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Research paper

The Lady from Basel's Barfüsserkirche – Molecular confirmation of the Mummy's identity through mitochondrial DNA of living relatives spanning 22 generations

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ABSTRACT

The identity of the mummified Lady from the Barfüsser Church in Basel, Switzerland has been unsolved for decades, despite the prominent location of the burial place in front of the choir screen. A recent multidisciplinary research approach came up with a possible candidate, Anna Catharina Bischoff who died in Basel in 1787 with an age of 69 years (1719–1787). To verify the identity of the mummy, genealogists of the Citizen Science Basel discovered three living individuals of the maternal lineage of two different family branches, separated from Anna Catharina Bischoff by up to 22 generations. In this study we compare the ancient mitochondrial DNA of the mummy recovered from a premolar to the mitochondrial DNA of these three candidates. Initially the mitochondrial hypervariable regions I and II of the living individuals were screened using the Sanger sequencing method. This was followed by a mitochondrial capture approach and next generation sequencing to enrich for the whole mitochondrial genome of the mummy and one living person. A full mitochondrial genome has been recovered of both individuals sharing an identical haplotype. The sequence was assigned to the mitochondrial haplogroup U5a1+!16192 including two private mutations 10006G and 16293C. Only by using an interdisciplinary approach combining ancient DNA analysis and genealogy a maternal lineage of a non-noble family spanning 22 generations could be confirmed.

1. Introduction

In 1975 during renovation works at the Barfüsserkirche in Basel (Switzerland), a former Franciscan church, the mummified human remains of a female individual have been discovered. For more than 40 years the identity of this well-preserved crypt mummy remained unknown. This, however, changed during a recent interdisciplinary reanalysis of the mummy that was led by the National History Museum of Basel and that provided novel precious insights into her life history and identity.

1.1. The discovery of the mummy

After the reformation in 1527 the monastic Barfüsserkirche underwent a successive profanation and was turned into a salt deposit in 1799. Due to the severe damage to the masonry by the salt it was decided to completely refurbish the church in 1975 which was accompanied by an archaeological rescue excavation [1]. On the 20th of October in 1975 a surprising finding was made. Three consecutive burials were found in a brick-build shaft grave without a grave slab. This burial chamber II, lying in a row with six other brick-build burial chambers had a very prominent position under the central nave in front of the choir screen. In addition, burial chamber II was right next to the central aisle of the church (Fig. 1A). Two entirely preserved wooden coffins and below a

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pile of bones of a former burial were uncovered. The upper burial contained an almost completely skeletonized female corpse, whereas the middle burial (burial 15) contained an almost complete, well-preserved female mummy. This mummy became known as the Lady from Basel's Barfüsserkirche (Fig. 1B) [2].

1.2. A general description of the mummy

The naturally mummified female body has been detected in a plain fir wood coffin. Apart from the lower limbs and the calvaria the mummy is very well preserved. Beside the mummified body itself major parts of her dress could be recovered. The Lady from the Barfüsserkirche was a small woman, with a body size of 142 cm, who suffered from severe obesity [2]. Her age of death between 55 and 70 years has been estimated based on the articular surfaces of the pubic bone, the advanced spinal degeneration, and the tooth cementum annulation [2]. First analyses including a dissection of the mummy were performed in the 80's of the last century. This showed that not only the outer part of the mummy, but also her inner organs are perfectly preserved. During the examination of the mummy, red spots were found on the skin and inner organs with the highest concentration in the lungs and the diaphragm. Chemical analysis revealed that the red stains are composed of mercury sulphide, a substance used to treat bacterial infections at that time. Due to both, indicative skull bone lesions and the signs for intoxication with mercury it was assumed that the mummy suffered from syphilis [2–4]. Further computer tomographic based imaging analysis revealed atherosclerotic calcifications in the abdominal artery and gall stones in the gallbladder [5]. During her lifetime she has lost all teeth of the maxilla and in the mandible only carious incisors, canines and premolars remained. This overall clinical picture suggests that the mummy most likely had a nutrition rich in fatty meat and sugar [2].

1.3. First indications for the mummy's identity

In Switzerland, it has been a widespread practice to bury people inside churches since the early Middle Ages. However, this favoured custom has been reserved for wealthy people and the clergy [2,6]. Hence, the question arises, who this mummy buried in such an outstanding position in close neighbourhood to influential families of the old Basel could have been.

Based on the location and archaeological investigations of the grave site the mummy was initially indirectly dated to the post-Reformation time period after 1528 [2]. First radiocarbon dating has been performed with parts of her dress that had been tucked between her upper arm and her torso so that the textile could not belong to a secondary dressing from a later time point. This dating resulted in a time period between 1647 and 1805, which fits to the cut and style of the dress that belongs to a fashion trend commonly found between 1750 and 1830. A further radiocarbon dating of an inner organ sample of the mummy revealed a time period between 1635 and 1797. This direct dating was highly supported by dendrochronological analysis of the coffin that suggests a time period after the year 1748 [2].

First indications for the identity of the mummy were found in the State Archive of the Canton of Basel City. The Burial Registry (1380–1741) revealed that the last entombment within the former Franciscan church took place in 1794. A historical list of tombstones in the Barfüsserkirche describes the localisation of 110 numbered family graves inside the church and importantly provides all names of the people that were buried between 1760 and 1790 [2]. The possible identity of the mummy could be further restricted by looking for a female candidate that died between 1748 and 1790 at an age between 50 and 70 years [5].

In addition, the clothes, her well-fed body, and her burial place imply that the Lady belonged to the upper class of post-reformed Basel.

The key, however, to narrow further down the search for the mummy's identity was the discovery of previously unread archival records in 2017. During reconstruction works in 1843 all gravestones that have not been previously removed inside the church have been eliminated. The newly discovered text of the construction manager Blendinger reveals a connection between the removed gravestone eleven and the number 105 on the list of tombstones: the grave of a well-established Basel family, the Bischoffs [2]. Both the archaeological findings and the historical documents revealed a possible candidate for the identity of the mummy, Anna Catharina Bischoff, who died in Basel in 1787 at an age of 69 years.

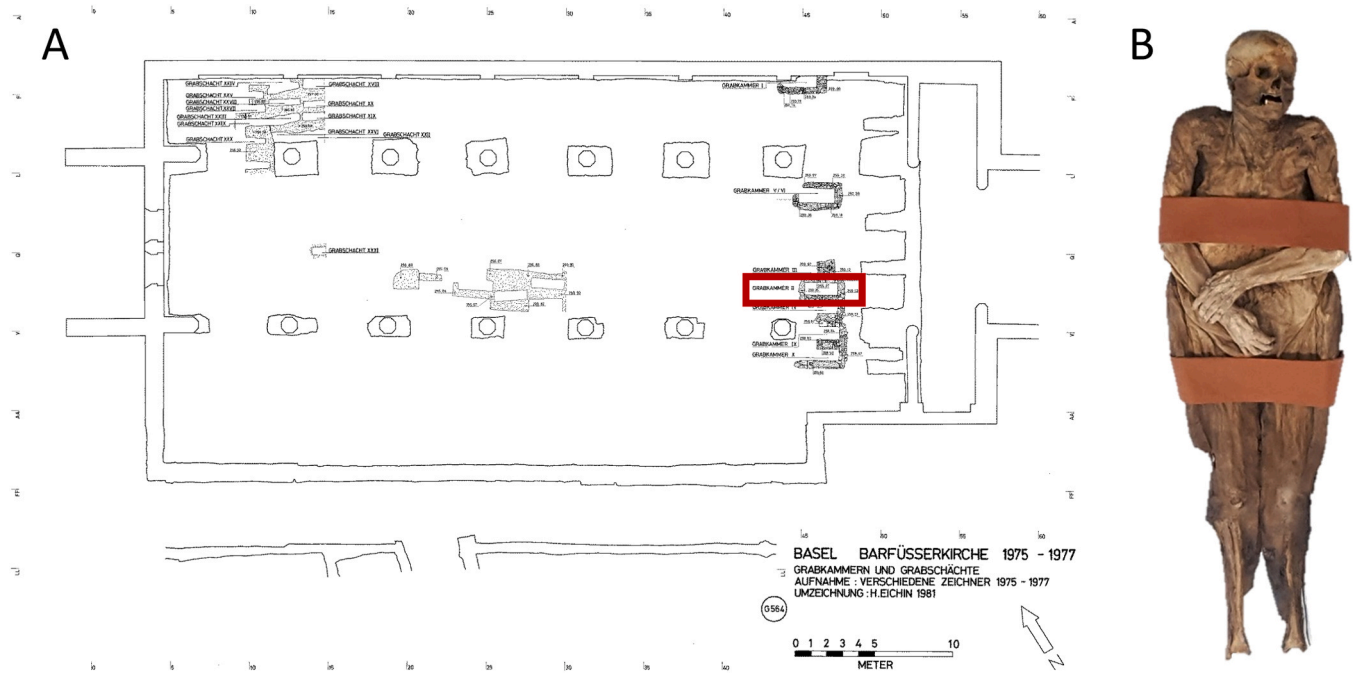


Fig. 1. (A) Prominent location of the brick-build burial chamber (red rectangle) right in front of the choir screen and next to the centre aisle inside the Barfüsserkirche (© Archäologische Bodenforschung, 1975/6 – Plan „Grabkammer und Grabschächte (G564)", modified by H. Eichin 1981). (B) The "Barfüsser mummy". (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Once the possible identity had been proposed, genealogists were able to generate a family tree (Fig. S3) based on records of birth, marriages and deaths stored in different archives. Thereby, the genealogists were able to detect living possible relatives of the maternal lineage of the mummy. After this tremendous archival detective work, our aim was to validate the genealogist's findings by comparative molecular analysis of the mummy with living descendants of her maternal lineage.

The genealogists succeeded in finding two living candidates for this molecular analysis by tracing the maternal family tree of Anna Catharina Bischoff seven generations backwards into the year 1512 to Justina Froben, the daughter of the famous Basel book printer Froben. Only with Justina Froben it was possible to find an uninterrupted matriline spanning 15 generations to today's descendants, a pair of siblings born in Basel in 1928 and 1938 [2]. In a later finding a third still living relative could be identified in Ohio (USA) separated only by nine generations, one generation backwards and eight generations forward following the matriline of the sister of Anna Catharina Bischoff (Fig. 2).

1.4. Aim of the study

In this paper, we aim to shed light on the identity of the "Barfüsser mummy" by validating a genetic relationship spanning over 22 generations based on genealogical records, with the help of ancient DNA (aDNA) analysis. For that purpose, DNA was extracted from the mummy and three possibly related living relatives of two different family branches and, subsequently, the mitochondrial DNA was analysed by using a polymerase chain reaction (PCR) based approach, followed by next-generation sequencing (NGS) and a capture approach to enrich for the complete mitochondrial genomes.

2. Materials and methods

2.1. Biological material

Ancient DNA analyses have been performed on a premolar (tooth 34) (Fig. S1) of the mummy which is housed in the Natural History Museum of Basel. For the comparative analysis with three possibly related living relatives we received samples taken with a buccal swab sampling device of a pair of siblings from Basel (Switzerland) born in 1928 and 1938 and a candidate from Ohio (USA) born in 1929. For all three living individuals a written consent has been obtained to take buccal swab samples and to perform the following analyses.

2.2. Molecular analyses

Our first goal was the reconstruction of the full mitochondrial genome of the mummy using a capture-sequencing approach. Therefore, the DNA of the mummy tooth has been extracted in the ancient DNA facility of the Eurac Research - Institute for Mummy Studies in Bolzano, Italy. Initially the premolar of the mummy has been cleaned with 3% hypochlorite and UV irradiated on two sides for 10 min before grinding the whole tooth to powder. First a pre-digestion step of 30 min has been applied to ~250 mg powder as described in Damgaard et al. [7]. Next DNA was extracted from the pre-digested powder using a Silica-column-based extraction as described by Rohland et al. [8] and modified by Gamba et al. [9]. A single-indexed library out of 25 µl extracted DNA was constructed based on Mayer & Kircher [10]. To enrich for the mitochondrial DNA an in-solution capture approach with the modern human global baits panel of Arbor Biosciences following the manual's (v3.02) suggestions for aDNA has been performed. The captured library was sequenced on an Illumina HiSeq 2500 platform using a 101 bp paired-end sequencing kit. To receive a higher coverage of the mtDNA genome the captured dataset has been merged bioinformatically using SAMtools merge (v.1.9) [11] with previously sequenced shotgun datasets which were produced in the same way as the mtDNA capture dataset however without enrichment.

DNA of the buccal swab samples of the two living individuals from Basel were extracted and processed in a modern DNA laboratory in Bolzano (Italy). The DNA has been extracted using the Gentra Puregene Buccal Cell Kit (Qiagen). The hypervariable region (HVR) I and HVRII were analysed by using the classical Sanger sequencing method covering the region between 15973 and 472 bp (F: Dloop-L 15973-P-S; R: mtDNA-Dloop-H495-P-S). PCR based analyses have been performed by BMR Genomics. To further strengthen the hypothesis that the mummy

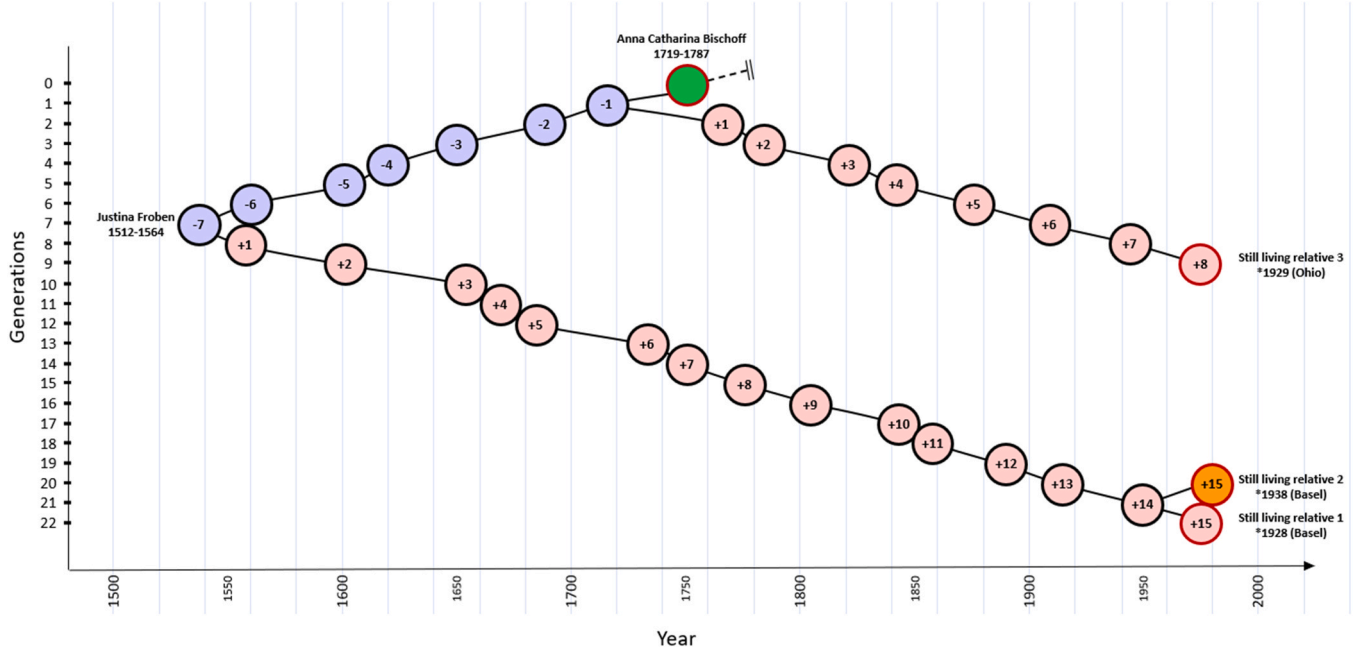


Fig. 2. Two branches of the condensed family tree of the matriline of Anna Catarina Bischoff. Red circled are the individuals of which DNA analyses have been performed. In green the mummy and in orange the living relative of which the mtDNA capture has been performed. -‖ Anna Catharina Bischoff has had children but no matriline to still living descendants of the female line has been discovered. (An extended family tree can be viewed on Ancestry.com). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and the still living individuals really share the same mitochondrial haplotype the complete mitochondrial genome of the modern male sample (still living relative 2 of Fig. 2) was analysed by the same NGS methods and the same mtDNA capture as previously described for the mummy DNA. Before the library preparation the DNA was sheared to fragments of about 150 bp using an ultrasonicator (Covaris). The fragmented modern DNA was subsequently transformed into a dual-indexed DNA library and subjected to the same capture-sequencing approach as described for the mummy.

For an independent confirmation the individual from Ohio and a second buccal swab sample of the female individual from Basel have been investigated using Sanger sequencing in the laboratory of the forensic genetics unit of the University Center of Legal Medicine in Lausanne (Switzerland). The first two hypervariable domains of the control region (HVRI and HVRII) were analysed following the methodology described in [12].

2.3. Bioinformatics analyses and authentication

The raw read pairs were assembled using PEAR (v.0.9.10) [13] with a minimum number of overlapping bases of 25 bp and a minimum length of assembled sequences of 25 bp. The QualityFilterFastQ.py script [14] has been applied to eliminate reads with 5 bases below the quality threshold of 15. Reads were aligned to the human reference genome (build hg19) and the mitochondrial reference genome (rCRS) [15] respectively using BWA (v.0.7.16a) [16] with a seed length of 1000. Data has been converted into BAM files using SAMtools (v.1.9) [11] removing reads with a mapping quality below 25. To remove read duplicates the tool DeDup (v.0.11.3) [17] has been applied. Contamination estimates of the mitochondrial sequences have been established with the tool Schmutzi [18] to authenticate the retrieved sequencing data. In addition, MapDamage2 (v.2.0.8) [19] has been used to retrieve deamination patterns of the sequencing data to authenticate for aDNA of the mummy's sample and to construct a new BAM file in which quality values of mutations most likely due to ancient DNA damage are downscaled. Rescaled BAM files were converted into VCF files using VCFtools (v.0.1.13) [20]. The mitochondrial haplogroups were assigned using HaploGrep 2.0 [21,22] based on PhyloTree built 17 [23]. All received single nucleotide polymorphisms (SNPs) were re-evaluated visually using SAMtools tview (v1.9) [11]. To visualise the coverage plot and mutations to the rCRS sequence of the modern and the ancient mtDNA genomes the tool Circos (v.0.69.6) [24] has been used. The genetic sex has been identified using a script especially designed for ancient DNA [25].

2.4. Biostatistical analyses

Statistical significance for the sequenced alternative alleles were calculated via binomial test with a significance value of $p = 0.5$ using R (version R-4.0.3).

To determine the significance of the genetic findings, a likelihood ratio (LR) was assigned for the mummy's identity being Anna Catharina Bischoff given the achieved mitotype. For the calculation of the LR only the control region of the mitogenome has been considered and recommendations of Buckleton et al. [26] were followed.

3. Results

3.1. Mummy DNA

With the capture-sequencing approach of the mtDNA of the mummy a complete mtDNA genome has been retrieved with an average coverage of 819.9 (SD 174.2). Human DNA contamination has been low with only 0–2%. Further aDNA authentication has been confirmed by showing a C to T transition of the first position on the 5′ end on 10.8% of mtDNA reads (Fig. S2).

After an alignment to the rCRS 24 SNPs and one insertion have been discovered spread throughout the whole mitochondrial genome (Fig. 3 + Table S1). The mitochondrial haplogroup was assigned to U5a1+! 16192. Furthermore, based on Haplogrep2 two private mutations were detected: one global private mutation (10006G) and one local private mutation (16293C). All results were confirmed by checking also visually for the correctly received mutations. The high base coverage of at least 380 times of each SNP and the low p-values for the alternative alleles of max. $p = 2.65E\text{-}104$ (Table S1) make the obtained results significant.

In addition, the genetic analysis confirmed the female sex of Anna Catharina Bischoff.

3.2. Modern DNA

With the Sanger sequencing of the two siblings from Basel six SNPs and one insertion in comparison to the rCRS [15] were discovered (16256T, 16270T, 16293C, 16399G, 73G, 263G, 315.1C). This result was independently confirmed with one of the siblings in the laboratory in Lausanne. In addition, in the mtDNA of the third living candidate, the candidate of Ohio, the same characteristics were detected.

The complete mtDNA genome of the living male relative has been sequenced with an average coverage of 5761.0 (SD 965.7). After the alignment to the rCRS 24 SNPs and one insertion have been discovered that are identical to the mutations of the mummy's mtDNA genome (Fig. 3 + Table S1). Contamination with human DNA has been low (0–2%) and C to T transition of the first position on the 5′ end occurred only on 0.2% of mtDNA reads as expected for modern DNA (Fig. S2). The modern mtDNA has been assigned to the same haplogroup as the mummy's mtDNA, haplogroup U5a1+!16192.

3.3. Comparison of ancient and modern DNA

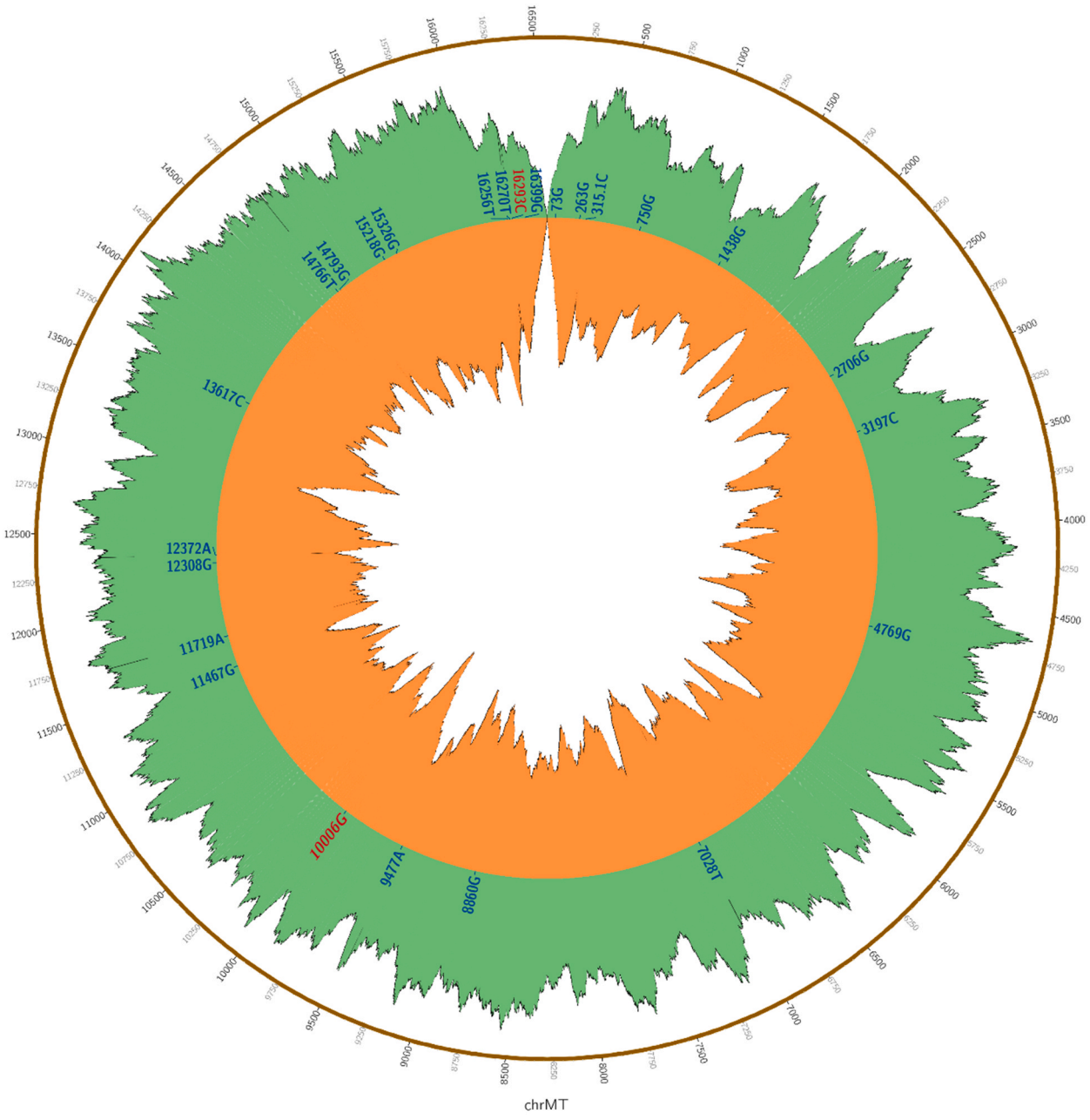
Initially, the PCR based analysis of the modern individuals' mtDNA targeting the HVR1 showed a 100% similarity to the sequence of the mummy's mtDNA including the local private mutation 16293C. More important, the full mtDNA genome of the modern individual is completely identical with the mtDNA genome of the mummy sharing all 24 SNPs and one insertion including the two private mutations. All SNP positions were sequenced with high coverage showing the alternative allele with significant p-values ($p \leq 2.65E\text{-}104$) (see Table S1). Thus, the mummy and the modern individual from Basel share the same mitochondrial haplotype which provides support for the proposition that the mummy and the modern individuals from Basel belong to the same matriline.

In order to determine the significance of this finding, the probability of the analytical results given the proposition that the Lady from Basel's Barfüsserkirche is Anna Catharina Bischoff as well as the probability of these results given the alternative proposition that this is an unknown person maternally unrelated to the living relatives of Anna Catharina Bischoff has been considered. The ratio of these two probabilities is called a likelihood ratio (LR). A LR in the order of 8000 was assigned.

For details of the sequenced datasets please refer to Table S2. All sequenced mtDNA datasets have passed the quality control of EMPOP (W. Parson, pers. communication) [27,28]. Data are available from the European Nucleotide Archive under accession no. PRJEB44723.

4. Discussion

In this study, we analysed the mitochondrial DNA of the mummy from Basel's Barfüsserkirche and three living possible relatives of two different family branches separated by up to 22 generations. In order to verify the identity of the female mummy based on genetic analysis, genealogists were looking for living descendants of the maternal lineage. We therefore focused in our molecular analysis on the mitochondrial genome, which is inherited only by the mother. All analysed individuals share the identical sequence at the HVR 1 and 2. Importantly, the two



	Mean coverage	SD	Contamination	Haplogroup	Private mutations			
					Global	Coverage	Local	Coverage
Mummy	819.9	174.2	0-2%	U5a1+!16192	A10006G	811	A16293C	510
Modern	5,761.0	965.7	0-2%	U5a1+!16192	A10006G	6.018	A16293C	5.125

Fig. 3. Comparison of mtDNA sequencing results between the Barfüsser mummy and the still living possible relative. Green: base coverage of the completely covered mtDNA data of the mummy; orange: base coverage of the completely covered mtDNA data of the modern individual; in red: the two private mutations. For a better visualisation only 1/10 of the genetic data of the modern individual has been used for the circos plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

individuals of which we have the full mitochondrial genome share the same haplotype including 24 SNPs and one insertion with two notable private mutations. The uniparental inheritance of mtDNA in combination with the fact that several thousand copies can be found within a single cell makes it an ideal marker to analyse the kinship of a deceased person based on degraded ancient DNA [e.g., 29,30]. The exclusively maternally inherited state justifies the fact that mtDNA sequences of siblings and all maternal relatives are identical, except if mutations occur [31–33]. The mutation rate of mtDNA is currently estimated to be in the range of one mutation per 70 generations [34] or $2–3 \times 10^{-7}$ mutations per generation [30]. Based on these mutation rates, the finding of an unchanged haplotype over 22 generations, as in our study, is well possible. In addition, we received identical results for two different uninterrupted matrilines for 22 and respectively nine generations to today's living relatives, which further validates our results.

The retrieved full mitochondrial genomes show both a low rate of human contamination (0–2%), and a high and significant coverage of all sites including the SNP loci. Therefore, we consider the listed SNPs as correctly assigned. The very low observed background at the SNP loci can be explained by further reasons then just modern human contamination. The HiSeq 2500 instrument from Illumina that has been used in our study has a sequencing accuracy of 99.9% [35]. This could result in one incorrectly sequenced bp in 1000 sequenced bps which does not explain the amount of observed background alleles. Besides sequencing errors, different biological mechanisms like the occurrence of nuclear mtDNA pseudogenes (numts) or heteroplasmy may also explain the low but present background of the reference allele. Numts are known to be co-enriched but normally in such a low level that the calling of the authentic mtDNA genome sequence is not influenced [36]. In a study of Payne [37] it was shown that heteroplasmy occurs in every healthy individual with at least one single base mutation in more than 0.2% of the mitochondria. All those mentioned mechanisms create only little variation which would fit with our results. To finally exclude the possibility that the observed mutations were introduced by the bioinformatic filter steps for aDNA damage, we checked that no SNP has been created based on rescaling. A circos plot created with the BAM file before rescaling (not published) is congruent to the shown circos plot based on rescaled data (Fig. 3). Therefore, a calling of SNPs that is due to damage patterns can be rejected as the SNP with the lowest coverage is still covered 380 times.

The mtDNA genome of the mummy from the Barfüsserkirche shows a sequence that is similar to those of the living relatives. A LR was assigned considering that the mitotype of this study was not observed within the EMPOP database (https://empop.online/) that includes data for the control region of 8039 Europeans (V4/R13, search 26.01.21). This database presently contains the full mtDNA genomes of only 726 Europeans, which would have resulted in a smaller LR. Therefore, only the control region has been considered to achieve a good compromise between the number of mitotypes of European origin present within the database and the discrimination power of the mtDNA control region. The achieved LR means that the mitotypes are in the order of 8000 times more likely if the mummy from the Barfüsserkirche is Anna Catharina Bischoff, rather than if this is an unknown person maternally unrelated to the living relatives of Anna Catharina Bischoff. Using the verbal scale presented in the ENFSI guideline [38], the support of the DNA findings can be qualified as strong.

Taken together, based on the presented authentication criteria, including the statistically high significance of the sequenced SNPs, the high sequencing coverage of the whole mitochondrial genome, the authentication of aDNA of the mummy through the presence of damage pattern (Fig. S2) and due to the identical sequences of the ancient and the modern individual, the detected mtDNA haplotypes can be considered as valid. The genetic results in combination with every other scientific and historical information, the authors think that it is reasonable to conclude that the Lady from Basel's Barfüsserkirche is Anna Catharina Bischoff (1719–1787).

The discovered haplotype belongs to the macrohaplogroup U5 which is a typical western Eurasian haplogroup and is considered to be the oldest haplogroup in Europe as it has been found to be the most common clade in Mesolithic hunter-gatherers [39–43]. The subhaplogroup U5a1 has a coalescence date of 16,200 yBP and was found among the original Proto-Indo-European speakers [40]. Nowadays, about 6% of the central European population belongs to the haplogroup U5a [39,40]. However, the haplotype that has been sequenced in this study contains two private mutations. A polymorphism is considered as a local private mutation if it is not associated with the assigned haplogroup but occurs at least once in the PhyloTree database related to another haplogroup. A global private mutation on the other hand is a polymorphism that is neither present in the assigned haplogroup nor in the complete PhyloTree database [21]. The global private mutation A10006G (tRNA gene) is already known, e.g. in MITOMAP [44], but occurs only in 0.018% (9 out of 51,192) of the present full-length mtDNA datasets associated to six different haplogroups. The local private mutation A16293C (HVR1) occurs in 0.270% (138 out of 51,192) of the full-length genomes in MITOMAP but is associated mainly to the haplogroups M, A, or I. So far, there is only one record in GenBank (KF933042.1) that combines both private mutations and has a predicted haplogroup U5a1!16192 originating from a person living in Pennsylvania, USA. The occurrence of two private mutations in the haplotype of the investigated mitochondrial genome in combination with an extensive genealogical research allowed us for the first time to verify an uninterrupted matriline of 22 generations based on the whole mitochondrial genome.

There exists a continues interest in kinship analyses of human remains especially among the nobility. With the advent of ancient DNA analysis this kinship studies received a powerful new tool to compare ancient human remains with potential modern relatives. The most famous case of molecular kinship analysis on ancient remains is most likely the identity reconstruction of Tsar Nicholas II that has been buried in a mass grave together with the remains of his family, the Romanovs, after their execution by Bolshevik revolutionaries in 1918. Fragments of the mtDNA obtained of the putative bones of the Tsar were compared to the mtDNA of two living maternal relatives, Countess Xenia Cheremeteff-Sfiri and the Duke of Fife. To identify the remaining individuals of the Romanov family, their mtDNA has been compared to the mtDNA of Prince Philip, the Duke of Edinburgh, who belongs to the same matriline as Tsarina Alexandra. Thereby obtained results helped to identify the bones of the Romanovs, the last royal family of Russia [45,46]. Another example for the identification of a noble man of the past is the study performed on the putative human remains of King Richard III from England. In 2012, a skeleton has been excavated in a monastery in Leicester, which is known as the last resting place of the King in the 15th century. MtDNA samples obtained of two genealogically linked maternal still living relatives, separated by 19 and 21 generations were compared to the mtDNA sequence of the excavated remains. In addition to the perfect match of the mtDNA sequences, DNA predicted hair and eye colour of the archaeological remains could be compared to an early portrait of King Richard III which strengthened the correct identification of the skeleton as the remains of King Richard III [47]. However, in both cases mtDNA analyses have been performed only with the classical Sanger sequencing method and in the case of King Richard III only on the control region of the mtDNA genome.

Besides analyses on aristocratic families, there also exist already identity reconstruction studies of non-noble archaeological individuals. As an example, in the province of Québec, Canada bones from an unmarked grave have been genetically matched with biparental markers to the family tree of living individuals of this region as contemporary individuals have a known genealogy collected in one database tracing back to the founder population of the 17th century [48].

In another study [49], the genetic maternal background of a man from more than 200 years ago has been reconstructed based on genomic data of 182 contemporary individuals belonging to five generations of his descendants. Since his mother has been an African slave, he

introduced a recent African genetic input into the Icelandic gene pool by immigrating to Iceland in 1802. Therefore, the African genome and a possible origin of the mother could be calculated by analysing recombination patterns of African DNA fragments within the five contemporary generations.

Moreover, in the field of bioarchaeology kinship analysis of deceased individuals are of increasing importance, in particular for the analysis of multiple burials [e.g., 50–52]. Burials of two or more people in a common grave are often considered as family burials, although the archaeological record in general does not allow to proof a relationship. Therefore, aDNA analysis has the capacity to verify the presence of possible genetic relationships among the buried individuals.

In contrast to previous studies, for the first time the identity of a non-noble deceased female individual has been reconstructed following an uninterrupted matriline over 22 generations. In earlier studies in which historical individuals were linked genetically to living relatives, mtDNA analysis has often only relied on a few informative SNPs. Furthermore, historical records often provided further specifications that were helpful for an identification, such as a portrait made during the lifetime of the deceased individual [e.g., 45,47]. In addition, family trees of noble families are in general better recorded as the family links of the common people and genealogical records of female-line lineages especially of non-noble individuals are usually more difficult to track over multiple generations due to the change of surname on marriage [47].

This study shows the potential that a connection can be made between people over a huge number of generations, even with non-aristocratic persons. Especially for an important historical person or an important archaeological finding in combination with good local historical records there is the chance to find and analyse the direct line to the modern population and to examine the continuity of families. However, in analyses on the mitochondrial level, the genealogy must be included always in order to achieve a solid assessment, since an identical haplotype does not imply a direct kinship. This is also evident in all the other studies mentioned above [45,47–49]. At the same time, this study shows that the analysis of aDNA is a good tool to support genealogical investigations and can support the identification of ancient individuals. Therefore, the here presented case of the Lady from Basel's Barfüsserkirche is a good example for the importance of interdisciplinary research where archaeology, genealogy, and genetics must support each other to receive a well-grounded result.

The identity reconstruction of the mummy is an important step in the exploration of the everyday life of an upper class woman in 18th century Basel. Based on those first promising results further genetical studies on the Lady from Basel's Barfüsserkirche are planned to focus on her phenotype as well as on the occurrence and development of diseases.

CRediT authorship contribution statement

Christina Wurst: Methodology, Software, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Frank Maixner:** Methodology, Writing – review & editing, Supervision, Project administration. **Vincent Castella:** Validation, Formal analysis, Investigation, Writing - review & editing. **Giovanna Cipollini**: Validation, Investigation, Writing – review & editing. **Gerhard Hotz**: Methodology, Resources, Writing – review & editing, Supervision, Project administration. **Albert Zink:** Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fsigen.2021.102604.

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