from above (shown in the excavation photo, Fig. 5). This stone likely fell from the fourth cover block on the roof when the robbers opened the hole (Fig. 4), whose position is approximately above the tibiae. The fact that the stone broke and overturned the tibia and that the upper body bones were fragmented and scattered on the floor (Fig. 6), indicates the body was skeletonized before the plundering, after which the remains were progressively covered with the soil fill. All of the above exclude a later, secondary burial after the plundering.

This ISM individual was aged 25–35 years at death, as determined by his dentition and also from other bones, and had a stature of about 167 ± 3 cm as discussed in the osteological/odontological section. The Sr isotope results of the petrous bone (Fig. 15), which mineralizes from birth to about 2 years of age, indicates that the ISM was probably born in the Vergina area, but two enamel samples from maxilla-A and mandible-A (Fig. 15) indicate that he moved and did not reside in his youth in the area of Vergina and/or Pella until at least the age of seven years. The most probable regions for his childhood are Northwest Greece or further north in Upper Macedonia or the Peloponnese, based on current knowledge of baselines from those regions. However, assuming only partial diagenetic alterations of his leg bones, he could have spent the last 10–20 years of his life in the greater Pella region, as shown from the Sr isotopes measured from those bones.

The radiocarbon dating and other scientific results given above for the male individual (ISM) inhumed in Tomb I to whom most of the bones “on the floor” (in-situ and commingled) and “in the fill” belong, exclude any association of this burial with Philip II of Macedon (died in 336 BC), as proposed by some authors.

This individual died and was buried between 388 and 356 BC, several decades before the assassination of Philip II. The last three years of this range fall within the beginning of Philip's reign, which started in 359 BC, maintaining the possibility that Philip II may have ordered the tomb's construction and the funeral/burial of this individual.

It is not our role or expertise to elaborate on who the ISM individual might be, except to provide a few comments based on the literature. As described by the excavators (Andronikos, 1984 and Drougou personal communication), Tomb I (“The Tomb of Persephone”) and Tomb II (“The Tomb of Phillip”) were both initially covered by their own individual tumuli, with the Tomb II tumulus overlapping and partially covering the tumulus above Tomb I. This may indicate a family connection between the two (Kyriakou, 2016). Later, both tombs and the heroon above were covered by the Great Tumulus. Adjacent to Tomb

I, it has been speculated that the above-ground heroon is an argument in favor of Amyntas III, the father of Philip II, as the occupant of Tomb I, although Andronikos (1984) seems to connect the heroon with Tomb II. In any case, according to Andronikos (1984) and Hammond (1991), only two kings of the Argead line were reported to have received worship in this way: Amyntas III having an ‘Amyntaion’ at Pydna, and Philip II worshipped at Amphipolis ‘as a god’ (Hammond, 1991).

Amyntas III, who died in 370/369 would fit the radiocarbon date range of the ISM, except that the reported ‘advanced’ age at his death does not agree with the osteological and odontological results of this work, indicating a young/middle-aged adult. His descendants, Alexander II (died in 368/367 BC) and Perdiccas III (died in 360/359) also fit in the radiocarbon age range, but their ages and physical conditions at death, along with the possibility of other “royals” or high-status candidates for Tomb I are beyond the scope of this paper.

For an independent historical discussion on possible identities, see David Grant's Academia webpage <https://independent.academia.edu/DavidGrant16>.⁹

5.2. “The female” burial

Three female bones found on the floor were identified among the 23 analyzed by DNA (Table 2 and Suppl Table S2.1): Maxilla-B (DEM-3237) (identified in the excavation drawing in Cluster Γ, Fig. 6), a right petrous bone (DEM-3246), and a left petrous (DEM-3247). The unsided femur fragment (DEM-3128), unassigned by DNA, is most likely also female, as explained in Section 4.2.

The three (out of the four) female bones dated (DEM-3237, 3246 and 3128) give radiocarbon dates that group together with the male bones (Figs. 11 and 12) and fit very well into the one-phase-burial model of the “on the floor” bones (Fig. 13). The R-combined test of the three dated bones passes the χ^2 -test indicating that they most likely belong to the same female individual, returning a combined calibrated age of 399-359 calBC (84 %) and 276-234 calBC (11.6 %) within a total probability of 95.4 % (Fig. S4.7). The age of 399-359 calBC with the highest probability, should be the dating range adhered to along with the conclusion that the bones were already skeletonized by the time the tomb was plundered. Applying a collagen offset correction (see Supplementary section S4.3) to the combined date of these three female bones results in a corrected date of 389-351 calBC (Fig. S4.9) at the latest, taking into account that a collagen offset correction may not be applicable to bones other than the long ones (femora, tibiae, humeri, etc.). In any case, this age range with or without correction is identical to the age range for the ISM burial. This dating also excludes any association with Cleopatra, Philip II's wife (as suggested by some authors) who was murdered shortly after Philip's death in 336 BC by Olympias, Philip's fifth named wife (Pausanias 8.7.7; Justin 9.7.12; Plutarch, *Life of Alexander* 10.8).

According to her dentition and suture obliteration of the maxillary bone, this female was between 18 and 25 years of age at death. The Sr isotope analysis of her tooth enamel and her right petrous bone indicates this female was likely born and lived in the area of Pella/Vergina in her childhood, and given the fact she was buried in Vergina, she most likely lived all her life in this area, contrary to the male who lived elsewhere in the first seven years of his life (or elsewhere after a couple years from his birth). In addition, her diet, as indicated by the C and N isotopes, was different than the ISM's, being higher in $\delta^{15}\text{N}$ (Fig. 14) (richer in animal protein?).

The consistent dating of the male and female bones implies a possible double burial of a man and a woman in the same period within the first half of the 4th c. BC. The very few identified female bones (one maxilla, two petrosas and a femur fragment), compared to an almost complete set of male bones, including the in-situ ones, could serve to question a

⁸ In this period in Vergina and elsewhere in Macedonia the tombs can be oriented with their axis north-south or east-west. When the orientation is east-west, like Tomb I, the heads' position depends on the gender. The men have their heads to the west and women to the east (Kottaridi, 1997 and the references there in; Duiti, 2017; Charalampidis, 2019).

⁹ David Grant is a scholar in ancient Macedonian history, who authored a book on the Vergina Great Tumulus Tomb finds (Grant, 2019).

woman's burial in the tomb. However, the original presence of a female in the tomb is supported by the associated finds, like the few fragments of gilded beads probably from a necklace, the marble shell¹⁰ and the Eleusinian myth of the *Abduction of Persephone* depicted on the wall - reportedly appearing more often in women's tombs (LIMC, 2009), - although the latter is rejected by Huber (2019). This has raised the question of whether this tomb was originally designed for a female burial, an important woman of the royal court. The construction of the tomb, closed from all sides with large stones and a ceiling originally covered with wooden boards topped with heavy limestone blocks would, according to Andronikos (1994), exclude a second burial after the first was completed and the tomb was closed. If this is true, it would imply that the burial of the male and female would have taken place at the same time, hence a double burial. But where are the rest of her bones?

As discussed previously, both Plutarch (*Life of Pyrrhus* 26.6) and Diodorus (*Library of World History* 22.12.1), describe the plundering by the greedy Galatians around 274/3 BC, reporting that they grabbed the valuable artefacts and scattered the bones around in a deliberate insulting and arrogant action. This would explain the destruction and scattering of the bones belonging to the male, especially the upper part of the body where the valuable objects may have been. However, many of his broken bones are still in the tomb, although some are missing. It seems illogical then to assume that they threw all of the woman's bones out of the tomb but left most of the man's inside. Besides, given the height of the tomb (3m) and the small opening in the roof and also the shelves or other construction just behind the looters opening on the west wall (Fig. 3B), it would have made it rather difficult and pointless for the looters to deliberately throw all her bones out of these holes. Also, if all her bones were deposited outside the tomb, they might have been found by the excavators in 1977, as they found minute golden pieces and other small objects dropped by the looters outside the tomb.

Assuming that the presence of even these few female bones, which date to the same period as the male remains, in addition to the other material evidence pointing to a male-female double burial in the Tomb, makes the lack of most of her bones hard to explain. However, a similar situation occurs in the plundered tombs of Stenomakri Tumulus at Vergina, dating generally to the same period as Tomb I. In the inhumed burials of Tomb Γ, there were many of the male bones present after plundering, but only very few from a female, although the material evidence points to the presence of a female (Kyriakou, 2016).

One possible explanation for the missing female bones, may be that the woman was most probably heavily ornamented with lots of gold, silver and other jewelry all over her body (chest, arms, hands, legs and feet) as described for other burials in this same area (Kottaridi, 2020b), so the looters could have, in haste, put all her bones with the ornaments in a bag which they took away with them for later scrutiny, dropping some bones in the process like maxilla-B and the other bones. They did not do the same for the male, probably because his body was not so richly decorated, apart from perhaps his upper skeleton, which they threw about.

There is not enough evidence to help us further characterize the presence of this female in the tomb and her relationship to the male. Perhaps further aDNA analyses and historical/archaeological research, based on the results of this paper, could shed more light on her identity and possible relationship with the man.

Speculation that Pyrrhus' Gallic mercenaries looted all the royal tombs in 274/3 BC when they descended on Aegae combined with the possibility that the human remains and the grave goods are from secondary burials in the reused empty tombs after that date (Hall, 2014), cannot be sustained by our results for Tomb I. We have shown that all

the adult bones date to 389-351 calBC and that the bodies were skeletonized when the plundering took place.

5.3. Fetus/perinate bones

All the fetus/perinate bones, representing at least six different non-adult individuals and found in the tomb (either "in the fill" or "on the floor") date more than two centuries later than the adults (150 calBC to 130 calAD). Hence, they are clearly unrelated to the primary adult burials. This also applies to the fetus/perinate bones transferred together with adult bones to AMTh, and which some authors associated with Philip's and Cleopatra's newborn (Bartsiokas et al., 2015, 2023). They all date to the Roman period.

That dating indicates that Tomb I was partly visible during the Roman period and the looters' openings were accessible so it may be hypothesised (in line with similar burial conventions observed at other opened tombs) that grieving parents of dead newborns from the Roman period recognized this place as a ready-to-use deep grave for disposing their dead. Disposing of dead infants in an underground void, e.g., a well (Bourbou and Themelis, 2010; Chenal-Velarde, 2006; Liston et al., 2018) or in an old tomb, was not an uncommon practice in antiquity, especially in the Roman period. A parallel situation was found in Vergina in another tomb close to the Great Tumulus, where more than 200 skeletons of fetuses/perinates had been found (obviously disposed of) inside the tomb. They also date to the Roman period (second half of the 2nd c. BC), determined by the pottery found with them (Kottaridi, 2020c).

5.4. Animal bones

The animal bones dumped inside the tomb through the looter's openings, some with butchery marks, also date to the same period as the fetuses/perinates, although their dates tend to accumulate more in the range 0-130 calBC, the later part of the fetus/neonate range, and may have been connected with sacrificial rites or simply with food consumption.

Human activity in the Roman period at Vergina has been documented (Drougou et al., 2019; Kyriakou and Tourtas, 2015), however, the fact that Tomb I was accessible during the Roman period was, up until now, unknown and unexpected. The tomb openings, through which the fetus/perinate and animal bones were disposed, were found by the excavators to have been deliberately closed with stones and other materials (Figs. 3 and 4), probably by some people of authority who were aware of the historical importance of the tombs.¹¹ An initial sealing up of the openings would logically have been undertaken by Antigonos Gonatas, who, it has been proposed, constructed the Great Tumulus to protect the remaining tombs from further looting. This could have been any time after the Gallic incursions of Tomb I (274/3 BC) and before Gonatas' death (ca. 239 BC). However, the presence of nonadults and animal bones in Tomb I, which date to the Roman period according to radiocarbon evidence, is indisputable proof that Tomb I was accessible for a time during the later Roman period. The *terminus ante quem* date when all human activity in the tomb stopped is 130 calAD. It is most likely, that Tomb I, being at the periphery of the Great Tumulus (Fig. 1), was partially exposed in the Roman period due to soil erosion or some other environmental event, and became accessible. A final covering up that brought it to the state it was found in 1977 was probably due to a substantiated landslide.¹² Assuming the Roman occupiers had no

¹¹ The same situation was observed in the Tombs of the Stenomakri Tumulus where the tombs were also plundered by the Gaulish Celts around 274/273 BC and the holes were closed up by stones and other material. However, in this case the looters' holes must have been closed shortly after the Celtic destruction and were not accessible during the Roman period, unlike Tomb I'.

¹² A landslide has been reported to have occurred in the 1st c. AD and marked the definitive end and abandonment of the city of Aegae (Kottaridi, 2011, 2020c).

¹⁰ The marble shell is thought to be a "crying symbol" of Aphrodite and is found in many forms in the iconographic repertoire of the goddess (born from the foam of the sea) and hence probably associated with a woman (S. Drougou personal communication).

ancestral loyalties or ties and no interest in protecting a looted and empty tomb, the question of who finally sealed or resealed the openings of the tomb remains a historical conundrum.

6. Conclusions

A combined scientific approach using: aDNA analysis for biological sex determination, osteological/odontological observations for complementing the DNA analysis and estimating the age at death, stature and other features, radiocarbon dating, stable isotope analysis of C, N and Sr-isotope analysis, was performed on the skeletal remains in Tomb I found beneath the Great Tumulus at Vergina (Aegae). These results indicate that all the analyzed adult skeletal remains in the tomb are male and belong to the same male individual. Exceptions are three or four bones that were identified as most certainly belonging to a single female. Bayesian analysis modeling of the radiocarbon dates of all the “on the floor” bones (male and female) showed they belong to one depositional phase that dates from 404 to 362 calBC.

More specifically, the in-situ and in anatomical/supine position leg bones are male and the body has the accustomed orientation for a male burial of that period. In addition, all the analyzed commingled bones on the floor are also male, except three or four that are female. The male individual to whom all the male bones belong is estimated to have an age at death of 25–35 years and a stature of about 167 cm. Combining the radiocarbon dates of the in-situ and all the other male bones “on the floor”, which were precisely recorded and clearly related to the primary male burial, an overall date in the range of 400–367 calBC was determined, and if we allow for a possible collagen offset, this date becomes 389–355 calBC at the latest.

The few female bones, including a maxilla, two petrous bones (left and right) and a femur diaphysis fragment appear to belong to the same female individual. The radiocarbon dating of these female bones gives a combined date of 399–359 calBC and if a collagen offset correction is applied, this becomes 389–351 calBC, tightly correlating with the date of the male. This female was aged 18–25 years according to the osteological and odontological examination. The same dating suggests that the male and female were most likely entombed together, taking also into account that this type of tomb structure (with no door and massive limestone slabs for the walls and roof) would not allow any new burials once it was closed.

It is an interesting question why only a few of the female bones were found in the tomb, in contrast with the male's who's in-situ leg bones and many of his other fragmented bones are still in the tomb, although the valuable adornment of her whole body may provide an explanation.

Contrary to the adult male and female individuals, all the nonadult (fetus/perinate) bones found in the tomb either “on the floor” or “in the fill”, as well as the animal bones, some with butchery marks, all gave dates in the Roman period (150 calBC – 130 calAD), hence they are clearly not related to the primary adult burials. The presence of fetus/perinates in the tomb indicates that the tomb was used as a burial place during the Roman period for disposing dead infants and animal remains. The openings created by the tomb robbers in 274/3 BC were obviously accessible during that period.

No further activities in Tomb I seem to have taken place after the early decades of the 2nd c. AD, when the final closing of the openings and concealment of the Tomb must have occurred. The excavators found both openings of the Tomb deliberately plugged up with stones and other materials. These results pose an interesting question under what circumstances Tomb I was revealed in Roman times, who sealed or resealed the openings made by looters and by what action either human or natural the tomb was finally concealed.

The Sr-isotopes of teeth enamel from the male and female revealed that the in-situ male (ISM) lived, in his early years (at least up to 7) of his life, away from the area of Vergina and Pella, but, the value of his petrous bone tentatively suggests that the ISM individual could have originated from the local area of Vergina. Furthermore, assuming only

partial diagenetic alterations of the male's femur and tibia fragments, their values may suggest that he could have lived in the greater Pella region in the remaining years of his life. The exact location during his youth is not easy to pinpoint.

According to the existing general Sr-isotope baseline database, possible regions could have been Northwest Greece and further north in Upper Macedonia or regions in the Peloponnese. Contrary to the male, the female has a Sr isotope signature indicating she probably was a native of the greater Pella region and spent her early childhood in that area and apparently died there as well.

Given the unique and special features (superb frescoes, mythological scenes) of this tomb, and its likely connection with the shrine above and the dates of the skeletal remains, we can assume that the male burial must have been that of a high-status individual (perhaps a king who died at a young/middle adult age and was buried several decades before Philip II's assassination). The female died in the same period as the male and at a young adult age. She was most probably buried with him, however the evidence for her is limited.

Despite ongoing questions, our results have now clarified the date, biological sex, age at death and geographical origin of the male and female occupants of Tomb I. These results create a solid scientific foundation on which historical and archaeological research on their identities can be based.

CRedit authorship contribution statement

Yannis Maniatis: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Konstantina Drosou:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Miren Iraeta Orbegozo:** Validation, Formal analysis, Data curation. **Dorothea Mylopotamitaki:** Validation, Formal analysis, Data curation. **Terence A. Brown:** Supervision, Methodology, Funding acquisition. **Keri Brown:** Validation, Methodology, Formal analysis. **Robert Frei:** Writing – review & editing, Validation, Methodology, Formal analysis, Data curation. **Sahra Talamo:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation. **Hannes Schroeder:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Theodore G. Antikas:** Supervision, Resources, Formal analysis, Conceptualization. **Laura Wynn-Antikas:** Writing – review & editing, Validation, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Data availability statement

The raw DNA sequencing data are available for download via the European Nucleotide Archive (ENA) under Project Accession Number PRJEB87529. All other results are provided in the manuscript and the Supplementary Materials.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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