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Archaeological questions and genetic answers: Male paternal kinship in a copper age multiple burial from the eastern Italian Alps

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ABSTRACT

In 2010, a detailed anthropological study regarding two adult individuals and one foetus-newborn buried in a Copper Age (ca. 3000–2700 cal. BC) multiple grave site found in Ora/Auer in the eastern Italian Alps (Alto Adige/ Südtirol) was published. This exceptional archaeological finding provides a rare insight into an inhumation prehistoric ritual discovered within a natural alpine rock shelter.

Due to the presence of an infant in the grave, the authors were doubtful of the anthropological male sex assignment given to both adult individuals found there. Additionally, correlation of non-metric traits suggested a possible kinship between them. To determine the biological sex and to investigate genetic relatedness, we performed a paleogenetic investigation (shotgun and enrichment data of ~2 million SNPs) of the two adults.

We successfully analyzed the ancient DNA of these individuals, confirming that biologically, both were males (XY). Moreover, through kinship analyses and data from unilinear-transmitted markers (Y-Chromosome and mitochondrial DNA), we detected a first-degree paternal kinship (most likely father-son).

This study underlines the importance of interdisciplinary dialogue between archaeology, anthropology and palaeogenomics, demonstrating how the latter can significantly support the interpretation of funerary contexts.

1. Introduction

In 2010, Rizzi and colleagues published a detailed anthropological and taphonomic study of an exceptional archaeological find in Alto Adige/Südtirol (hereinafter referred to as South Tyrol), located in the eastern part of the Italian Alps (Fig. 1a). Inside a natural niche at the base of a high cliff in the present municipality of Ora/Auer (Fig. 1b) in the Adige Valley, human remains of three individuals were found in primary deposition (Fig. 2a). Two were adults of approximately 30 (Ind. A) and 40+ years of age (Ind. B). The third individual was a foetus-newborn with an estimated gestational age of 38–40 weeks *in utero* (Ind. C). Osteological samples were radiocarbon (^{14}C) dated to the early, but not initial, Copper Age (Ind. A: LTL-3607A 4279 ± 45 BP, 3021–2705 cal. BC [95.4%]; Ind. B: LTL-3607A 4268 ± 35 BP, 3008–2707 cal. BC [95.4%], Tecchiati, 2013). Among items found in the grave were a red deer antler tool and some bone beads which are postulated to be associated with the burial (Rizzi et al., 2010).

There are several reasons why this burial site is particularly unique and important. First, findings of inhumed individuals in this territory are extremely rare and only a few cases have been reported in the literature (De Marinis, 2003; Steiner et al., 2017; Tecchiati, 2011). In fact, archaeological evidence dated to the Copper Age and to the Early Bronze Age suggests a complex funerary practice in South Tyrol as well as the Northern Alps that was more ritual than intentional (Baur, 2006; Tecchiati, 2013; Tecchiati et al., 2016). The ritual involved different kinds of body manipulations (e.g., exhumation, burning, fragmentation), which ended with deposition of the burned human remains often together with cultural objects and animal bones (e.g., Barbiano/Barbian Gostner in Coltorti et al., 2010; Dal Ri et al., 2002; Millan Stockner in Tecchiati, 2013). Moreover, the incinerated bones were sometimes surrounded by stone circles like those found at Varna Circonvallazione in Isarco Valley, South Tyrol (Tecchiati, 2014).

Second, Copper Age burial sites with clear tomb structures in natural rock shelters, such as the one found in Ora/Auer, are very rare in South Tyrol (Tecchiati, 2013). This is in contrast to the neighboring Trentino region where this funerary practice is found more often (Mottes and Nicolis, 2019). There are some other similarities to the Trentino area, including the discovery of another foetus buried in an Early Bronze Age

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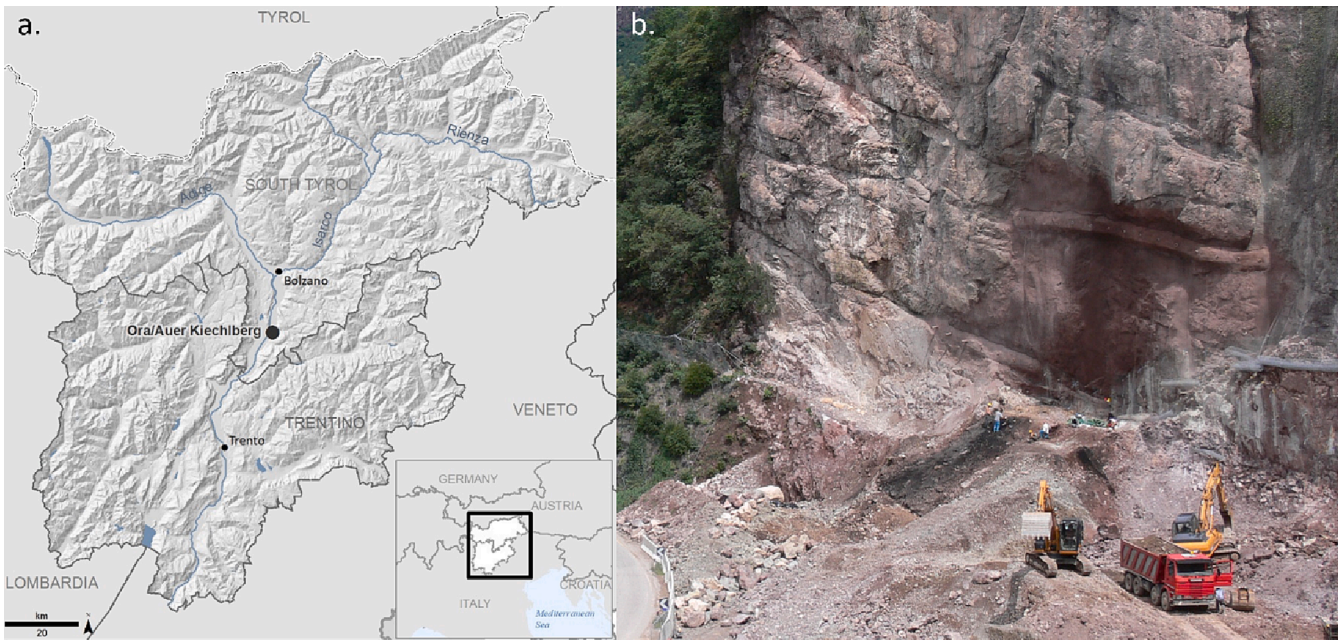

Fig. 1. a. Map displaying the location of Ora/Auer in the Adige Valley in Alto Adige/Südtirol. b. Excavation of the natural rock niche where the burial site was discovered in 2007 (photo courtesy of Jasmine Rizzi).

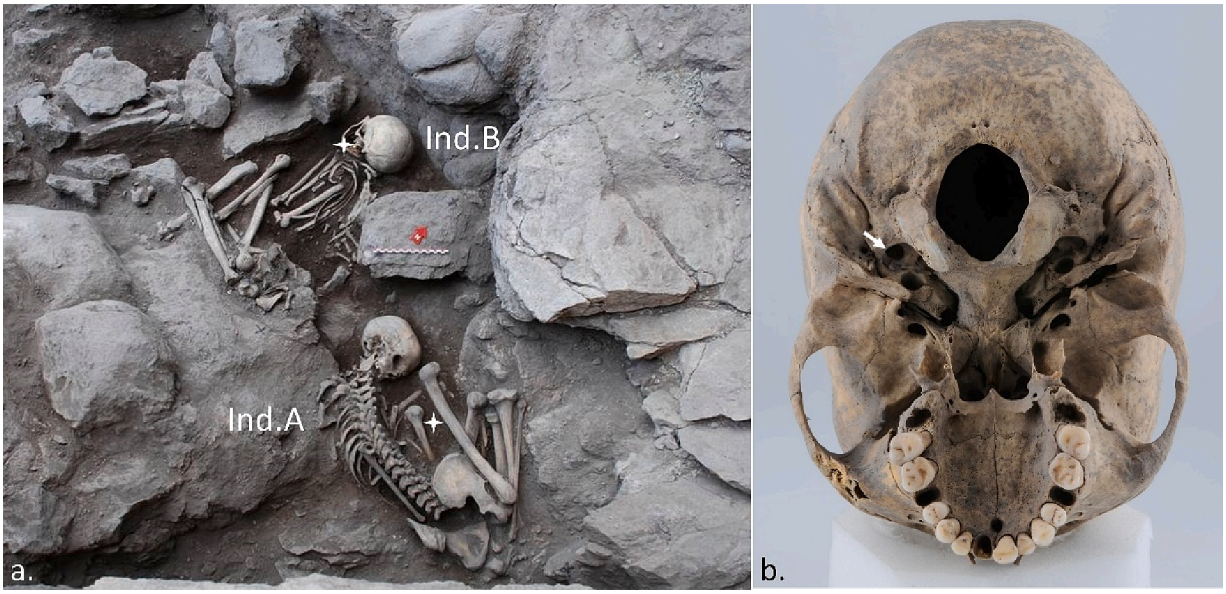

Fig. 2. a. The original positions of Ind. A and B found in the natural rock shelter at Ora/Auer (Rizzi et al. 2010, modified). White crosses show where the osteological remains of Ind. C (the foetus-newborn) were found at the time of discovery. b. Ind. A cranium basal view shows the hole on the left PP (arrow) that was sampled for genetic analysis.

vase at Ora/Auer that dated to the later phases of usage of the tomb (burial in *pithos*, Nicolis, 2001).

In their study, Rizzi and colleagues (2010) used morphological and morphometric methods to postulate that the two adult individuals (Ind. A and Ind. B) were male. However, they doubted this sex estimation conclusion due to the presence of the foetus-newborn (Ind. C) originally found on the chest of Ind. B, as indicated by the taphonomic investigation. This initial discovery suggests that Ind. B could be a female who was buried together with her child. The burial site at Ora/Auer may therefore have represented a family burial. Additionally, the authors report that both adult individuals exhibited the same cranial and post-cranial non-metric traits (i.e., lambdoid ossicles, suprameatal spines and depressions, fusion of the *os trigonum* with the astragalus as well as the third femoral trochanter, Rizzi et al., 2010), suggesting a possible kinship. In the absence of genetic analyses, classic osteology was used to infer a relationship between individuals through the presence of non-metric or epigenetic traits (Berry and Berry, 1967). The latter are skeletal and dental variants considered to be bio-distance indexes (Lippi, 2009). However, the analysis of non-metric traits present methodological limitations as unrelated individuals could share morphological traits by chance (Vai et al., 2020). In fact, these traits only give some preliminary indications to infer kinship that need to be genetically validated to provide a reliable result (Ricaut et al., 2010).

To further explore this rare prehistoric find and clarify ambiguities in

the interpretation of anthropological results, we performed a paleogenetic analysis to answer two specific questions: 1) are the two adults biological males?; 2) are they genetically related?

Ancient DNA (aDNA) analyses were done on nuclear and unilinear transmitted markers (mitochondrial DNA and Y-Chromosome) of Ind. A and B found at the Ora/Auer site. Unfortunately, a paleogenetic analysis of the foetus-newborn (Ind. C) was not possible due to the paucity and poor preservation of the infant's immature bones.

2. Materials and methods

During rescue excavations done in 2007, a burial site was unearthed in Ora/Auer by the Archaeological Office of the Autonomous Province of Bolzano/Bozen. As shown in Fig. 2a, Ind. A was originally found lying on the left side in a crouched position. The taphonomic analysis suggested that this inhumed individual underwent various phases of displacement inside the grave due to soft tissue decomposition, gravity effects, and small-sized animals (rodents) that caused disarticulation of the joints (Rizzi et al. 2010). Ind. B (Fig. 2a) was buried in contracted position, but differently from the other individual, he was lying on the right side. Ind. B moreover presented clear signs of rodent tooth-marks on the surface of some bones. The immature skeletal remains of Ind. C were most affected by taphonomic agents, particularly by rodents "which had an erosive action" on the bones (Rizzi et al., 2010: 41).

For the paleogenomic analysis, left petrous parts (PP) of the temporal bones still anatomically connected to the cranium (Fig. 2b) were sampled from both adult individuals.

For each sample, approximately 150 mg of powdered bone was collected from the inner part of the PP (Fig. 2b) using a drill (Pinhasi et al., 2015) in a dedicated pre-PCR area of the aDNA laboratory of Eurac Research in Bolzano (Italy) following all stringent rules required for aDNA analyses. DNA samples were then extracted using a purification method based on silica columns (Gamba et al., 2014) and double-stranded genomic libraries were constructed (Meyer and Kircher, 2010). These were then sent to an external company (Macrogen) for shotgun sequencing [100 bp paired-end (PE), Hiseq2500 and 150 bp HiSeq-X systems, Illumina]. This first molecular screening was finalized to assess the authentication and good preservation of aDNA from the samples. These were then enriched for more than 2 million polymorphic sites in the human genome using the in-solution target capture kit myBaits ® Expert Human Affinities – Prime Plus (Arbor Bioscience). This includes three different target sets: 1) *Prime 1240 K* includes 1.24 million population-informative SNPs (Single Nucleotide Polymorphisms); 2) *Y Chromosome 46 K* targets sites on the Y Chromosome; and 3) *MitoTrio* probes which cover the complete mtDNA genome. For both samples, the amount of library input for the enrichment reached 1000 ng – the quantity recommended in the protocol for successful enrichment (Human Affinities, Version 1.0, 2021 – Daicel Arbor Bioscience). This procedure was adjusted in terms of hybridization period by increasing the time to 40 h instead of 16 h suggested by the protocol.

Bioinformatic analysis of the sequenced reads (shotgun and capture data) was performed. Reads were trimmed and merged (PEAR) (Zhang et al., 2014) if they overlapped by at least 25 bp and had a minimum length of 25 assembled sequences. The QualityFilterFastQ.py script (Kircher, 2012) was applied to eliminate reads with 5 bases below the quality threshold of 15. Reads were then aligned to the Genome Reference Consortium Human Build 37 (hg19) and revised Cambridge Reference Sequence (rCRS) (Andrews et al., 1999) with BWA (Li and Durbin, 2010) using a minimum mapping quality set at 25. Duplicates were removed by using Dedup (Peltzer et al., 2016). Damage patterns among the ancient reads were tracked and quantified (fragmentation and misincorporation patterns) by using mapDamage (Jónsson et al., 2013). Contamination estimates based on mtDNA data were inferred by using Schmutzi (Renaud et al., 2015). Those on X-chromosome data were estimated applying the method implemented in ANGSD (Analysis of next generation Sequencing Data) (Rasmussen et al., 2011).

The two bam files obtained for each sample from molecular screening and enrichment were then merged for a total of 552,688 (Ind. A) and 1.019,831 (Ind. B) SNPs sites hitting on the 1.240 K panel and were used for kinship analyses.

This was performed using three different methods: READ, TKGWV2 and lcMLkin. The method implemented in READ (Relationship Estimation from Ancient DNA; Kuhn et al., 2018) calculates and normalizes pairwise mismatch rates in non-overlapping windows across the whole genome (pseudo-haploid data). The normalization was carried out using standard parameters (i.e. median of all average P0s). The other two methods, TKGWV2 (Thomas Kent Genome-Wide Variants 2; Fernandes et al., 2021) and lcMLkin (Lipatov et al., 2015), use genotype likelihoods and population allele frequencies to infer genetic relatedness between individuals. In both cases, analyses were performed with default parameters. TKGWV2 is used to infer kinship up to the 2nd degree and lcMLkin to the 5th degree.

Molecular sex determination was inferred by calculating the ratio of the total merged sequences aligning to the X and Y Chromosomes (Skoglund et al., 2013).

Y Chromosomal haplogroups were assigned using *Yleaf* software v2.2 (Ralf et al., 2018) with standard settings, while classification of the mtDNA haplogroups was performed by applying Haplogrep 2.4.0 (Kloss-Brandstätter et al., 2011) and the most recent up to date phylogenetic tree of worldwide human mitochondrial DNA variation.

The recovery, sampling and all the analyses performed in this study were authorized by the competent authority (13.2 Archaeological Office, Autonomous Province of Bolzano/Bozen, Italy).

3. Results and discussion

Molecular screening revealed good preservation and quality of aDNA for both adult individuals. Bioinformatic analyses of shotgun sequencing reads showed typical damage patterns for aDNA and low contamination from modern human DNA using mtDNA data (average 3%). The percentage of reads mapped to the human reference genome (hg19) was 7.3% and 24.8% for Ind. A and Ind. B, respectively (Table SM1 and Table SM2). Additionally, bioinformatic analysis of sequencing reads obtained after enrichment showed very good human endogenous content in both samples (>92%) and mean coverage on 1240 K sites of 0.448 in Ind. A and 0.827 in Ind. B. Low contamination from modern mtDNA was confirmed (average 1–2%) and is based on a higher coverage of the mitogenomes (31.5X and 172X for Ind. A and Ind. B, respectively). Low contamination estimates (Ind. A, 1.9–2.4%; Ind. B, 1–1.1%) were also inferred using nuclear X chromosome data (Table SM3). The final mean genome coverage based on merged data was 0.07 X and 0.34 X for Ind. A and Ind. B, respectively (Table SM4).

Successful recovery of aDNA from both individuals made it possible to answer our two main questions.

First, ancient molecular analysis confirmed that the two adults were biologically male (XY). Molecular sex estimations were based on several human reads that were much higher (1,262,31 for Ind. A and 4,250,379 for Ind. B) than the number needed by the method to obtain a reliable estimate (about 100,000 human sequences; Skoglund et al. 2013; Table SM2). Therefore, any previous speculation of their sex estimations made by Rizzi and her colleagues was clarified. This highlights that presence of an infant in a multiple burial does not necessarily imply the presence of a female.

There are other examples cited in the literature in which the biological sex of ancient individuals diverged from the initial assumption based on archaeological records. This is the case for individuals buried in double or multiple tombs, particularly when the bodies are found placed next to each other. In these cases, the natural hypothesis is to presume that they are a man and a woman. For instance, the two "Lovers of Mantova" (Italy), which were intentionally buried hand-in-hand, were therefore considered a loving couple (Vazzana et al., 2018). However, an Amelogenin protein analyses of tooth samples from these

Table 1
Summary of the genetic results for the two adults found in Ora/Auer. Abbreviations: Anthro ID = Anthropological ID; 1240 K Sites (All) = number of total sites hitting on the 1240 K dataset. Mol Sex = Molecular sex assignment; Haplogroups of the mitochondrial DNA (mtDNA) and Y-Chromosome. Kinship results obtained by applying three methods (lcMLkin, READ and TKGWV2) and final kinship interpretation based on all data.

Anthro ID	1240 K Sites (All)	Mol Sex	mtDNA haplogroup	Y-Chromosome haplogroup	Kinship (lcMLkin)	Kinship (READ)	Kinship (TKGWV2)	Relation
Ind. A	552.688	XY (Male)	J1c + 16261 + 189	G2a2b2a1a1b1	Parent-offspring	1st degree	1st degree	Father-Son
Ind. B	1.019,831	XY (Male)	K1a	G2a2b2a1a1b1				

two individuals revealed that they were both males (Lugli et al., 2019). Another example is seen where several couples were buried in a Bronze Age double grave in Spain. In this case, they were believed to be married couples, corroborating the existence of heterosexual monogamous marriages during that time period (Castro et al., 1993). However, recent radiocarbon dating has shown that the individuals belonged to different generations, demonstrating the deceased were more likely descendants of one another and not married couples (Esparza et al., 2017). Our study, together with these cases, illustrate the importance of critically reconsidering gender perspectives that have been applied to past societies, as was recently pointed out by Turek (2019).

The second aim of this work was to investigate whether the two individuals from Ora/Auer were genetically related. The application of three methods to infer relatedness based on genomic data identified a first-degree relationship between the two males (e.g., father-son, brothers). Additionally, one method (lcMLkin) specifically detected a parent-offspring relationship (Table 1 and Table SM5). Moreover, data from the unilinear transmitted markers, which are almost exclusively transmitted by only one parent to their offspring, indicated kinship at paternal level. Indeed, Y-Chromosome haplogroup analysis found the same lineage in both males (haplogroup G2a2b2a1a1b1) while those based on the mtDNA data unambiguously assigned two different maternal haplogroups for Ind. A and Ind. B (K1a and J1c + 16261 + 189, respectively). This moreover suggests a different genetic history at maternal level for the two individuals, the further investigation of which is beyond the scope of this paper (Table 1 and Table SM4). Taking all the genetic results into consideration, we exclude the possibility that the two men were brothers, thus most likely indicating that they were father and son.

The age-at-death estimation performed by Rizzi and colleagues (2010) could also be consistent with a father-son relationship. Indeed, there was only a ten-year age difference between the two men (Ind. A ~ 30 years old, Ind. B 40+ years old). However, considering that the anthropological age-at-death is the result of an estimation, the gap could also have been greater, up to 20 years or more.

Radiocarbon dating ranges also support the almost contemporaneity of the two relatives.

4. Conclusions

The effectiveness of interdisciplinary dialogue combining archaeology, anthropology, and paleogenomics is well represented in this study. We successfully obtained the genetic sex and biological relatedness of two Copper Age adult individuals, thus answering some questions remaining from previous anthropological and taphonomic investigations. This study also shows the important role that paleogenomics plays in better understanding prehistoric funerary contexts which would otherwise be difficult to interpret based on archaeological data alone. This study is part of an ongoing palaeogenomic project performed on several ancient human remains from the eastern Italian Alps in order to broaden our understanding on the genetic and social structure of prehistoric and protohistoric individuals from this alpine region.

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.

Data availability

The four FASTQ files for shotgun and capture generated in this study are available at the European Nucleotide Archive (ENA) with the accession number PRJEB58428.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2023.104103.

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