Y-chromosomal analysis identifies the skeletal remains of Swiss national hero Jörg Jenatsch (1596–1639)

Cordula Haas a,* Natallia Shved b, Frank Jakobus Rühli b, Christina Papageorgopoulou c, Josephine Purps d, Maria Geppert d, Sascha Willuweit d, Lutz Roewer d, Michael Krawczak e

a Institute of Legal Medicine, University of Zurich, Switzerland
b Centre for Evolutionary Medicine, Institute of Anatomy, University of Zurich, Switzerland
c Laboratory of Anthropology, Department of History and Ethnology, Demokritos University of Thrace, Greece
d Department of Forensic Genetics, Institute of Legal Medicine and Forensic Sciences, Charité-Universitätsmedizin, Berlin, Germany
e Institute of Medical Informatics and Statistics, Christian-Albrechts University of Kiel, Germany

1. Introduction

1.1. History (adapted from a review [1] of the Jenatsch biography by R. C. Head [2])

Jörg (or Georg) Jenatsch (Fig. 1) was an important political figure in Graubünden (or Grisons, the largest and easternmost canton of present-day Switzerland) during the Thirty Years’ War (1618–1648). At the time, the small federation of the “Three Leagues” (German: “Freistaat der drei Bünde”) had become strategically important and therefore a focus of wide political interests. Wedged between the Swiss Confederation, Habsburg Tyrol, Venice and Spanish Milan, the self-governing rural communities of Graubünden controlled the important Valtellina valley. Whenever Spain wanted to send soldiers from northern Italy to the southern Netherlands in the early 17th Century, they had to pass the Valtellina. Consequently, the Spanish, French and Venetians all tried to gain a foothold in the Valtellina, and in Graubünden as a whole, through patronage, military intervention and downright bribery. Jenatsch, who as a young man became a Calvinist minister, emerged as one of the leaders of the mostly Protestant faction allied with Venice. Despite being a man of the cloth, he showed little reluctance to participate in acts of violence, including assassination and brutal murder. Among his victims were members of the influential “von Planta” family, local nobles who were closely allied with Spain. Keen on taking revenge, they forced Jenatsch into temporary exile. The former clergyman now had to live in Venice for some years and, in the end, became a professional soldier and military entrepreneur. This position turned out an important stepping stone for social advancement, and Jenatsch tried to persuade Ferdinand II, Emperor of the Holy Roman Empire, to grant him a title of nobility and a fief in the 1630s. He was about to achieve this goal when he was assassinated in a tavern in Chur, in 1639. By the time of his death, Jenatsch had undergone a profound change of identity, both religiously and politically, by converting to Catholicism. He had also put an end to
his close collaboration with France and had sought patronage and protection in Innsbruck and Vienna. In the 19th Century, Jenatsch became a sort of local and national (Swiss) hero, particularly after the famous novel Jörg Jenatsch by Swiss author Conrad Ferdinand Meyer (1825–1898) had been published in 1876 [3]. In 1987, a French-Swiss film adaptation (Jenatsch) by Daniel Schmid revived the story [4].

1.2. Exhumation of the skeleton in 1959

According to contemporary reports, Jenatsch was buried in the cathedral of Chur [5]. Due to subsequent renovation works and several rearrangements of the tomb slabs in the cathedral, however, the exact place of the tomb became unknown. The presumed Jenatsch grave was found in 1959 by Swiss anthropologist Erik Hug who identified the skeleton as Jörg Jenatsch on the basis of its clothing and of injuries to the head (Fig. 2). The skeleton was reburied in 1961, though without clothing and ornaments. Hug regularly reported his findings in public lectures but he never got round to publishing a scientific paper about this case. With Hug’s death in 1991, all documents of his Jenatsch research disappeared. A long adventurous quest was initiated by Manuel Janosa of the Grisons Archeological Service and involved, among others, Hug’s lawyer, an anthropologist friend of Hug and the dean of the Einsiedeln monastery. In 2009, Hug’s documents were eventually detected in a safe inside the monastery shop [5,6].

1.3. Re-exhumation of the skeleton in 2012

Based upon the rediscovered Hug documents, the exact place of the Jenatsch grave could be localized inside Chur cathedral. The documents also contained a blood-soaked piece of fabric, purportedly Jenatsch’s clothing, which ignited the idea of a kinship analysis. The fabric was analyzed at the University of Zurich (Institutes of Anatomy and Legal Medicine) and three male members of the Jenatsch family were traced. The Jenatsch family tree was reconstructed (Fig. 3) by historian and genealogist Paul Eugen Grimm. Unfortunately, no Y-STR profile could be generated from the blood stain, and the only way out of this deadlock was to collect new sample material. The bishop of Chur gave permission to exhume the skeleton again, which was done in March 2012.

The goal of the present study was to clarify whether the three male family members and the skeleton shared identical Y-chromosomal markers. This would argue strongly in favor of the skeleton belonging to the Jenatsch family and therefore, because no other male relative has ever been connected to the find, of being Jörg Jenatsch himself.

2. Materials and methods

2.1. DNA extraction

Three male descendants of a common ancestor shared with Jörg (named Anton Jenatsch) gave permission for genetic analysis aimed at confirming the authenticity of the skeletal remains. DNA was extracted from buccal swabs of both, the descendants and the excavator, using the QIAamp DNA Mini Kit (Qiagen).

Initially, an attempt was made to extract DNA from the bloodstains on the piece of clothing belonging to Jörg Jenatsch. An expert report from the Institute of Legal Medicine in Berne from 1959 attested that these spots were most probably blood [6], but at present no additional blood tests were performed. Samples were taken from at least two different locations using cotton swabs, and DNA was isolated with the QIAamp DNA Mini Kit. The extraction was performed twice following a DNA purification protocol for dried blood spots provided by the manufacturer, except for an increase of the volume of all buffers used before the washing steps, and of the incubation times.

From the historic skeleton, material from a bone (femur, diaphysis compacta) and a tooth (first right molar, M1/46, lower jaw) was subjected to DNA analysis. These samples were taken during the exhumation by two experienced researchers, with all necessary precautions. After UV radiation to decontaminate the surface, the samples were pulverized with a cryogenic mill (6770 Freezer/Mill™, SPEX SamplePrep). Two DNA extractions (bone B1, B2, B3 and tooth T1 powder) were performed at a dedicated ancient DNA laboratory (Center for Evolutionary Medicine, Institute of Anatomy, University of Zurich) with adequate precautions and negative controls. A third DNA extraction (bone B4 and tooth T2 powder) was performed at a forensic laboratory (Institute of Legal Medicine, University of Zurich), also taking appropriate care. To ensure the highest possible reliability, some of the most general and widely accepted guidelines for aDNA work were followed [7,8]. These included, for example, the use of negative controls and the analysis of multiple extracts per sample. As was to be expected, an inverse correlation was observed between the amplification efficiency and the size of an amplification product, reflecting the degradation and damage of the ancient DNA template. DNA was extracted either with phenol-chloroform and silico-column clean-up [9] (aDNA laboratory) or using an in-house method whereby the bone powder is first carefully decalcified [10], then extracted and purified with the QIAamp DNA Mini Kit (forensic laboratory).
2.2. Y-STR analysis

DNA extracts were amplified using the AmpFISTR Yfiler PCR amplification kit (Applied Biosystems AB, now Life Technologies) \[11\] and the PowerPlex Y23 kit (Promega) \[12\], according to the manufacturers' instructions. Analysis with the PowerPlex Y23 kit was performed in two different laboratories, namely at the Institute of Legal Medicine, University of Zurich, and the Institute of Legal Medicine, Charité Berlin. Amplicons of the PowerPlex Y23 loci were up to 425 bp in length, and 30 amplification cycles were run. PCR products were separated and detected with Genetic Analyzers 3500 (Zurich) or 3130xl (Berlin). One microliter of the amplified sample was added to 10 μl Hi-Di Formamide (AB) and 1 μl CC5 ILS 500 Y23 (Promega). The following electrophoresis conditions of operating the Genetic Analyzers were adhered to in Zürich and in Berlin (in brackets): polymer POP-4, 24 s (10 s) injection time, 1.2 kV (3 kV) injection voltage, 15 kV run voltage, 60 °C, 1270 s (1800 s) run time, Dye Set G5 (FL, JOE, TM-ET, CCR-ET, CC5). Raw data were analyzed with the Genemapper ID-X Software Versions 1.2 (1.1.1) (AB). A threshold of 50 RFUs was used for peak detection.

2.3. Y-SNP analysis

The Y-SNP analyses were performed at the Institute of Legal Medicine, Charité, Berlin. DNA extracts were amplified with self-designed multiplexes based upon the SNAPSHOTSTM technique (AB). The three multiplexes comprised 21 Y-SNPs sufficient to define the most common European haplogroups. Amplicon lengths of PCR multiplexes I-III were up to 340 bp, most of them were below 200 bp. The PCR and SBE reactions included 32 and 25 amplification cycles, respectively. PCR, SBE and clean-up reactions for multiplexes I and II were performed according to \[13\] and for multiplex III as follows: PCR: 3 μl multiplex Mastermix (Qiagen), 0.8 μl H₂O, 1.2 μl Primer mix (Table 1), 1 μl DNA were amplified 95 °C/15 min, 32× (94 °C/30 s, 57 °C/90 s, 72 °C/60 s), 72 °C/10 min. PCR clean-up: 2 μl ExoSAP IT and 5 μl PCR product were incubated 37 °C/60 min followed by 75 °C/15 min. SBE reaction: 1.8 μl H₂O, 1.5 μl SNAPSHOT Reaction mix, 1.2 μl Primer mix
Table 1
PCR and SBE primer sequences used for haplogroup R-specific multiplex III.

<table>
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<tr>
<th>SNP</th>
<th>Branch</th>
<th>Primers (5'-3')</th>
<th>Size (bp)</th>
<th>Amplicon (bp)</th>
<th>SNP</th>
<th>Conc. (µM)</th>
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<td>M157</td>
<td>R1a1b</td>
<td>F: GAGAGGATATCAAAATTTGGR: TAGCTTAAACACACAGTTC</td>
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<td>229</td>
<td>A/C</td>
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<td>M269</td>
<td>R1b1b2</td>
<td>F: TGGTACAAATAGAGGGR: AAGGGCGTGGGAGGGC</td>
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<td>152</td>
<td>T/C</td>
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<tr>
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</tbody>
</table>

SBE primers

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<th>Primer sequence (5'-3') target specific sequence black, neutral sequence gray</th>
<th>Size (bp)</th>
<th>Orientation typing</th>
<th>Conc. (µM)</th>
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<td>Reverse</td>
<td>0.18</td>
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<tr>
<td>M124</td>
<td>ACAACTTCATATTATATATAC</td>
<td>22</td>
<td>Reverse</td>
<td>0.18</td>
</tr>
</tbody>
</table>

(1 Table 1). 1.5 µl cleaned PCR product were amplified 25 × (96 °C / 10 s, 50 °C / 5 s, 60 °C / 30 s). SBE cleanup: 1 µl SAP and 6 µl SBE-product were incubated 37 °C/60 min followed by 85 °C/15 min. Purified SBE products were separated and detected with a 3130xl Genetic Analyzer. One microliter of the amplified sample was added to 15 µl Hi-Di Formamide and 0.1 µl of Size Standard LIZ 120 (all from AB). The following electrophoresis conditions were used for the 3130xl Genetic Analyzer: polymer POP-4, 22 s injection time, 2 kV injection voltage, 10 kV run voltage, 60 °C, 2000 s run time, Dye Set E5 (R110, R6G, TAMRA, ROX, LIZ). Raw data were analyzed with the Genemapper ID Software Version 3.2 (AB). A peak detection threshold of 50 RFUs was used for declaring positive results.

2.4. Biostatistics

The goal of the biostatistical analysis was to quantify how much more likely than not it was that the exhumed skeleton was Jörg Jenatsch. The necessary likelihood calculations were carried out twice, once following the exact approach of Kayser et al. [14] and once under a systematic reduction of the genotypic information used. Exact likelihood calculations require knowledge of the population frequencies of the haplotypes involved [14], and these are difficult to obtain for comprehensive, and therefore rare, haplotypes [15,16]. Moreover, nothing is usually known about the population frequencies of haplotypes at the time of origin of historic specimen. Therefore, only the seven loci defining the so-called ‘core haplotype’ [17,18] were included in the exact calculations. In a second analysis, we circumvented the problem of inaccurate haplotype frequency estimation by reducing the employed genetic information to mere mismatch counts (see below). Since, substantially less population data were available in the Y chromosome Haplotype Reference Database (YHRD) [19,20] for the 23 PowerPlex Y23 loci than for 17 Yfiler loci, the second analysis was based upon the Yfiler loci only. At the time of inquiry (release 42, 1 February 2013), YHRD included 23,445 haplotypes from western Europe for the seven core haplotype loci, 8134 entries for the Yfiler loci, but only 590 full PowerPlex Y23 haplotypes. Population frequencies of relevant haplotypes were estimated from these data by means of the augmented count estimate (k + 1)(n + 1), where k denotes the respective haplotype count and n is the database size. Likelihood calculations were based upon an average mutation rate of S = 10⁻³ for all Y-STRs, a figure that has been reported as an appropriate approximation in the literature before [21–23].

3. Results

3.1. DNA analysis

No Y-STR profile could be obtained from the bloodstains on the piece of clothing with the Yfiler kit, because of the low quality of the extracted DNA. The skeletal remains were of archeological origin so the DNA was degraded and present at low copy number, as expected. This notwithstanding, partial Y-STR and complete Y-SNP profiles could be generated (Tables 2 and 3).

Since initial tests with the PowerPlex Y23 kit provided better results for the bone samples than the Yfiler kit (data not shown), all subsequent analyses were performed with the former. Fourteen PCR amplifications revealed partial profiles that could be assembled into a complete PowerPlex Y23 profile, with reproducible results for each locus (Table 2). The PowerPlex Y23 profiles of the three living family members were concordant but differed from the PowerPlex Y23 profile of the skeleton at three loci, DYS456, DYS458 and DYS635, of which are also included in the Yfiler kit (Table 2). The only male involved in the 2012 exhumation was the excavator himself, but his PowerPlex Y23 profile was completely different from that of the Jenatsch males (Table 2). All other staff working with the skeleton was female, thereby obviating the risk of contamination. Extraction- and PCR-negative controls were all negative, except for one extraction negative control (NB3) that showed two single peaks (Table 2).

Y-SNP analysis yielded an identical haplogroup, R1b1b2a2 g, for Jörg Jenatsch and the three living family members (Table 3). The excavator carried a different Y-SNP haplotype (haplogroup I) of presumably northern European origin (Table 3). Extraction- and PCR-negative controls were all negative.

3.2. Biostatistics

We assumed that J0, the grandfather of the three genotyped males J1, J2, and J3 carried core haplotype 14-13-29-24-12-13-13 because his grandsons shared this haplotype (Table 2). Since the skeleton carried the same haplotype, the likelihood of the null hypothesis that the skeleton does not belong to Jörg Jenatsch’s male lineage equals

\[ L(H_0 : D) = g \cdot h, \]

where D denotes the genotype data, g is the current frequency of the haplotype in question, and h is its haplotype frequency in the
Table 2

Y-STR haplotypes of three living members of the Jenatsch family (J1, J2, J3), the excavator involved in the exhumation at Chur cathedral, and several pieces of bone (B1–B4) and tooth (T1 and T2) from the presumed Jenatsch skeleton.

The Y-STR analyses were performed at the Center of Evolutionary Medicine in Zurich (A), the Institute of Legal Medicine in Zurich (Z) and the Institute of Legal Medicine, Charité, Berlin (B). Alleles in brackets had peak heights below the peak detection threshold of 50 RFUs. N = extraction negative controls.

<table>
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<th>Sample</th>
<th>Extraction</th>
<th>PCR</th>
<th>Core set</th>
<th>Yfiler</th>
<th>PowerPlex</th>
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<td>Yfiler</td>
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<td>PowerPlex</td>
</tr>
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Reference samples

J1 A Z 14 13 29 24 12 13 13 11/15 15 12 14 19 15 15 11 24 22 12 13 17 19 10
J1 A B 14 13 29 24 12 13 13 11/15 15 12 14 19 15 15 11 24 22 12 13 17 19 10
J2 A Z 14 13 29 24 12 13 13 11/15 15 12 14 19 15 15 11 24 22 12 13 17 19 10
J2 A B 14 13 29 24 12 13 13 11/15 15 12 14 19 15 15 11 24 22 12 13 17 19 10
J3 A Z 14 13 29 24 12 13 13 11/15 15 12 14 19 15 15 11 24 22 12 13 17 19 10
J3 A B 14 13 29 24 12 13 13 11/15 15 12 14 19 15 15 11 24 22 12 13 17 19 10
excavator A Z 15 13 31 25 11 11 13 14/15 15 10 12 19 14 17 11 23 29 13 11 18 17 10
excavator A B 15 13 31 25 11 11 13 14/15 15 10 12 19 14 17 11 23 29 13 11 18 17 10

Extraction 1 (2 pieces of bone)

Bone B1 A B 13 (29/30) 12 13 11 14 19 (17) 23 22 17 19
Bone B1 A B No results
NB1 A B No results
Bone B2 A B 13 13 19 23,24 22 13 17,19 19
Bone B2 A B 13 16

Extraction 2 (bone and tooth)

Bone B3 A B 24 12 13 12 14 19 22 11 13 17
Bone B3 A B 13 12 13 14 19 22,(26) 12 13 17 19
Bone B3 A B No results
Bone B3 A B No results
Tooth T1 A B No results
Tooth T1 A B No results
NT1 A B No results
NT1 A B No results

Extraction 3 (bone and tooth)

Bone B4 Z Z 12 11/15 15 14 16 19 23 22 17 19
Bone B4 Z Z 14 13 29 12 13 13 11/15 15 14 16 19 23 22 13 17 19 10
Bone B4 Z Z 12 11/15 12 14 19 23 12 13 17 19
Bone B4 Z Z 13 29 24 12 13 13 11/15 14 16 19 23 22 12 13 17 19
Bone B4 Z Z 14 13 29 12 13 13 11/15 19 16 19 23 22 12 13 17 19
Bone B4 Z Z 13 29 24 12 13 13 (11/15) 12 19 19 23 22 17 19
Bone B4 Z Z 13 29 24 12 13 13 11/15 19 19 23 22 17 19
Bone B4 Z Z 14 13 29 12 13 13 (15) 12 19 19 23 22 17 19
Bone B4 Z Z 13 24 12 13 13 (15) 12 19 19 23 22 17 19
Tooth T2 Z Z No results
population of origin of the skeleton. Under the alternative hypothesis that the skeleton is in fact Jörg Jenatsch, it can be assumed that Anton Jenatsch, the most recent common ancestor (MRCA) of Jörg Jenatsch and J0, carried the same haplotype as the other males. Otherwise, multiple mutations would have to be invoked that yield only minor contributions to the overall likelihood. Thus, the likelihood of the alternative hypothesis (approximately) equals

\[ L(H_A : D) = f \cdot 0.995^{7 \times 12} = f \cdot 0.656, \]

where \( f \) is the haplotype frequency of interest in the population of origin of the MRCA and factor \( 0.995^{7 \times 12} \) reflects the lack of mutation at all 7 loci in all 12 meioses separating Jörg Jenatsch and J0 under the alternative hypothesis (Note: 0.995 equals one minus the average mutation rate of \( 5 \times 10^{-3} \)). Haplotype frequencies \( f \) and \( h \) were unknown but had to be approximated by current haplotype frequency \( g \), so that the likelihood ratio simplified to

\[ \frac{L(H_A : D)}{L(H_0 : D)} = \frac{g \cdot 0.656}{g^2} = \frac{0.656}{g} \]

Core haplotype 14-13-29-24-12-13-13 was observed 73 times among the 23,445 western European entries in YHRD. This yielded an augmented count estimate of \( g = 3.15 \times 10^{-3} \) and a likelihood ratio of 207.8. In other words, when only the core haplotype information is taken into account, it is >200 times more likely that the skeleton is Jörg Jenatsch than that it belongs to a different male lineage.

We also tried to make inferential use of the more comprehensive Yfiler data available to us (Table 2). At three of the additional loci, namely DYS456, DYS458 and DYS635, the skeleton and the (identical) haplotypes of the three grandsons of J0 showed a mismatch by one repeat. Inspection of YHRD revealed that neither these two haplotypes nor any of their most parsimonious intermediates were present in the database, rendering exact likelihood calculations potentially unreliable. Therefore, we choose to evaluate only the observed mismatch number and to disregard the actual haplotype information. Under the alternative hypothesis, a one-repeat mismatch at exactly three of 17 loci would arise in 12 meioses with probability

\[ L(H_A : D) = \left( \frac{17}{3} \right) \cdot 0.94^{14} \cdot 0.06^3 = 0.06176 \]

Here, 12 times \( 5 \times 10^{-3} = 0.06 \) (approximately) equals the locusswise probability of a single one-repeat mismatch arising in 12 meioses.

The likelihood of the null hypothesis, \( L(H_0 : D) \), was evaluated empirically by estimating, from the western European part of YHRD, the probability that two randomly drawn Yfiler haplotypes exhibit exactly three mismatches. Considering all haplotypes, this probability was found to be \( 6.44 \times 10^{-3} \). However, the Yfiler haplotype distribution in YHRD is heavily skewed in that the database contains 7512 singletons (92.4%). When only these haplotypes were taken into account, the probability of interest was estimated to be \( 3.08 \times 10^{-3} \). Relating the likelihoods of the two hypotheses to one another therefore implies that, taking the information for the 17 Yfiler loci and the three single step mutations properly into account, the alternative hypothesis is still 20.0 times more likely than the null hypothesis.

4. Discussion and conclusion

Our goal was to clarify, with the help of three living male members of the Jenatsch family, whether the skeleton exhumed

### Table 3

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from Chur cathedral is that of Jörg Jenatsch. The DNA analysis of an approximately 400 year old bone is challenging, and the success prospects clearly depended upon the conditions of the biological material. Fortunately, even though DNA from the presumed Jörg Jenatsch skeleton was degraded, a complete PowerPlex Y23 profile could be generated from all three extractions. The novel PowerPlex Y23 kit provided superior results compared to other, more common Y-STR kits. SNP-analysis was a less severe problem because small DNA fragments (mostly below 200 bp) were amplified.

Contamination, at least from the second exhumation, could be ruled out because the only male involved in handling the skeleton had completely different Y-STR and Y-SNP profiles. We were fully aware that the analyzed bones also could have been contaminated during the first exhumation, because bones used to be brushed with bare hands for cleaning and Erik Hug showed the original skull during public lectures and on television. However, the Y-STR and Y-SNP profiles of the skeleton and the three living members of the Jenatsch family were so similar that they clearly argued in favor of a blood relationship rather than (random) contamination.

The skeleton and the three living family members carried the same Y-SNP-haplogroup, R1b1b2a2g. In YHRD, R1b1b2a2g occurs in 132 of 2357 western- or middle-European (frequency: 5.6 × 10^-2), meaning that this haplotype is quite common in the target area. Therefore the match on its own did not provide sufficient evidence to allow reliable identification of the skeleton. Comparison of the PowerPlex Y23 profiles of the skeleton and the three living family members revealed three discrepancies and 20 matches. Bearing in mind that, under the hypothesis that the skeleton is that of Jörg Jenatsch, each of these mutations would have occurred in one of 12 meioses, such an observation may well have been compatible with the presumed identity. Indeed, conservative biostatistical evaluation of the data suggested that it was at least 20 times more likely than not that the Chur skeleton is Jörg Jenatsch. In addition, our calculations were based upon the 17 loci of the Yfiler kit only, due to the scarcity of population data, and did not allow for the fact that the profiles under study matched for six additional STRs. If the conservative assumption were made that the probability of observing exactly three mismatches between two unrelated western-European Y-chromosomal haplotypes is the same for the PowerPlex Y23 kit as for the 17 Yfiler loci, a likelihood ratio of 36 would emerge. Finally, two of the additional markers, DYS570 and DYS576, are rapidly mutating with mutation rates >10^-3 [24,25]. The fact that we did not find a mutation at any of these loci argues further for the presumed relationship. Since no other male relative has ever been connected to the find, our analysis therefore strongly suggests that the Chur skeleton is that of Jörg Jenatsch.

Our study highlights the power of Y-chromosomal analysis for the identification of male lineages, but also revealed some of its limitations. We demonstrated that distant family branches indeed can be traced back to common ancestors using Y-chromosomal data, even if some of the individuals involved lived hundreds of years ago. However, when it comes to the biostatistical evaluation, particularly of Y-STR data, the notorious lack of population data from the time and region of origin of the presumed forebears turns out a limiting factor. Marker sets in forensic use undoubtedly will be expanded in the future because additional markers are always useful for better discrimination. In addition, slowly mutating simple single-copy Y-STRs are advantageous for paternity testing and anthropological studies [25]. However, analyzing more and more loci will not necessarily add to the power of positive male lineage identification because the evidential value of matches becomes increasingly difficult to quantify when the haplotype in question gets too rare [15,16]. In this respect, the amount of information that Y-STRs can provide in terms of positive male lineage identification will likely obey a “law of diminishing return”.

The Jenatsch case belongs to a series of cases where particular historical hypotheses were tested genetically. These include the investigation of skeletal remains of the Romanov family, Russia’s last monarch ([1198] [26–28] and of Austria’s patron saint Leopold III (12th century) [29], of the putative skulls of Friedrich von Schiller ([1805] [30] and Wolfgang Amadeus Mozart ([1791] [31], and the recent identification of King Richard III of England ([1485] (press release of February 4th 2013 [32]). In addition to genetic testing, many of these remains were subjected to other state-of-the-art analyses. In the Jörg Jenatsch case, these included CT-based investigations, stable isotopes analyses for the reconstruction of diet and origin, and a re-evaluation of anthropological and pathological findings. Although many mysteries of history (fortunately) will never be solved, despite all the latest technologies available to scientists, the present study undeniably highlights the potential benefits of aDNA analysis for historic research.

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