

Beyond simple kinship and identification: aDNA analyses from a 17th-19th century crypt in Germany

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ABSTRACT

Ancient DNA (aDNA) analysis is a powerful tool in multidisciplinary research on human remains, potentially leading to kinship scenarios and historical identifications. In this study, we present a genetic investigation of three noble families from the 17th to 19th centuries AD entombed in burial crypts at the cloister church of Riesa (Germany). Tests were aimed at identifying anticipated and incidental genetic relationships in our sample and the implications thereof for the assumed identity of the deceased. A total of 17 individuals were investigated via morphological, radiographic and aDNA analysis, yielding complete and partial autosomal and Y-STR profiles and reliable mtDNA sequences. Biostatistics and lineage markers revealed the presence of first to third degree relationships within the cohort. The pedigrees of the families *Hanisch/von Odeleben* and *von Welck* were thereby successfully reproduced, while four previously unknown individuals could be linked to the *von Felgenhauer* family. However, limitations of biostatistical kinship analysis became evident when the kinship scenario went beyond simple relationships. A combined analysis with archaeological data and historical records resulted in (almost) unambiguous identification of 14 of the 17 individuals.

1. Introduction

Autosomal, Y-chromosomal and mitochondrial DNA analyses are powerful methodologies in the identification of ancient human remains [1,2]. The identification of these remains is of special interest in cases of historically significant individuals. In such cases, anthropologists seek to verify the identity of the deceased by comparing genetic lineages and enhancing conclusions from osteological and archaeological evidence [3].

However, to interpret the results, we need to make a priori assumptions about the identities of the individuals through contextual information and anticipate shared family pedigrees with modern living descendants [4,5] or historical relatives whose identities are known [6,7]. Contextual information might include the burial location, characteristic artifacts or clothing, provenance, dating, congruent age and sex estimations, diseases, or perimortem injuries [8–11]. At best, all these factors can favor a presumed identity and can be verified by comparison of the genetic lineage with known modern and historical individuals. It is nonetheless essential to be aware of the pitfalls that such historical identifications may present, especially when sampling ambiguous,

ancient remains that might have been replaced, manipulated or contaminated in the past [12–14].

With the increasing potential of DNA analyses, the focus has shifted from identifications of royal [7,11] or other important figures [15] to locally influential individuals or families [16–18]. Post-medieval family crypts offer a unique opportunity for multidisciplinary research by enabling synoptical comparisons of the historical, archaeological, anthropological and genetic evidence [17,19–21]. Due to favorable environmental conditions, the inventory of such crypts is often preserved, including the coffins and clothes as well as the corpses [22–24]. The identity of the entombed individuals is usually known from inscriptions on the coffin or through historical records providing information on the life history of the deceased [25,26]. However, the available biographical data are not always sufficient to unambiguously correlate historical records with the preserved remains, especially when the coffins are not labeled or when looters have disturbed the burials [17,27].

In this study, we present a genetic investigation of three noble families from the 17th to 19th centuries AD, entombed in burial crypts at the cloister church of Riesa (Germany). Our aim was to test for

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anticipated and incidental genetic relations and assess the implications of the presence and absence thereof for the assumed identity of the deceased.

2. Background

Riesa manor was an estate on the Elbe river whose owners were members of the lesser Saxon nobility. Christoph Felgenhauer (1577–1639) was a commoner who made a career under the Electors of Saxony and was ennobled in 1624 [28]. Riesa manor became the family estate and soon received market rights, resulting in the development of a flourishing city [29]. Later, the family held a second estate at Hirschstein Castle. The estates were managed by Christoph Ludwig (1650–1707) and Johann Christoph von Felgenhauer (1633–1705), the grandsons of Christoph von Felgenhauer. During their regime, the owners of Riesa and Hirschstein manors used the former cloister church as a patronage church and burial place [30]. Their family vault was the crypt below the altar, a subterranean groined vault (Fig. 1). The Felgenhauer family held Riesa manor until 1716; afterwards the estate was acquired by the commercial counsellor Johann Christoph Hanisch (1708–1774) whose descendants were ennobled in 1790 as the Barons von Odeleben. In 1824, Curt Robert Freiherr von Welck (1798–1866) purchased the estate. In 1828 the new estate owner opened the sealed crypt below the altar and arranged for an official documentation of the crypt's contents [31,32]. According to his report, several bodies were preserved as mummies of "leathery" appearance. Of a total of 50 coffins, 20 less well-preserved inhumations were subsequently removed from the crypt and transferred to another location [33]. The 30 remaining coffins were numbered and information regarding the coffin (color, material, and decoration), the deceased, the clothing, the state of preservation and the year of death (if available) was recorded [34]. This documentation from 1828 constitutes the background for the current identification of the

coffins, although they were later rearranged multiple times. However, despite the eviction of some and movement of other interments, the inventory is considerably less disturbed than in other crypts [24], since the relocation of the remains was performed under careful consideration of the original setting. Historical sources, such as the church register, as well as family chronicles and later correspondence and photographs, allowed us to reconstruct the changes which the crypt underwent over time [33,35]. In 1856, Curt Robert von Welck decided to found a new crypt for himself and his family [36,37]. This barrel vault is located in the northeastern corner of an annexe to the church and is nowadays referred to as the "northern crypt" (Fig. 2). Between 2016 and 2018, the preserved coffins and mummies from both crypts were documented and investigated by a team led by A. Alterauge [35,38].

3. Material and methods

Samples for aDNA analysis were taken from 17 individuals, including 12 from the crypt below the altar and 5 from the northern crypt. The individuals were supposed to belong to three different families: von Felgenhauer, Hanisch/von Odeleben, and von Welck. According to the coffin inscriptions and the report from 1828, two individuals could be attributed to the von Felgenhauer family, four individuals to the Hanisch, and five to the von Welck family. The identity of six individuals was unknown (Table 1).

All the bodies underwent a morphological investigation in order to estimate the sex and age of the deceased [39,40]. Since they were either mummified and/or dressed, only very basic information on the biological profile could be collected. All coffins containing human remains were therefore X-rayed on site with a mobile device (Examion® PX-20 BT Plus X-ray tube; Examion® X-DR portable detector) in anteroposterior and/or lateral projection [41–43]. The bodies were left in place during the radiological examination. Morphological sex



Fig. 1. View of the northern side of the crypt below the altar. Coffins 27, 28 and 10 (from left to right), standing on stone benches, show striking similarities, with black surfaces and an absence of coffin handles. The mummy in the glass case was not analyzed in this study. (Photo: Amelie Alterauge).



Fig. 2. View of the eastern corner of the northern crypt with coffins N1, N2 and N3 (from right to left) (Photo: Steffen Giersch, Dresden; courtesy of Protestant Parish of Riesa).

Table 1

List of sampled individuals. The red, green and blue colors correspond to the families von Felgenhauer, Hanisch and von Welck, respectively. *The identity of Marie Clara von Welck was verified from an assessment of sex and age. (For interpretation of the references to color in this table legend, the reader is referred to the web version of this article.)

	Coffin No.	Sample	Morphological sex	Based on	Morphological age	State of preservation	Ascribed identity
Crypt below the altar	6	femur	indet.		34th-36th week (in utero)	skeletonized	Son of Hans Christoph von Felgenhauer, still-born on 20 March 1685
	10	navicular	female	genitals, X-rays	18-25 years	mummified	Maria Magdalena von Felgenhauer, née von Binäur (1655-1676)
	11	2 teeth	indet.		8-10 years	mummified	unknown
	13	foot phalange/tissue	female	X-rays	40-60 years	partly mummified	unknown
	13D	patella	female	X-rays	25-40 years	partly mummified	unknown
	16	foot phalange	male	X-rays	50-70 years	mummified	Johann Christoph Hanisch (1708-1774)
	17	tooth	male	X-rays	50-70 years	mummified	Ernst Gottfried Hanisch, Freiherr von Odeleben (1743-1808)
	19	femur	indet.		28th-30th week (in utero)	skeletonized	Ernst Georg Franz Hanisch (1782)
	20	parietal	indet.		32th-34th week (in utero)	skeletonized	Leopold Ernst August Hanisch (1777)
	27	pars basilaris	indet.		3-5 years	mummified	unknown
	28	tibia	indet.		5-7 years	mummified	unknown
	X	hand phalange/tissue	male	genitals, X-rays	22-30 years	mummified	unknown
	Northern crypt	N1	pars petrosa	indet.		4-8 months	skeletonized
N2		humerus	indet.		7-9 years	mummified	Otto Heinrich Ernst von Welck (1856-1863)
N3		humerus/pars petrosa	indet.		6-9 months	skeletonized	Sarah Elisabeth von Welck (1855-1856)
N4		foot phalange	male	genitals, X-rays	60+ years	mummified	Curt Robert von Welck (1798-1866)
N5		tooth	female	genitals, X-rays	25-35 years	mummified	Anna Editha von Welck (1829-1856)

determination relied either on the presence of genitalia or on the radiographic images of the pelvis and skull. Skeletal parameters such as supraorbital ridges and the mastoid process on the skull (Fig. 3), the mandibular shape, the greater sciatic notch and the sub-pubic angle on the pelvis were considered.

The state of dentition (Fig. 3), skeletal maturation (e.g. presence/fusion of epiphyses) (Fig. 4) and degenerative changes were considered for the estimation of age-at-death [39,44–46].

Whenever possible, bone samples were taken at an accessible and inconspicuous location to minimize tissue damage. For this reason, samples come from different skeletal elements, e.g. teeth, hand or foot bones, and skull fragments. Possible contamination was avoided through protective clothing, sterilization of sampling tools and sampling by only one person. If sample weight was sufficient for both stable isotope and aDNA analysis, the bone fragment was cleaned with distilled water in an ultrasonic cleaning bath (Thermo Fisher Scientific, Reinach) and ground to powder in a mixer mill (MM400, Retsch) (samples 6, 10, 19, 20, 27, N2). Stable isotope analyses of the individuals will be published in a separate study. Otherwise, the plain bone fragment was treated according to the protocol described below (samples 11, 13, 17, 13D, 16, 28, X, N1, N3, N4, N5).

3.1. DNA extraction

DNA was extracted at the Zurich Institute of Forensic Medicine. Precautionary measures were taken to prevent contamination: regular UV-treatment and/or chemical sterilization of all working surfaces and instruments, spatial separation of pre- and post PCR DNA analysis, plastic disposables with a certified purity grade according to ISO 18385. Negative controls were included for all experiments. STR profiles for all staff that had worked with the ancient samples were available and confirmed the absence of contamination from the researchers.

Different skeletal elements (petrous bone, teeth, long bone fragments, hand or foot bones) were used for DNA extraction. The previously untreated bones and teeth were mechanically cleaned with a scalpel and then washed sequentially in biopure H₂O, 5% Neodisher (Sanaclean, Zug), biopure H₂O, and 70% ethanol. Bone powder was produced using a milling machine (Proxxon). Teeth were frozen with liquid nitrogen in a metallic mortar and crushed with a mortar and pestle. About 100 mg of the sample was used for DNA analysis. The DNA extraction was performed according to the PrepFiler® BTA Forensic DNA Extraction Kit User Guide, including BTA and PrepFiler lysis buffers and several purification steps with magnetic beads, with the following adaptation: for



Fig. 3. Lateral radiographic image of coffin 10, assumed to be that of Maria Magdalena von Felgenhauer, née von Büchau (1655–1676). The absence of supraorbital ridges and the vertical forehead indicate female sex. The fused humeral head and good state of dentition, including an erupted third molar with unfinished root development (red rectangle), suggest young adult age (18–25 years). Metal components of the coffin (nails) and an earring appear as radiodense objects on the image. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Fig. 4. Photograph and corresponding radiograph of coffin 6, containing the still-born son of Johann (Hans) Christoph von Felgenhauer, born 20 March 1685. Based on long bone length and skeletal maturation, the individual had an estimated age-at-death of 34–36 weeks (in utero). The coffin inscriptions in lead paint, coffin nails and wires used to thread feathers appear as radiodense objects on the radiographic image. (Photo: Steffen Giersch, Dresden; courtesy of Protestant Parish of Riesa).

each 100 mg of bone/tooth powder all reagent amounts were doubled. The DNA was eluted in 65 µl elution buffer. From two friable bone samples (coffins 13 and X), DNA was extracted with a conventional chelex extraction, then concentrated (Amicon Ultra Centrifugal Filters, Sigma-Aldrich, Buchs) and purified (QIAamp DNA Mini Kit, Qiagen, Hombrechtikon), according to standard protocols. DNA quantity was assessed using the QuantiFluor® ONE dsDNA system and the Quantus™ Fluorometer (both from Promega, Dübendorf). DNA was stored at -20 °C.

3.2. STR analysis

DNA extracts were amplified using the AmpFLSTR™ NGM Select™ [47] and the NGM Detect™ [48] PCR amplification kits (both from Thermo Fisher Scientific), according to the manufacturers' instructions. 30 amplification cycles were run with both STR kits. Amplicons of the STR loci were up to 450 bp (NGM Select) and 380 bp (NGM Detect) in length. Genetic sex of the individuals was determined by amelogenin analysis, included in the NGM Select and NGM Detect kits.

For Y-STR analysis, DNA extracts were amplified using the PowerPlex® Y23 System (Promega) [49] and the Yfiler™ Plus (Thermo Fisher Scientific) [50] PCR amplification kits, according to the manufacturers' instructions. PowerPlex Y23 amplicons were up to 425 bp in length, the Yfiler Plus amplicons were up to 478 bp in length.

PCR products were separated and detected with a Genetic Analyzer 3130xl or a Genetic Analyzer 3500. In general, a peak detection threshold of 50 rfu was used for declaring positive results. Exceptionally, lower peaks were called manually. Raw data were analyzed with the Genemapper ID-X Software Version 1.4 (Thermo Fisher Scientific).

3.3. mtDNA analysis

Whole mitochondrial DNA (mtDNA) was sequenced using massively parallel sequencing technology. Mitochondrial DNA was quantified using a Taqman assay targeting a 105 bp fragment [51]. 1500 mtDNA copies were amplified in 10 µl reaction volumes and 21 PCR cycles using the Precision ID™ mtDNA Whole Genome Panel (Thermo Fisher Scientific). The assay amplified 162 short overlapping amplicons (the average amplicon size was 163 bp) that covered the entire mtDNA in two primer pools each containing 81 primer pairs. The manufacturer's protocol was followed, with one exception: the two 10 µl amplification reactions from primer pool 1 and 2 were handled separately using the same barcode and only equimolar-pooled after library quantification. This enabled detection of inhibition of either of the two amplification reactions. Ion Xpress™ barcode adapters were used for sample labeling. After library quantification with the Ion Library TaqMan™ Quantitation Kit (Thermo Fisher Scientific), libraries were diluted to 25 pM and equal volumes were pooled. Clonal amplification and sequencing of the libraries was done on an Ion Chef™ and an Ion S5™ instrument, respectively, using the Ion S5™ Precision ID Chef & Sequencing Kit and Ion 520 chips (all from Thermo Fisher Scientific). Reads were mapped to the revised Cambridge reference sequence (rCRS) [52] in Torrent Suite™ (v.5.10.1) and additionally mapped to the human genome hg19 to detect nuclear mitochondrial sequences (Numts). Variant calling was done with the Torrent Variant Caller plugin (v.5.10-11) applying the recommended forensic nomenclature [53]. The Integrative Genomics Viewer (IGV, <http://software.broadinstitute.org/software/igv>, [54]) was used to visually review variant calls. For point heteroplasmies a frequency threshold of 10% was applied; for length heteroplasmies, only the dominant form was reported. Indels at position 309 were omitted due to the uncertainty of long homopolymer detection using the Ion Torrent technology. Mitotypes were entered in the EMPOP database (<https://empop.online>, v4/R13, [55]) for quality control, phylogenetic alignment and haplogroup (most recent common ancestor MRCA) assignment. Phylogenetic alignment was based on PhyloTree (<https://www.phyloree.org>, build 17, [56]).

3.4. Biostatistics

The *familias* software delivers probabilities for various family constellations through likelihood ratios [57,58]. The Blind Search module within *familias* has proven to be a valuable tool for reconstructing parentage and kinship, even when the data do not represent a classical mother-child-father trio, but instead are deficient (e.g. missing individuals), complicated (e.g. inter-familial marriage) or include mutations [57,59]. Allele frequencies of 16 STR loci from a Swiss population sample were used for calculations [60]. For rare alleles a frequency of 0.01 was applied. With the Blind Search module a relationship search was performed for the 17 individuals. The search made a pairwise comparison with all persons against each other person and calculated a likelihood ratio (LR) for each selected relationship. The following relationships were analyzed: parent-child, full siblings and half siblings (cannot be distinguished from uncle-nephew/aunt-niece). *Familias* Version 3.2 was used for this study.

4. Results

Due to the constant ventilation and low humidity in the crypts, most of the bodies were preserved in a good state as natural mummies (Table 1). Only the fetal and infant remains were skeletonized. Bone and/or soft tissue preservation was good for all individuals, as evidenced by tissue rigidity and collagen content. Soft tissue characteristics, such as genitalia and facial and scalp hair, were also preserved.

4.1. Morphological data

Of the 17 analyzed mummies, 11 individuals were male and 6 were female (Table 2). Genetic sex determination was in accordance with the genitalia of individuals where these were present (coffins 10, X, N4, N5) as well as with individuals' gender-specific names (coffins 16, 17, 19, 20, N1, N2, N3) (Table 1). For the remaining adult individuals, 13 and 13D, the morphological sex determination based on the X-rays could be confirmed by amelogenin DNA-analysis, while for the subadult individuals, the sex determination uniquely relied on the genetic analysis. In case of individuals 6 and 11, the DNA-based sex determination challenged historical information deriving from the survey of 1828, which had been uncritically handed down.

Regarding age estimation, there were three fetuses (coffins 6, 19, 20), two infants of 1 year old or less (coffins N1, N3), four children of up to 10 years old (coffins 11, 27, 28, N2), and eight adults (18-70 years; coffins 10, 13, 13D, 16, 17, X, N4, N5) in our sample. For the individuals with an ascribed identity, the age estimation based on the radiographic images and/or skeletal maturation coincided with the reported age-at-death. For the unidentified individuals, the precise age estimation was used to narrow down potential candidates.

4.2. STR analyses

Most STR profiles displayed the well-known ski slope pattern for degraded DNA, where high molecular weight STR markers show decreased peak heights and/or allelic drop out. For this reason, the autosomal STR analysis was performed with two STR kits that complemented each other (NGM Select and NGM Detect), in that the same markers were designed as short amplicons in one kit and as long amplicons in the other kit and vice versa. From each individual, up to 13 replicate STR analyses were performed. The resulting partial profiles could be assembled into eight further complemented and nine full consensus profiles (Table 2). Within the partial consensus profiles, 9-15 of the 16 loci were present. From two individuals (11 and N3) two different samples were analyzed; 2 teeth and humerus/pars petrosa, respectively, with concordant results. Reference profiles of staff handling the samples were also analyzed to exclude them as contributors. All the individuals showed different autosomal STR profiles.

Table 2

Autosomal STR results of the 17 deceased individuals. Amelogenin (Amel) shows the sex determination: X,X = female; X,Y = male. - = no result.

Samples	D10S1248	vWA	D16S539	D2S1338	Amel	D8S1179	D21S11	D18S51	D22S1045	D19S433	TH01	FGA	D2S441	D3S1358	D1S1656	D12S391	SE33
coffin 6	14,15	16,16	11,12	18,20	X,Y	10,13	30,2,32	14,16	11,15	13,14	7,9,3	21,24	11,14	14,16	11,15.3	16,18	17,19
coffin 10	13,14	15,19	9,11	17,25	X,X	11,12	28,29	14,17	15,18	14,15	6,9,3	20,24	11,11	16,19	15,19.3	18,19	14,14
coffin 11	13,14	-	11,12	19,19	X,Y	13,13	30,30	14,15	11,16	13,13	-	-	11,11	-	-	-	-
coffin 13	-	14,17	11,11	17,18	X,X	13,15	-	15,16	11,16	13,15.2	6,9	20,25	10,10	15,15	15,15	18,18	20,30.2
coffin 13D	13,14	15,17	9,11	17,19	X,X	12,13	29,30	14,17	15,18	15,17.2	6,7	22,24	11,11	18,19	-	-	14,23.2
coffin 16	13,15	14,17	9,11	17,21	X,Y	10,14	29,31	13,20	14,15	13,15.2	9,9	21,25	14,14	15,16	16,16	18,22	19,23.2
coffin 17	15,16	17,20	9,13	21,23	X,Y	14,16	29,32.2	17,20	15,19	13,15.2	9,9,3	22,23	11,14	15,18	14,16	18,22	13,19
coffin 19	14,15	17,18	11,13	20,23	X,Y	12,16	29,32.2	17,18	15,16	13,14	9,9,3	23,24	11,14	15,18	13,16	22,23	19,26.2
coffin 20	13,15	18,20	11,13	20,23	X,Y	13,14	29,29	-	15,16	14,15.2	-	-	11,14	15,18	14,16.3	-	-
coffin 27	13,13	14,16	11,13	20,26	X,Y	12,15	28,28	16,16	11,15	12,13	6,9	18,20	10,11	14,16	17.3,17.3	17,18	16,20
coffin 28	15,15	18,19	9,9	18,18	X,Y	15,15	30,31.2	13,14	11,14	12,13	-	20,21	-	16,18	-	19,21	15,16
coffin X	13,14	17,18	11,11	18,19	X,Y	13,15	30,31.2	15,16	15,16	13,15	9,9,3	20,22	10,11.3	17,18	12,12	-	28.2,30.2
coffin N1	15,15	17,18	11,13	19,20	X,X	13,13	29,29	12,16	11,16	14,14	6,9	19,25	10,14	15,15	-	-	-
coffin N2	14,15	16,16	11,13	19,20	X,Y	14,15	29,31.2	12,16	11,16	14,14	7,9,3	25,26	10,10	15,15	14,18	17,19	23.2,24.2
coffin N3	14,15	16,16	12,13	17,20	X,X	13,15	-	-	11,15	14,14	-	-	10,10	15,17	-	-	-
coffin N4	14,14	17,17	11,13	20,24	X,Y	13,15	30,31.2	14,16	16,17	14,15	7,9,3	19,25	10,14	17,18	13,16.3	18,22	14,27.2
coffin N5	14,14	16,17	11,13	20,20	X,X	14,15	30,31.2	16,17	15,16	14,15	7,9,3	21,25	10,10	15,17	14,16.3	18,19	14,24.2

To review the paternal lineages, Y-STRs were analyzed for the 11 male individuals. Most regions on the Y-chromosome are passed on without recombination from fathers to sons, and therefore all members of the same paternal lineage share the same Y-haplotype. Analyses of Y-STRs were performed using two different Y-STR kits. For each individual, up to 6 replicate Y-STR analyses were performed. The resulting partial profiles could be assembled into eight further complemented and three full consensus profiles (Table 3). Within the partial consensus profiles, 9–26 of the 27 loci were present. We found three groups of individuals that shared male lineages, corresponding to the families von Felgenhauer (red), von Welck (blue) and Hanisch (green). The coffin 11 Y-STR profile was very incomplete (18 loci missing), but the 9 present loci fully coincided with the coffin 6 Y-STR profile. Coffins 27, 28 and X showed individual Y-STR profiles that did not fit into any of the three paternal lineages. The one male staff member that handled the samples was also analyzed and could be excluded as contributor (data not shown).

4.3. mtDNA analysis

To review the maternal lineages, mitochondrial DNA was analyzed for 14 individuals. Mitochondrial DNA is passed on without recombination from a mother to both sons and daughters, and therefore all members of the same maternal lineage share the same mitotype. Complete sequences of the entire mtDNA genome were generated from all 14 individuals with a mean amplicon coverage ranging from 555 to 2355 reads. The only coverage dip below 20 was observed in amplicon mt_95 (position 9840–9958; amplicon coverage = 10) from coffin 20. From the 14 individuals, 6 different mitotypes were found (Table 4). Within the

Table 3

Y-STR results of the 11 deceased male individuals. The red, green and blue colors represent shared male lineages (corresponding to the families von Felgenhauer, Hanisch and von Welck, respectively). The red and blue numbers are single mismatches in one Y-STR locus. - = no result. (For interpretation of the references to color in this table legend, the reader is referred to the web version of this article.)

Samples	DY5576	DY5389 I	DY5448	DY5389 II	DY519	DY5391	DY5481	DY5549	DY5533	DY5438	DY5437	DY5570	DY5635	DY5390	DY5439	DY5392	DY5643	DY5393	DY5458	DY5385	DY5456	YGATAH4	DY5627	DY5460	DY5188	DY5449	DY5387/51
coffin 6	17	13	19	29	13	11	22	12	12	12	15	17	24	25	13	13	-	13	17	11,14	16	13	24	11	-	29	35,36
coffin 11	17	13	-	-	-	11	22	-	12	-	-	17	24	-	-	-	-	13	17	-	-	-	-	-	-	-	-
coffin 16	20	13	20	30	16	10	22	11	13	11	14	18	23	25	10	11	11	13	15	11,14	17	13	17	10	42	32	37,38
coffin 17	20	13	20	30	16	10	22	11	13	11	-	18	23	25	10	11	-	13	15	11,14	17	-	-	10	42	-	-
coffin 19	20	13	20	30	16	10	22	11	13	11	14	18	23	25	10	11	-	13	15	11,14	17	13	17	10	42	32	37,38
coffin 20	20	13	20	-	16	10	22	-	-	11	14	19	-	25	10	-	-	13	15	-	17	13	-	10	-	-	-
coffin 27	18	14	19	30	14	11	21	13	12	12	15	17	24	24	12	14	10	13	16	11,14	16	12	21	11	39	29	35
coffin 28	18	14	20	33	14,15	10	29	12	-	10	-	20	21	-	11	12	-	14	15	15	15	-	-	11	-	-	-
coffin X	20	13	19	29	14	11	22	15	12	12	14	18	25	23	12	14	-	13	18	11,14	16	12	21	10	37	29	-
coffin N2	16	14	20	31	15	11	23	12	12	11	14	19	23	25	10	11	-	13	15	11,14	16	12	18	12	41	32	37
coffin N4	16	14	20	31	15	11	23	12	12	11	14	20	23	25	10	11	11	13	15	11,14	16	12	18	12	41	32	37

Table 4

Whole genome mitotypes of the 14 analyzed individuals. Variants depict the position and the difference relative to rCRS. Colors indicate shared mitotypes. *Amplicon mt_159 (16,222–16,341) of the coffin N3 sample exhibited two sequence variants with equal abundance (both ca. 40%): one contained only 16,222 T and the other contained the variants 16,294 T, 16,296 T and 16,304 C but not 16,222 T. As the variants are linked, a heteroplasmic event happening at 4 positions at the same time is very unlikely. Phylogenetic data strongly favors the latter sequence variant as the true sequence variant and the sequence variant containing 16,222 T was interpreted as contaminant reads (either Numt or sample contamination). (For interpretation of the references to color in this table legend, the reader is referred to the web version of this article.).

coffin	10	13D	28	13	27	19	20	N1	N2	N3	N5	11	6	X
HG (MRCA)	V23			C5c1a		K1b1b1		T2b8					H	V7a
mitotype	72C	72C	72C	73G	73G	73G	73G	73G	73G	73G	73G	73G	146C	72C
	263G	263G	263G	249-	249-	263G	263G						189R	263G
	315.1C	315.1C	315.1C	263G	263G	315.1C	315.1C	263G	263G	263G	263G	263G	315.1C	93G
	750G	750G	750G	315.1C	315.1C	460C	460C	315.1C	315.1C	315.1C	315.1C	315.1C	750G	195C
	1438G	1438G	1438G	489C	489C	750G	750G	709A	709A	709A	709A	709A	1438G	263G
	2706G	2706G	2706G	595.1C	595.1C	1189C	1189C	750G	750G	750G	750G	750G	4769G	315.1C
	4580A	4580A	4580A	750G	750G	1438G	1438G	930A	930A	930A	930A	930A	8838A	750G
	4769G	4769G	4769G	1438G	1438G	1811G	1811G	1438G	1438G	1438G	1438G	1438G	8860G	930A
	6734A	6734A	6734A	1670T	1670T	2706G	2706G	1888A	1888A	1888A	1888A	1888A	15326G	1438G
	7028T	7028T	7028T	2706G	2706G	2761T	2761T	2706G	2706G	2706G	2706G	2706G	16519C	2706G
	8860G	8860G	8860G	3552A	3552A	3480G	3480G	3338C	3338C	3338C	3338C	3338C		4580A
	15326G	15326G	15326G	4715G	4715G	4769G	4769G	4216C	4216C	4216C	4216C	4216C		4769G
	15904T	15904T	15904T	4769G	4769G	5264T	5264T	4769G	4769G	4769G	4769G	4769G		7028T
	16290T	16290T	16290T	7028T	7028T	5899.1C	5899.1C	4917G	4917G	4917G	4917G	4917G		7444A
	16298C	16298C	16298C	7196A	7196A	5913A	5913A	5147A	5147A	5147A	5147A	5147A		8860G
	16519C	16519C	16519C	7694T	7694T	6053T	6053T	7028T	7028T	7028T	7028T	7028T		11167G
				8584A	8584A	7028T	7028T	8697A	8697A	8697A	8697A	8697A		11899C
				8701G	8701G	8164T	8164T	8860G	8860G	8860G	8860G	8860G		15326G
				8860G	8860G	8860G	8860G	10463C	10463C	10463C	10463C	10463C		15904T
				9540C	9540C	9055A	9055A	11251G	11251G	11251G	11251G	11251G		16153A
				9545G	9545G	9698C	9698C	11719A	11719A	11719A	11719A	11719A		16183C
				10398G	10398G	9962A	9962A	11812G	11812G	11812G	11812G	11812G		16189C
				10400T	10400T	10289G	10289G	13368A	13368A	13368A	13368A	13368A		16298C
				10454C	10454C	10398G	10398G	14233G	14233G	14233G	14233G	14233G		
				10873C	10873C	10550G	10550G	14766T	14766T	14766T	14766T	14766T		
				11719A	11719A	11299C	11299C	14905A	14905A	14905A	14905A	14905A		
				11914A	11914A	11467G	11467G	15326G	15326G	15326G	15326G	15326G		
				12705T	12705T	11719A	11719A	15452A	15452A	15452A	15452A	15452A		
				13263G	13263G	12308G	12308G	15607G	15607G	15607G	15607G	15607G		
				14318C	14318C	12372A	12372A	15928A	15928A	15928A	15928A	15928A		
				14766T	14766T	14063C	14063C	16126C	16126C	16126C	16126C	16126C		
				14783C	14783C	14167T	14167T	16294T	16294T	16294T	16294T*	16294T		
				15043A	15043A	14384A	14384A	16296T	16296T	16296T	16296T*	16296T		
			15301A	15301A	14766T	14766T	16304C	16304C	16304C	16304C*	16304C			
			15326G	15326G	14798C	14798C	16519C	16519C	16519C	16519C	16519C			
			15487T	15487T	15326G	15326G								
			16093C	16093C	15946T	15946T								
			16223T	16223T	16093C	16093C								
			16234T	16234T	16195C	16195C								
			16288C	16288C	16224C	16224C								
			16298C	16298C	16311C	16311C								
			16327T	16327T	16519C	16519C								
			16518T	16518T										
			16519C	16519C										
			16527T	16527T										

Table 5

Likelihood ratios of the most probable relationships between the 17 individuals, without and with theta correction ($LR > 10$ and $LR > 1$, respectively). The highlighted relationships are the ones that fit best with the presumed pedigrees. The red, green and blue colors correspond to the families von Felgenhauer, Hanisch and von Welck, respectively. *half siblings cannot be distinguished from uncle-nephew/aunt-niece. (For interpretation of the references to color in this table legend, the reader is referred to the web version of this article.)

theta 0

Person 1	Person 2	Relationship	LR
10	13D	Parent-Child	8.83E+06
10	13D	Siblings	2.27E+06
N5	N2	Parent-Child	2.09E+06
N4	N5	Parent-Child	1.65E+06
N4	N5	Siblings	117675
10	13D	Half-siblings*	93854.2
N2	N5	Siblings	79028.2
17	19	Parent-Child	57452.3
17	20	Parent-Child	14167.2
N2	N5	Half-siblings*	11424.8
N4	N5	Half-siblings*	10333.5
17	19	Siblings	3505.64
16	17	Half-siblings*	3160.9
N3	N2	Parent-Child	3137.53
N1	N2	Siblings	2974.23
N3	N2	Siblings	2417.14
16	17	Siblings	1792.43
17	19	Half-siblings*	1069.87
17	20	Half-siblings*	688.377
17	20	Siblings	606.794
N5	N3	Parent-Child	594.01
20	N1	Parent-Child	172.742
N3	N2	Half-siblings*	157.933
N1	N2	Half-siblings*	109.864
N3	N5	Siblings	103.229
N3	N5	Half-siblings*	57.018
13	27	Half-siblings*	52.5134
X	13	Half-siblings*	41.5168
X	13	Siblings	39.1591
19	20	Siblings	36.1355
20	N1	Half-siblings*	24.6013
20	N1	Siblings	23.8897
N1	13	Siblings	18.5436
N1	13	Half-siblings*	16.6752
N1	N3	Half-siblings*	16.6057

theta 0.1

Person 1	Person 2	Relationship	LR
N4	N5	Parent-Child	2393.68
N5	N2	Parent-Child	2354.35
10	13D	Parent-Child	1446.18
17	19	Parent-Child	375.59
10	13D	Siblings	360.382
N4	N5	Siblings	225.01
N2	N5	Siblings	111.872
N3	N2	Parent-Child	100.312
N4	N5	Half-siblings*	95.3392
N2	N5	Half-siblings*	92.7274
10	13D	Half-siblings*	80.3248
17	20	Parent-Child	76.6924
N3	N2	Siblings	47.2614
17	19	Half-siblings*	32.4395
17	19	Siblings	30.5259
N1	N2	Siblings	29.8964
N5	N3	Parent-Child	27.7514
16	17	Half-siblings*	16.4325
N3	N2	Half-siblings*	14.4641
20	N1	Parent-Child	13.5657
17	20	Half-siblings*	12.8889
N1	N2	Half-siblings*	7.12206
N3	N5	Half-siblings*	6.95598
17	20	Siblings	5.52034
19	20	Siblings	5.51614
N3	N5	Siblings	4.77871
20	N1	Half-siblings*	4.65103
Mister X	13	Half-siblings*	3.24233
N1	N3	Half-siblings*	2.66488
N1	13	Half-siblings*	2.46668
16	17	Siblings	2.38919
19	20	Half-siblings*	2.08242

a relationship as ‘practically proven’, an LR of 39 as ‘highly likely’. Nevertheless, an LR of less than 499 (W-value < 99.8%) is insufficient for a definitive statement in sibship cases [62].

Since endogamy was common in noble families, including the families we investigated, population substructure may be an issue for LR calculations. Adjustments for population substructure can be made by using the kinship coefficient (theta). The kinship coefficient is defined as the probability that two homologous alleles sampled from each of two individuals are identical by descent. Including a theta correction in the LR calculations compensates for the potential to underestimate allele frequencies in subpopulations. Typically, values of theta in the range 0.01–0.05 are considered a conservative estimate of population

substructure, but higher values may occur [63,64]. However, to accommodate a possibly high degree of inbreeding, we re-calculated the LRs with a rather extreme theta of 0.1. In comparison, the kinship coefficient between a pair of half-siblings or uncle/nephew is 0.125. The results in Table 5 show that the LRs were visibly reduced when theta 0.1 was applied, but the ranking of the relationships was unchanged.

With the help of lineage markers (Y-STRs and mtDNA), we were able to strengthen our hypotheses for the assumed relationships, but also discovered unexpected connections. The individuals from coffins 6 and 11 were found to be paternally linked and could therefore be identified. Quite unexpected were the findings that the boy from coffin 28 was maternally linked to individuals 10 and 13D, and the boy from coffin 11

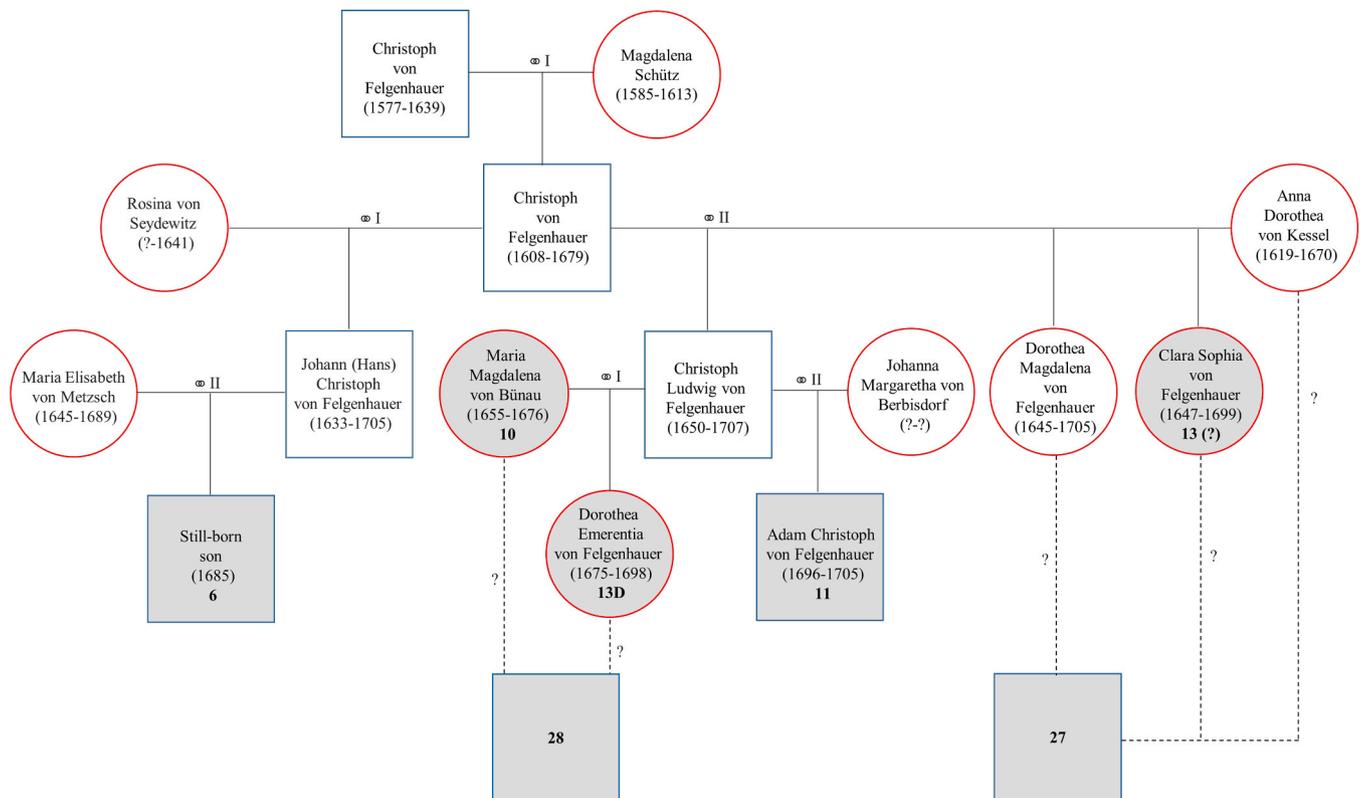


Fig. 5. Suggested pedigree of the von Felgenhauer family. Individuals highlighted in grey were investigated in this study (coffin numbers in bold type). Female individuals are indicated by their maiden names. Rectangles: males; circles: females. Dotted lines: genetically suggested, but historically not supported relationships. ∞ : marriage.

was maternally related to the von Welck family. Another revelation was that the presumed brothers 27 and 28 were not related, either paternally or maternally.

5. Discussion

The aim of our study was to test for genetic relationships between members of three noble families, entombed at the cloister church of Riesa, to verify or disprove the assumed identities of the deceased, and to identify several unknown individuals.

From the genealogies [65,66] and death registers [67], we were able to make reasonable assumptions about the identities of those who were buried in the crypts. But this only applied to the main lineages and core family members, while we had less information about by-lineages, e.g. out-marrying daughters. What we knew from the death register entries was that family members living at Riesa manor and at Hirschstein Castle were interred in the crypt. One obstacle for this study was that nearly all adult men of the von Felgenhauer and von Welck families married twice during their lifetimes and had offspring with both wives [28,37]. Some of these family members were not buried in Riesa, and possible genetic links between half-siblings or half-cousins could therefore be missing, which hampered the interpretation of the genetic relationships. Due to the partial clearing of the crypt in 1828, we were already lacking several individuals. Besides, we always had to keep the possibility of extra-pair paternity in mind, which would result in different Y-STR profiles of the male descendants [68]. Nonetheless, on the positive side, we were able to work from a priori information to limit potential family constellations by excluding statistical options where subadult individuals (<15 years) had offspring. Sampling was also limited to those individuals where bones or teeth could be easily accessed.

Our starting point were the individuals whose identity was explicitly stated on the coffin inscriptions or inscription plates (Table 1). For all

these individuals, estimations of their age and sex – both morphological and genetic – were congruent with their ascribed identity, and the style of the coffin and clothing could be taken as further supporting chronological evidence [38]. The identity of all 11 named individuals could be confirmed by genetic relationships. The identifications suggested in 1828 (and later) were, however, questionable when it came to the inhumations without coffin inscriptions. Here, the aDNA analysis provided clues by revealing kinship relations between identified and unknown individuals. Admittedly, we expected more direct kinship relations among our samples, but the lack thereof was also significant, since it revealed the presence of individuals who did not belong to the core family. Conflicting results between the aDNA results and historical sources called for a careful consideration of what might have led to the false assumed identity in order to find an alternative integration of the individual into the pedigree.

Our STRs can reliably detect first-degree relations, however, they are not informative enough to conclusively determine second degree and more distant relationships [69]. Further, STRs are not able to distinguish between symmetric relationships such as grandchild–grandparent, uncle–niece and half-siblings, which all have the same identical by descent (IBD) probabilities. In some cases, this problem can be solved by investigating lineage markers. Another alternative is to use some form of autosomal linked markers [70]. For resolving distant relationships large numbers of Single Nucleotide Polymorphisms (SNPs) can be analyzed instead of STRs, however, SNP array analysis was not applicable in the case of our ancient and scarce bone material.

Zvenigorosky et al. [71] remind us that the choice of allele frequencies affects LR calculations. They highlight specific issues (both false positives and false negatives) that prevent the confirmation of second-degree kinship or even full siblingship. We used allele frequencies estimated from 668 unrelated individuals of Caucasian appearance living in different parts of Switzerland [60]. The Swiss

cohort had previously been compared to 24 European populations and showed that the genetic variability was evenly distributed among these populations [72]. We therefore believe that our applied Swiss allele frequencies were a good approximation for LR calculations of the German nobles, considering that they lived only 200–400 years ago.

Since endogamy was practiced in the investigated families, we adjusted our LR calculations for population substructure using a kinship coefficient θ of 0.1. The resulting LRs were visibly reduced, but the ranking of the relationships remained unchanged. We conclude that our calculations were not significantly affected by population substructure.

However, with the help of uniparental markers (Y-STRs and mtDNA), which are passed down unchanged along the paternal and maternal lines, we were able to obtain additional insights and strengthen and confirm our hypotheses.

5.1. von Felgenhauer family

Within the von Felgenhauer family (Fig. 5), we found three meaningful sets of relationships. The first concerned a son of Johann (Hans) Christoph von Felgenhauer (1633–1705) who was still-born in 1685 (coffin 6) (Figs. 4 and 5). The individual had a similar Y-STR profile to the child from coffin 11, which implies the same male lineage. Taking into account that both individuals were children, the lineage must have been transmitted through their fathers or grandfathers. Autosomal STRs do not support a close genetic relation, such as brothers or half-brothers. Nevertheless, with an estimated age of 8–10 years, a coffin dating to the early 18th century and the paternal relationship to individual 6, individual 11 could be identified as Adam Christoph von Felgenhauer (1696–1705), the half-cousin of the still-born child from coffin 6.

The second set of relationships concerned the individuals from coffins 10, 13D and 28. Maria Magdalena von Felgenhauer (coffin 10), née von Büнау (1655–1676), was the first wife of Christoph Ludwig von Felgenhauer (1650–1707). They married in 1671 and had three children (2 sons, 1 daughter). Since she had married into the Felgenhauer family, the close genetic relationship to individual 13D suggested that the latter was her daughter, Dorothea Emerentia von Felgenhauer (1675–1698), married name von Grünrod. The morphological age and sex estimation as well as the clothing were in accordance with the genetic results, although no remains from the original coffin, which could have been used for dating the interment, were preserved. The 5–7 year-old boy from coffin 28 shared the same maternal lineage with Maria Magdalena and Dorothea Emerentia, but he was not related to the male Felgenhauer branch. Since the autosomal DNA analysis does not support a close genetic relationship between the boy and both women, we can exclude a parent-child or sibling scenario. This would be in accordance with the historical records since neither woman had a child deceased at the age of 5–7 years or - in case of Dorothea Emerentia - a brother who died at this age. We reached the limits of historically based identification at this point, since we do not know whether there were additional (female) children of either woman, whether the maternal relation was transmitted via preceding generations or whether we were dealing with a case of extra-paternity in the lineage.

Due to typological resemblances, it was assumed that coffin 13 might contain Johanna Margaretha von Felgenhauer, née von Berbisdorf, second wife of Christoph Ludwig von Felgenhauer (1650–1707) [31], and that the two children (coffins 27 and 28) might be their sons (Fig. 5). Both children showed striking similarities in their funerary attire and grave goods, such as funeral wreaths and crosses [38]. This interpretation was challenged by the genetic analysis on several levels. Firstly, individuals 27 and 28 were not related to each other, which contradicted

the assumption that they were brothers. Secondly, neither of them was related either to individual 11 (presumed brother) or to individual 6 (presumed half-cousin). Thirdly, the death register did not report any male children of the above-mentioned parents who died between 3 and 7 years of age. Therefore, we concluded that individuals 27 and 28 did not belong to the paternal Felgenhauer lineage. Since individuals 27 and 28 had different Y-STR and mtDNA lineages from those of individuals 6 and 11 but also dated from the second half of the 17th century, we concluded that they were nonetheless Christoph von Felgenhauer's (1608–1679) and Anna Dorothea von Kessel's (1619–1670) grand- or great-grandchildren. Since we have already discussed the family constellation for individual 28, individual 27 was probably a son of a Felgenhauer daughter married into other families (e.g. Dorothea Magdalena von Gersdorff, née von Felgenhauer (1645–1705); Clara Sophia von Lechleidtner, née von Felgenhauer (1647–1699)) (Fig. 5). It was not unusual for married daughters and their offspring to be entombed in the family crypt [17], especially when their husbands did not have their own burial places. In this regard, the maternal relationship between individual 13 and 27 was of interest. Since we could possibly exclude Clara Sophia as parent, who only married at the age of 45 years, the boy might have been her sister's offspring. Dorothea Magdalena married in 1675 and had several children with her husband Caspar Christoph von Gersdorff. Those might have had offspring on their own. Thus, there are several possibilities for the identification of individuals 13 and 27.

Completely unexpected was the maternal relationship between Adam Christoph von Felgenhauer (coffin 11) and members of the von Welck family. This relationship was very difficult to reconstruct owing to the fact that female nobles usually took their husbands' surnames, making it very difficult to trace them over several generations. In case of Adam Christoph, we suspected that the maternal lineage was transmitted via one of his sisters, Johanne Eleonore, married name von Ende, or Erdmutha Sophia, married name von Schleinitz. In the case of neither sister were we able to trace their female descendants into the 19th century. It was nonetheless a remarkable coincidence that relatives of a child buried in the crypt below the altar were buried in nearly the same location 150 years later; this shows that Saxon nobles predominantly married among their own kind.

5.2. Hanisch/von Odeleben family

In contrast to the von Felgenhauer family, all the coffins of the Hanisch/von Odeleben and von Welck families carried inscriptions or inscription plates which facilitated the comparative analysis of their ascribed identity. The Hanisch family was represented by Johann Christoph Hanisch (1708–1774; coffin 16), his nephew Ernst Gottfried Hanisch, later von Odeleben (1743–1808; coffin 17), and the latter's children (Fig. 6) [73]. Age and sex estimations were in accordance with the suggested identities. We only tested four male individuals from this lineage, and the pedigree of the Hanisch/von Odeleben family could be successfully reproduced via DNA analyses. More importantly, the genetic investigation confirmed that the individual from coffin X was not related to the Hanisch family. In 1923, a 31st coffin was reported in the crypt, which had obviously been entombed there after the documentation in 1828. Oral tradition suggested that it could be the body of Ernst Otto Innocenz Freiherr von Odeleben (1777–1833), a cartographer in the service of Napoleon, who had been transported after his death from Dresden to the crypt in Riesa [74,75]. However, the morphological age estimation of the corpse raised doubts about this identification. Moreover, no such incident was reported in the diaries of Curt Robert Freiherr von Welck (pers. comm. Josef Matzerath, Dresden 2018), nor was there

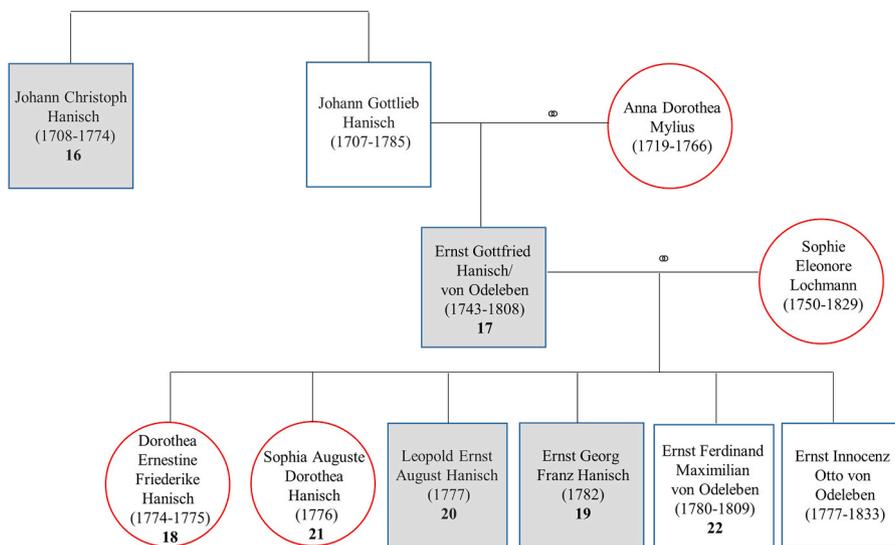


Fig. 6. Suggested pedigree of the Hanisch/von Odeleben family. Individuals highlighted in grey were investigated in this study (coffin numbers in bold type). Female individuals are indicated by their maiden names. Rectangles: males; circles: females. ∞: marriage.

any entry in the death register. The absence of affinities in Y-STRs, mtDNA and autosomal STRs finally demonstrated that the individual did not belong to the Hanisch/von Odeleben family.

5.3. von Welck family

The pedigree of the von Welck family was more intertwined [36,37], but first- and second-degree relations became evident during DNA analysis (Fig. 7). While Anna Editha von Welck (coffin N5, 1829–1856) could be identified as the mother of Otto Heinrich Ernst (coffin N2,

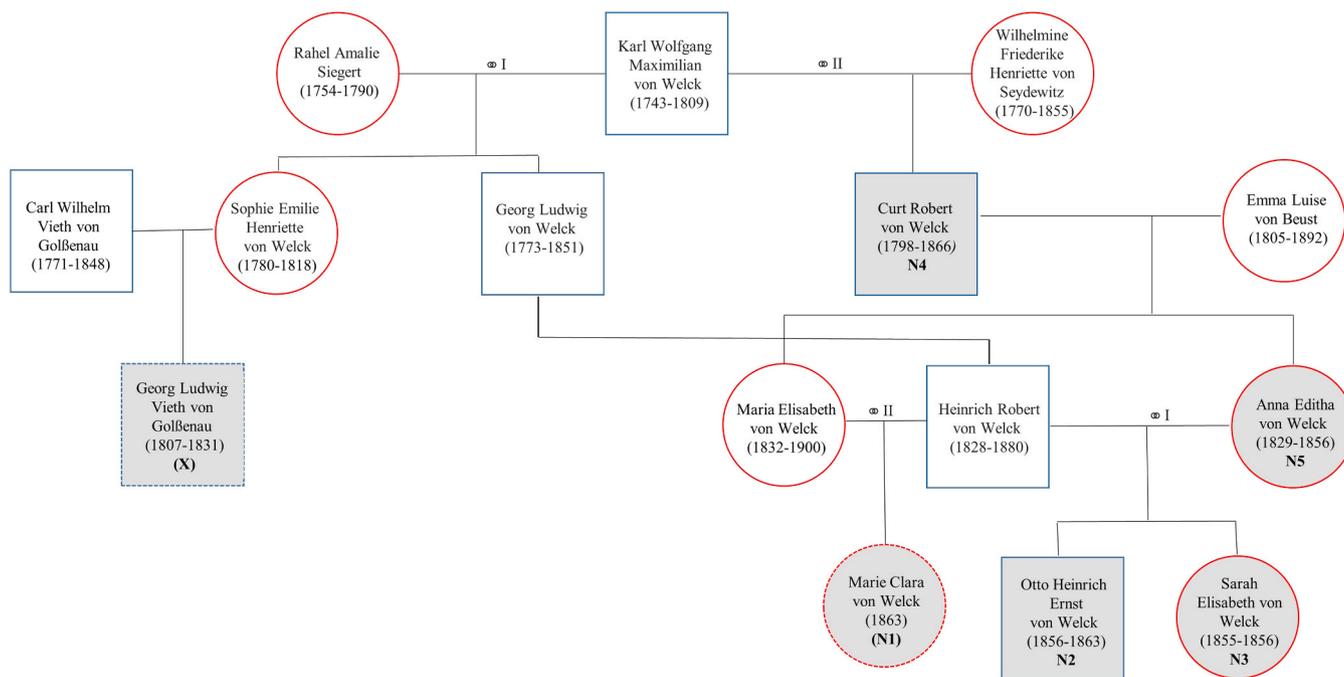


Fig. 7. Suggested pedigree of the von Welck family. Individuals highlighted in grey were investigated in this study (coffin numbers in bold type). Female individuals are indicated by their maiden names. Rectangles: males; circles: females. Dotted lines and coffin numbers in brackets: identification based on circumstantial evidence. ∞: marriage.

1856–1863) and Sarah Elisabeth (coffin N3, 1855–1856), she was also identified as the daughter of Curt Robert von Welck (coffin N4, 1798–1866). Otto Heinrich Ernst could be assigned to the male lineage of Curt Robert von Welck via Y-STRs; he was both his grandson and his grandnephew. However, the likelihood ratios were rather low for half-siblingships between N1 and N2 (LR = 110) and between N1 and N3 (LR = 17). The individuals N1, N2 and N3 are assumed to be related, not only as half-siblings (N1-N2/N3), but also as cousins and second cousins. Their exact relationship cannot fully be established via the genetic analyses. A possible explanation for the genetic similarity between N1, N2 and N3 is that several family members married relatives and had children, and the biostatistical calculations should therefore be interpreted with caution.

Even though the pedigree of the von Welck family could be successfully reproduced via DNA analyses (Fig. 7), this did not clarify the identity of individual X. Contextual information (death after 1828, male, 22–30 years, not Hanisch family) fits with the mention in the death register of the inhumation of Georg Ludwig Vieth von Golsenau (1807–1831) in the baronial crypt. Knowing that the northern crypt was not yet established at this time, we supposed that Curt Robert von Welck allowed his half-sister's son to be buried in the crypt below the altar. Due to the challenging familial relations of half-siblings and offspring with different maternal and paternal lineages, we were regrettably unable to support this assumption by genetic evidence from within the Riesa crypts. As far as we know, the descendants of the brothers of Georg Ludwig Vieth von Golsenau continued to live in Dresden but the lineage became extinct with the famous writer Ludwig Renn (1889–1979) [76]. Thus, we were no longer able to obtain comparative genetic material from modern living descendants.

6. Conclusion

The documentation of burial crypts in the cloister church of Riesa allowed high-quality recovery of extensive burial data. The interplay between anthropological and genetic research helped to verify or disprove ascribed identities and to elucidate those of hitherto unknown individuals. However, the limitations of biostatistical kinship analysis became evident when the kinship scenario went beyond first to third degree relationships. Without modern descendants, links to the family pedigree had to be confirmed by contextual information. Moreover, this study has increased awareness of the social complexity of pedigrees of noble families beyond the main lineage.

In summary, this study highlights the benefits of transdisciplinary research and mutual validation of data on historical human remains. In complex kinship scenarios, a single methodological approach is not sufficient to understand genetic relationships and confirm historical identifications.

Acknowledgements

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