Heliyon 8 (2022) e11731

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Research article

The genetic legacy of the Hunyadi descendants

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ARTICLE INFO

Keywords:
Ancient genomes
Hunyadi
Corvinus
Hungarian Nobel family

ABSTRACT

The Hunyadi family is one of the most influential families in the history of Central Europe in the 14th–16th centuries. The family's prestige was established by Johannes Hunyadi, a Turk-beater who rose to the position of governor of the Kingdom of Hungary. His second son, Matthias Hunyadi, became the elected ruler of the Kingdom of Hungary in 1458. The Hunyadi family had unknown origin. Moreover, Matthias failed to found a dynasty because of lacking a legitimate heir and his illegitimate son Johannes Corvinus was unable to obtain the crown. His grandson, Christophorus Corvinus, died in childhood, thus the direct male line of the family ended.

In the framework of on interdisciplinary research, we have determined the whole genome sequences of Johannes Corvinus and Christophorus Corvinus by next-generation sequencing technology. Both of them carried the Y-chromosome haplogroup is E1b1b1a1b1a6a1c ~, which is widespread in Eurasia. The father-son relationship was verified using the classical STR method and whole genome data. Christophorus Corvinus belongs to the rare, sporadically occurring T2c1+146 mitochondrial haplogroup, most frequent around the Mediterranean, while his father belongs to the T2b mitochondrial haplogroup, widespread in Eurasia, both are consistent with the known origin of the mothers. Archaeogenomic analysis indicated that the Corvinus had an ancient European genome composition.

Based on the reported genetic data, it will be possible to identify all the other Hunyadi family member, whose only known grave site is known, but who are resting assorted with several other skeletons.

1. Introduction

One of the most important periods in the history of Hungary is the few decades known in Hungarian historiography as the Hunyadi era, when Johannes Hunyadi (1407?–1456) and his son Matthias Hunyadi (1443–1490) successfully confronted the astonishingly rapidly expanding Ottoman Empire seeking to conquer Europe, and stopped them at the southern borders of Hungary. This significant feat earned them great fame and for Hungary the title of the Bulwark of Europe and of Christendom (Bárány and Györkös, 2009). The name Hunyadi became

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https://doi.org/10.1016/j.heliyon.2022.e11731
Received 4 March 2022; Received in revised form 11 October 2022; Accepted 11 November 2022

equivalent with the meaning of "leader, conqueror" in 16th Century English and Greek (Rászlai, 1994). The heroic deeds of the Hunyadis also made them folk heroes for Hungarians as well as Italians, Serbians, Croatians, Slovenians, Slovaks, Czechs, Ruthenians and Romanians (Magyar, 2021).

Johannes Hunyadi earned himself fame as an exceptionally talented general of Sigismund of Luxembourg, King of Hungary (1387–1437), and Holy Roman Emperor (1433–1437). He quickly rose through the ranks both in the military and the political arena: he became the biggest landowner of the country and used his significant resources to spearhead the defence against the Turks as commander in chief and from 1446 as Governor of the Kingdom of Hungary (Petrovics, 2010). Since he won almost all his battles, he was very popular. His last and perhaps most important battle was fought in July 1456 against the Ottoman armies at Nándorfehérvár (present day Beograd, Serbia) (Pálosfalvi, 2018). The bells tolling at noon are, to this day, a daily commemoration of this victory (Kovács, 2007). Johannes Hunyadi died from the plague three weeks after the Battle of Nándorfehérvár, which ended in victory for the Hungarians (Kubinyi, 2008).

The idea that one of his two sons, Ladislaus and Matthias, who received humanist education alongside their military training, could possibly occupy the Hungarian throne emerged while Johannes Hunyadi was still alive. However, after his untimely death, his older son was executed by King Ladislaus V (1453–1457). The king died shortly thereafter, and the Hungarian general Diet did elect Matthias, the younger Hunyadi as King of Hungary. Matthias, who took the throne as a *homo novus*, became one of the most significant monarchs of his age. Relying on his diplomatic skills and his Black Army, one of the best organized and combat-ready armies in Europe, he not only defended the southern borders of the country against a global empire, but also expanded the territories of the country: he conquered the eastern provinces of Austria and a part of Bohemia (Kubinyi, 2008). Matthias' name is still remembered around the world due to his patronage of literature, arts and sciences often praised by Italian humanists (Feuer-Tóth, 1990), and his founding of Bibliotheca Corvinus, the humanist royal library regarded in the 15th Century as the second largest European collection after the Library of Vatican (Csapodi and Csapodi-Gárdonyi, 1981).

Since he did not have an offspring from his wife, Beatrice of Aragon, Matthias intended to make his only and illegitimate son, Johannes Corvinus (1473–1504) his successor. After his sudden, unexpected death he was buried at the basilica of Székesfehérvár, the coronation and burial place of the Hungarian kings since the 11th century (Engel, 1987). Unfortunately, the Basilica was annihilated during and after the Turkish occupation of Hungary and his tomb was lost. His son was sidestepped after his death and the crown was bestowed upon Vladislaus II of the Jagiellon dynasty. Johannes Corvinus was given the title of Duke of Dalmatia, Slavonia and Croatia and continued to excel himself in the defence of the Hungarian border against the Turks. After his death in October 1504, he was put to eternal rest, according to his wish, in the Pauline monastery of Lepoglava. Nearly two years later his son, Christophorus, who was hardly six years old, also passed and was buried next to him. With him the Corvinus lineage ended (Schönherr, 1894).

The origin of the Hunyadi family were already in the focus of speculation in their day. According to most contemporary sources, he was the member of a noble family of Wallachian ancestry. However, there were several legends in circulation, especially during the reign of Matthias Rex. One of the best-known stories was created by Italian humanists and polished by Antonio Bonfini (†1502), which connected the Hunyadi family paternally to the Roman Corvinus family. On the other hand, Bonfini also recorded the oral tradition that Johannes Hunyadi was the illegitimate son of Sigismund of Luxembourg King of Hungary (1387–1437) and Holy Roman Emperor (1433–1437) (Kulcsár, 1993). Historians have tried to establish the veracity of these legends, but written sources do not allow us to clearly establish either the maternal or paternal origin of János Hunyadi.

In recent years, there has been an increasing emphasis in archaeogenetic research to identify the genetic origins of famous historical families. Papers were published on the genetic origins of Romanovs (Rogaev et al., 2009), Briger Magnusson, founder of Stockholm (Malmström et al., 2012) and Richard III (King et al., 2014). In Hungary, two members of the founding Árpád Dynasty were identified (Olasz et al., 2019), and their phylogenetic origins were elucidated (Nagy et al., 2021).

In this study, we aim to investigate the biological relatedness between the individuals buried in the Corvinus grave in the church of the Immaculate Conception of the Blessed Virgin Mary in Lepoglava and to define their genetic composition. This information will be crucial for possible identification of the remains of Matthias Rex from among the remains stored in the ossuary at Székesfehérvár.

2. Methods

2.1. Archaeological and anthropological examination

Radiocarbon analysis was performed to confirm the archaeological dating of the remains, i.e., to exclude the possibility of mixing up the bones from a post-medieval burial. The sampled rib fragment was measured in the Radiocarbon AMS facility of the Center for Applied Isotope Studies, University of Georgia. The conventional radiocarbon data was calibrated with the OxCal 4.4 software with IntCal 20 settings(Reimer et al., 2020).

Standard macromorphological methods were used during the osteoarchaeological examination. Age at death estimation was based on complex methods, such as the cranial suture closure (Rösing, 1977), the changes of the auricular surface of the ilium (Lovejoy et al., 1985), the changes of the pubic symphyseal surface (Brooks and Suchey, 1990), the epiphyseal closure (McKern and Stewart, 1957), the long bone length (Stloukal and Hanaková, 1978), and the teeth eruption (Ubelaker, 1999). The probable sex of the adult individual was estimated with the Éry-Kralovánszky-Nemeskéri method using standard macromorphological traits. However, the sex of the subadult is undeterminable based on these since the manifestation of secondary gender traits is incomplete (Éry et al., 1963). In addition, lesions described in the historical record (Schönherr, 1894) were used for personal identification during the paleopathological investigation which was based on the work of Otner (Ortner et al., 2003).

2.2. DNA extraction

Bone powder samples were collected from the petrous bone of skulls base (Sirak et al., 2017) and the molar roots at the burial site at Lepoglava, Croatia (Supplementary Material). After sample collection all pre-PCR steps were carried out in dedicated ancient DNA facilities at the Department of Archaeogenetics of the Institute of Hungarian Research and Department of Genetics, University of Szeged, Hungary. Details concerning the ancient DNA purification and library preparation method are given in (Neparáczki et al., 2017). DNA extraction quantity measurements were performed with the Qubit fluorometric quantification system. Five different DNA extractions were performed, three from Johannes Corvinus (two from pars petrosa bone powder and one from tooth root) and two from Christophorus Corvinus (one form pars petrosa bone powder and one from tooth root).

We estimated the endogenous human DNA content of each library based on low coverage shotgun data generated on iSeq 100 (Illumina) platform. The whole genome sequencing was performed on NovaSeq 6000 Systems (Illumina) using paired-end sequencing method (2 × 150 bp) following the manufacturer's recommendations.

2.3. STR analysis

PCR amplification for Y-STRs and Taqman assay for Y-SNPs were used as before (Dudás et al., 2019). DNA was amplified using the Promega

PowerPlex Y23 amplification kit for the aDNA samples according to the manufacturer's instructions. Fragment sizes and allele designations were determined with an ABI3500 Genetic Analyzer and GeneMapper ID-X v.1.4 software. For testing Y-SNP markers, amplifications of aDNA with TaqMan probes and the analysis of relative fluorescence of the PCR products were performed in an ABI 7500 Real-time PCR instrument using SDS.1.2.3 software as described in the manufacturer's manual.

We compared our STR data the public available database (yhrd.org) of world-wide populations for forensic geneticists and researchers that generates reliable Y-STR haplotype frequency estimates for Y-STR haplotypes to be used in forensic casework and kinship analysis. The forensic community has been proactive in establishing large quality-assured and publicly accessible databases of Y-haplotypes to support these issues.

2.4. NGS data processing

The adapters of paired-end reads were trimmed with the Cutadapt software (Martin, 2011) in paired-end mode. Sequences shorter than 25 nucleotides were removed. The datasets were aligned to GRCh37 (hs37d5) using Burrow-Wheels-Aligner (v 0.7.17) using the MEM command with reseeding disabled. Only properly paired primary alignments with ≥90% identity to reference were considered in all downstream analyses. Sequences for different lanes were merged by samtools (Li et al., 2009). PICARD tools (Wysoker et al., 2013) were used to mark duplicates and the mergeReads task with the options "updateQuality mergingMethod = keepRandomRead" from the ATLAS package (Link et al., 2017) to merge PE reads in the BAM files.

Ancient DNA damage patterns were assessed using MapDamage 2.0 (Jónsson et al., 2013) and read quality scores were modified with the Rescale option to account for post-mortem damage. Biological sex was assessed by the method described in (Skoglund et al., 2013). Mitochondrial genome contamination was estimated using Schmutzi software package (Renaud et al., 2015). Contamination for the male samples was also assessed by the ANGSD X chromosome contamination method (Rasmussen et al., 2011).

Mitochondrial haplogroup (Hg) determination was performed using HaploGrep (Weissensteiner et al., 2016). Mitogenome phylogenetic analysis was described in (Maár et al., 2021). Y chromosome haplogroup determination was performed using Yleaf (Ralf et al., 2018).

Haploid calling of whole genome samples were performed by the application of the ANGSD software package (version: 0.931-10-g09a0fc5) (Korneliussen et al., 2014) using the "-doHaploCall 1 -doCounts 1 -sites" options and the HumanOrigins and 1240 K site coordinates of the Reich laboratory datasets. Identified variants were lifted over to plink format. The relatedness analysis of the samples was performed on 1240 K datasets of the Reich laboratory by the pcangsd software package (version 0.99) (Meisner and Albrechtsen, 2018) using the "-inbreed 1 -kinship" options and.

Sequence data from different libraries of the same individuals were merged because they belonged to the same haplogroup at the individual level and were also mapped to a same site on the PCA. The newly produced aligned sequence data of the merged samples for the two individuals were deposited to the European Nucleotide Archive (http://www.ebi.ac.uk/ena) under the accession number: PRJEB47418.

2.5. Archaeogenomic analyses

Analysing the genetic affinity between our historical individuals and other present-day populations of interest, we used the smartpca tool from the Eigensoft package (Patterson et al., 2006), with the "lsqproject: YES" option. For the PCA background we used the pseudo haploid data of a set of Eurasian populations (Supplementary Table s1) from the Reich Lab Human Origins dataset. All samples were projected by the least square method.

Genome structure was assessed with unsupervised ADMIXTURE (Alexander et al., 2009) using Reich Lab Human Origins dataset. Closely related samples were excluded, and just samples with at least 50,000 overlapping SNP polymorphisms were used. After pruning the dataset for linkage disequilibrium in the plink software with the option—indep-pairwise 200 25 0.4 we ran 1000 replicates of the analysis for each K value (i.e., number of ancestral populations) between 2 and 8, and then examined the replicates with the lowest cross-validation error.

Outgroup-f3 tests were used to estimate shared drift between individuals/populations from 1240 K datasets of the Reich laboratory with the software qp3Pop from the AdmixTools package (Patterson et al., 2012).

Table 1. Summary of NGS data. Additional details are provided Supplementary Table s2. Total reads mapped to GRCh37 (million) are properly paired primary alignments with ≥90% identity to the reference genome.

Sample identifier	Johannes Corvinus	Christophorus Corvinus
Avg. coverage over genome (fold)	9.73	3.29
Avg. X chromosome coverage	5.35	1.83
Avg. Y chromosome coverage	3.84	1.51
Avg. mitochondrial coverage (fold)	1658.45	2287.22
Number of mitochondrial bases not covered	0	0
Age estimation (C14)	1459-1525; 1559-1632	1459-1525; 1559-1632
Y chromosome haplogroup (ISOGG, Yleaf)	E1b1b1a1b1a6a1c~	E1b1b1a1b1a6a1c~
Mitochondrial Hg (HaploGrep)	T2b	T2c1+146
Estimated X contamination (%)	0.43	0.51

3. Results and discussion

3.1. Archaeological and anthropological consequences

Carbon dating studies:

According to the radiocarbon analysis (conventional radiocarbon age is 360 ± 20), the sample can be dated between 1459 and 1632 CE with (95,4% probability). Within this time range, the probability for between 1459 and 1525 is 48,5% and for between 1559 and 1632 is 46,9%. Knowing the limits of the radiocarbon dating, the analysis confirmed the historical and archaeological dating of the sample (Table 1 and Supplementary Material).

Anthropological characteristics:

The state of preservation of the osteological material of Johannes Corvinus (Figure 1A) was rather good, except for a few areas where the surface of the bones was *post mortem* damaged.

According to the cranial suture closure, age at death was 29–35 years (Rösing, 1977; Vallos, 1937). However, the reliability of suture maturation methods for age at death estimation is questionable (Gruspier and Mullen, 1991). Because pathological conditions were detected on the pelvic bones, the examination of age-dependent characteristics of this region was problematic. Therefore, the assessment of the pubic symphyseal surface had to be excluded. Based on the examination of the auricular surface (Lovejoy et al., 1985), the age at death is between 30 and 39 years. However, this area was also slightly affected with pathological changes and post mortem damage, therefore we should be cautious with these results. Since the fusion of the epiphyseal flake was incomplete on the sternal end of the clavicle, according to McKern and Stewart (1957), the age at death can be estimated around the late twenties.

Due to pathological alterations of the pelvic bones and post mortem damages of the cranial base some of the morphological traits should be

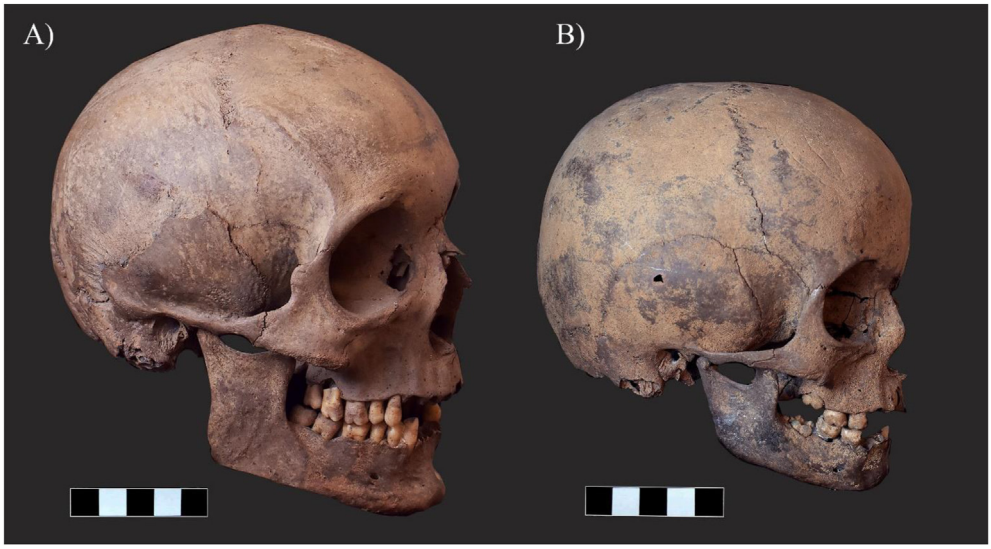

Figure 1. The cranium of A) Johannes Corvinus and B) Christophorus Corvinus from the right lateral view.

excluded during the sex determination. Based on 9 well observable sexual dimorphic skeletal traits the sex of the individual was male.

The paleopathologicals analysis of the bones revealed serious alterations of the left hip joint. These observations correspond to the written sources on the childhood trauma of Johannes Corvinus (Schönherr, 1894).

The fragmentary skeleton of Christophorus Corvinus revealed *post mortem* damages on the distal and proximal ends of the long bones, moreover the major part of the left facial bones was missing.

The age at death of Christophorus Corvinus (Figure 1B), was seven years (+/− 24 months) based on teeth eruption (Ubelaker, 1999) and approximately 7–8 years according to the long bone measurements (Stloukal and Hanáková, 1978). No pathologic changes cloud be detected on the observed skeleton.

The results of the osteoarchaeological examination (age at death of the individuals, sex and pathological changes of the adult individual) support the assumption that the skeletal remains from the ossuary of the church of the Immaculate Conception of the Blessed Virgin Mary in Lepoglava belonged to Johannes Corvinus and Christophorus Corvinus.

3.2. Uniparental data

3.2.1. Y chromosomal data (STR and Y chromosomal Hgs)

We obtained a full Y-STR haplotype profile from both aDNA samples using the PowerPlex Y23 PCR amplification kit (Promega, Madison, USA) (Supplementary Table s2). As the haplotype from the two individuals were the same, it confirms the assumption that the two individuals could be close paternal relatives. According to the statistical evaluation calculated (Supplementary Material) based on Y-chromosomal DNA tests, the probability that the two samples tested are from a shared paternal ancestry is 99.996%, which corresponds to "practically proven" oral statement.

We searched this haplotype consisting of 23 Y-STR loci for a hit in the YHRD database (www.yhrd.org, downloaded June 28, 2021, release R64) and found no matches among 23,998 haplotypes. Reducing the locus number to 17 (Y-filer loci) also failed to provide hits. Further reducing the locus set to 12 loci (PowerPlex Y kit) resulted in only one hit out of 296,798 haplotypes indicating that the remains have a rare haplotype.

Based on haplotype prediction, both samples can be classified into haplogroup E-M78 (E1b1b1a1) which was confirmed by testing the M78 SNP marker.

The E-M78 haplogroup may have been formed about 13,400 years ago (Adamov et al., 2015). Remains belonging to the E-M78 subgroup, dating from about 7000 years ago, were discovered in Avellaner cave, Spain (Lacan et al., 2011). Another E-M78 sample from the Sopot culture was found in Hungary (5000-4800 BCE) (Szécsényi-Nagy, 2015). This indicates that E-M78 men most likely arrived with Neolithic farmers from the Fertile Crescent to Europe and even Asia (Battaglia et al., 2009). Within a few centuries, haplogroup E-V13 became one of the most widespread male lineages in Europe, reaching far beyond the borders of Europe and the Mediterranean, as Asia (Cruciani et al., 2007).

After the STR study, a deeper classification was performed from whole genome sequencing data. The Corvinus were derived for the E1b1b1a1b1a6a1c~ haplogroup, based on SNPs BY4281 and BY4330 (Table 1 and Supplementary Table s3).

Ancient samples with paternal Hg E1b1b1a1b1a6a1 probably have widespread geographical and chronological distribution. One was excavated in Medieval Sardinia (Marcus et al., 2020) and another one was derived from the Otrar-Karatau culture of the Iron Age Kazakh steppe (Gnecchi-Ruscone et al., 2021), both sample belonged to: E1b1b1a1-b1a6a1~; E-CTS9320. The same sublineage of E-V13 (E1b1b1a1b1a) had been detected in the Carpathian Basin in Avar individuals (650–675 AD), elite Hungarian Conquerors (895–950 AD) (Neparáczki et al., 2019), and in a Medieval Hungarian nobleman (Nagy et al., 2021; Olasz et al., 2019) (Table 2).

3.2.2. Mitogenome analysis

The mitochondrial sequence of Johannes Corvinus belongs to haplogroup T2b with the unique polymorphism 3828G (Supplementary Table s4). The earliest representatives of Hg T2b haplogroup were detected in North-western Anatolia early Neolithic (ca. 6500 BC) individuals (Mathieson et al., 2015), indicating that T2b was already present among farmers in the Middle East before their arrival to Europe. Subsequently it was spread in southern Europe and later Neolithic farmers spread it throughout Europe (Pala et al., 2012).

Phylogenetic analysis using Median-Joining network revealed that the closest sequence matches to our T2b lineage are found in three Neolithic LBK individuals; one Bronze Age Bell Beaker and two early medieval samples from Germany; two Bronze Age samples from Great Britain; two Bronze Age Trzciniec samples from Poland, a Neolithic sample, which belongs to Lengyel culture from Hungary; a Bronze Age sample from Lithuania; a Late Chalcolithic sample from Turkey; two Longobard samples from Italy; one Punic sample from Spain; a medieval

Table 2. Details of the archaic samples which are closest Y chromosomal haplogroups.

Sample ID	Y ch. Haplogroup	Markers	Time period	References
Closest Y Hg' samples around the world				
KNT001.A	E1b1b1a1b1a6a1~	CTS9320	245–343 AD	Gnecchi-Ruscone et al. (2021)
SNN001	E1b1b1a1b1a6a1~	CTS9320	1300–1400 AD	Marcus et al. (2020)
Closest Y Hg' samples from the Carpathian Basin				
SzK/239	E1b1b1a1b1a	V13	650–675 AD	Neparáczki et al. (2019)
K2/6	E1b1b1a1b1a	V13	895–950 AD	Neparáczki et al. (2019)
HU53	E1b1b1a1b1a	L542	Not available	Olasz et al. (2019), Nagy et al. (2021)

sample from Finland; and one medieval sample from Romania (Supplementary Material).

Johannes Corvinus's maternal lineage probably originated from the Middle East with the spread of farming, and over time it became a common, widespread haplogroup throughout Eurasia.

Christophorus Corvinus's mitochondrial DNA was classified into the haplogroup T2c1+146 with the following private SNP polymorphisms: 200G, 783G, 9524G, 11914A and 12346T (Supplementary Table s4). The T2c1 maternal haplogroup is most likely of Middle Eastern origin (Pala et al., 2012). The maternal haplogroup of T2c1+146 was found to be predominant in Copper and Neolithic remains in Hungary (Lipson et al., 2017) and in the Middle Eastern remains from Bronze and Copper Age from Israel (Agranat-Tamir et al., 2020), Syria and Turkey (Skourtanioti et al., 2020), from Neolithic remains in Italy (Amorim et al., 2018) as well as from an LBK individual excavated in Germany (Haak et al., 2015).

Based on phylogenetic analysis, we can say that the T2c1+146 maternal lineage has been a relatively rare haplogroup in the past and has been present mainly in the Middle East and parts of Europe (Supplementary Material). Median-Joining network revealed that the closest sequence matches (6 nucleotides apart) can be found in Copper Age individuals from Turkey and Syria. In addition, a closely related linage was detected in an individual from the territory of the Copper Age Hungary, an individual from the territory of the Bronze Age Israel, and another individual from the LBK culture in Germany.

These results indicate that the maternal line of Christophorus Corvinus is an ancient branch from the Middle East, derived from early farmers, which was already present in Hungary in the Neolithic era. These data are in line with historical records about the origin of Beatrix Frangepán, the mother of Christophorus Corvinus, who had Mediterranean descent, related to the Aragon and Castile dynasty (Engel, 2001).

3.3. Archaeogenomics analyses

The whole genome sequence of the two individuals was tested for relatedness with the PCAngsd program, and we obtained 0.2437 value, which is very near to the 0.25 expected value for first-degree relatives if we compare pseudo-haploid genomes.

Genomes of Johannes Corvinus and Christophorus Corvinus map to the European side on the PCA plot, Christophorus is somewhat shifted southwards from his father, due to the Mediterranean ancestry received from his mother (Figure 2).

Unsupervised Admixture gave lowest cross-validation value at K = 7 (Supplementary Table s5). As kinship analysis indicated first degree relation between the two Corvinus, just Johannes Corvinus was left in the

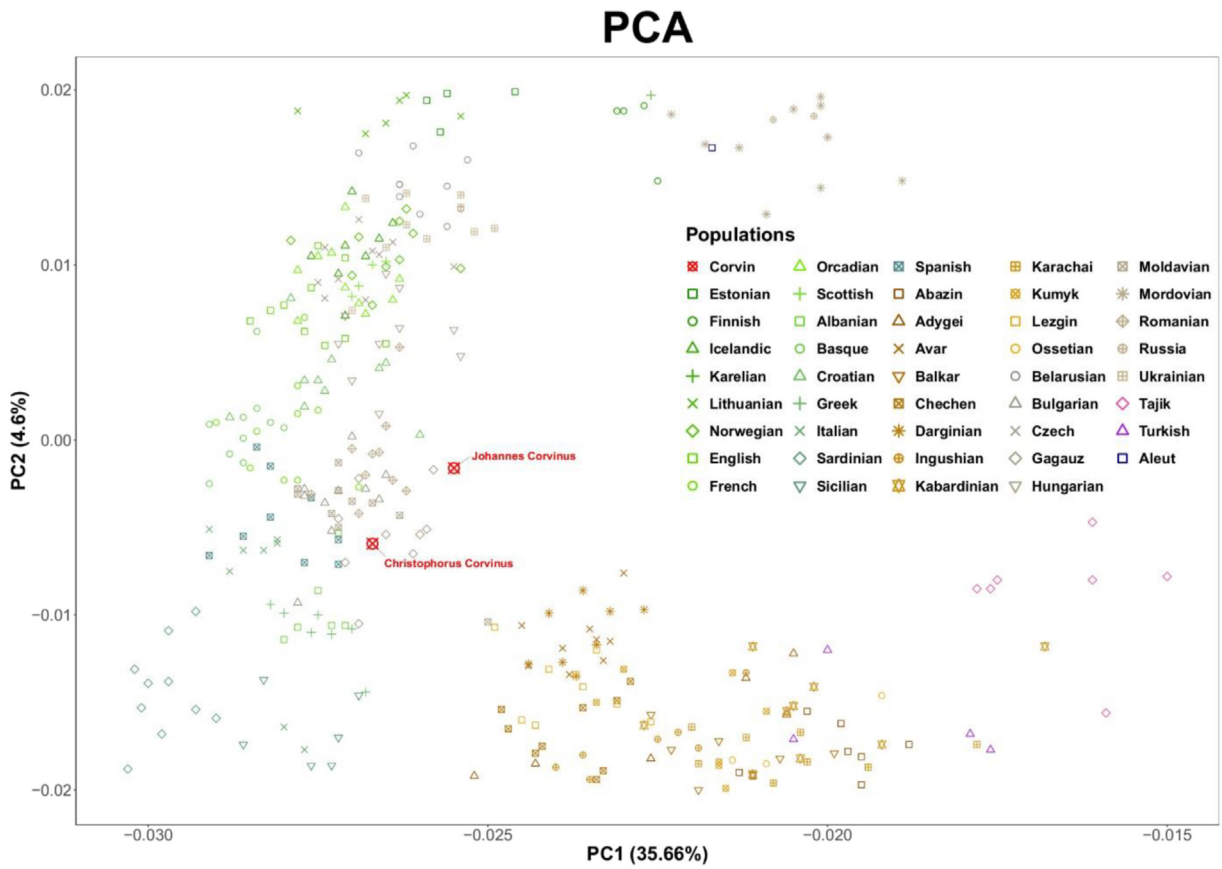

Figure 2. PCA analysis, genomes of Johannes Corvinus and Christophorus Corvinus were projected on modern European background. Studied samples are highlighted in red colour.

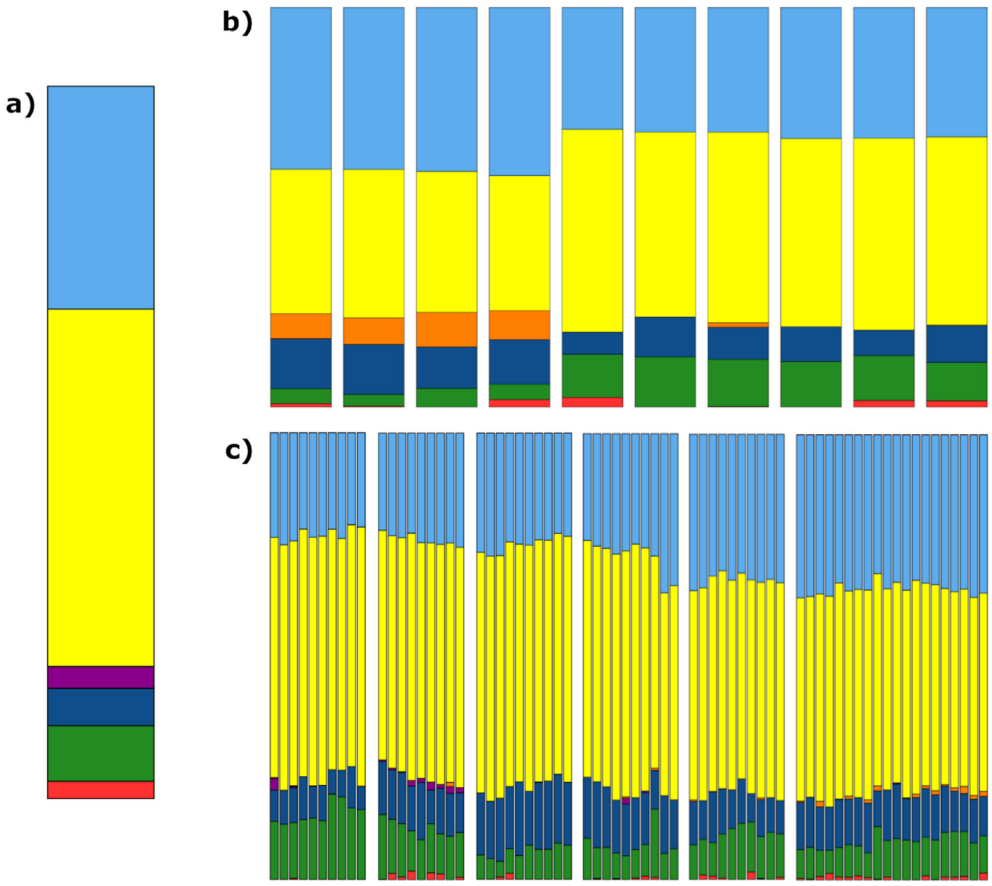

Figure 3. Model-based ancestry estimates of Corvinus with ADMIXTURE, K = 7; a = Corvinus; b = the closest clustered individuals to Corvinus from left to right: Vologda Oblast, Russia; Vologda Oblast, Russia; Mordovian; Mordovian; Romanian; Croatian; Hungarian; Croatian; Croatian and Romanian; and c = the closest clustered populations to Corvinus from left to right: northern Italy; Spain; Basque; France; Croatians and Hungarians; colours indicate the admixture component: blue = Ancient North Eurasian, yellow = Neolithic Anatolian, pink = Early Bronze Age, dark blue = Western Hunter Gatherer, green = Neolithic Iranian, orange = Nganasan and red = Han (Supplementary Table s5).

Admixture analysis. The Corvinus' genome contain the following Admixture component 50% Neolithic Anatolian, 31% Ancient North Eurasian, 8% Iranian Neolithic, 5% Western Hunter gatherer, 3% Early Bronze Age and 2% Han (Figure 3a). At the individual level, the top 10 most similar samples are from Russia (two Mordvinian and two Russian Vologda Oblast samples), three Croatians, two Romanians and one Hungarian individual (Figure 3b). Though in these most similar individuals on Figure 3b minor components show obvious differences,

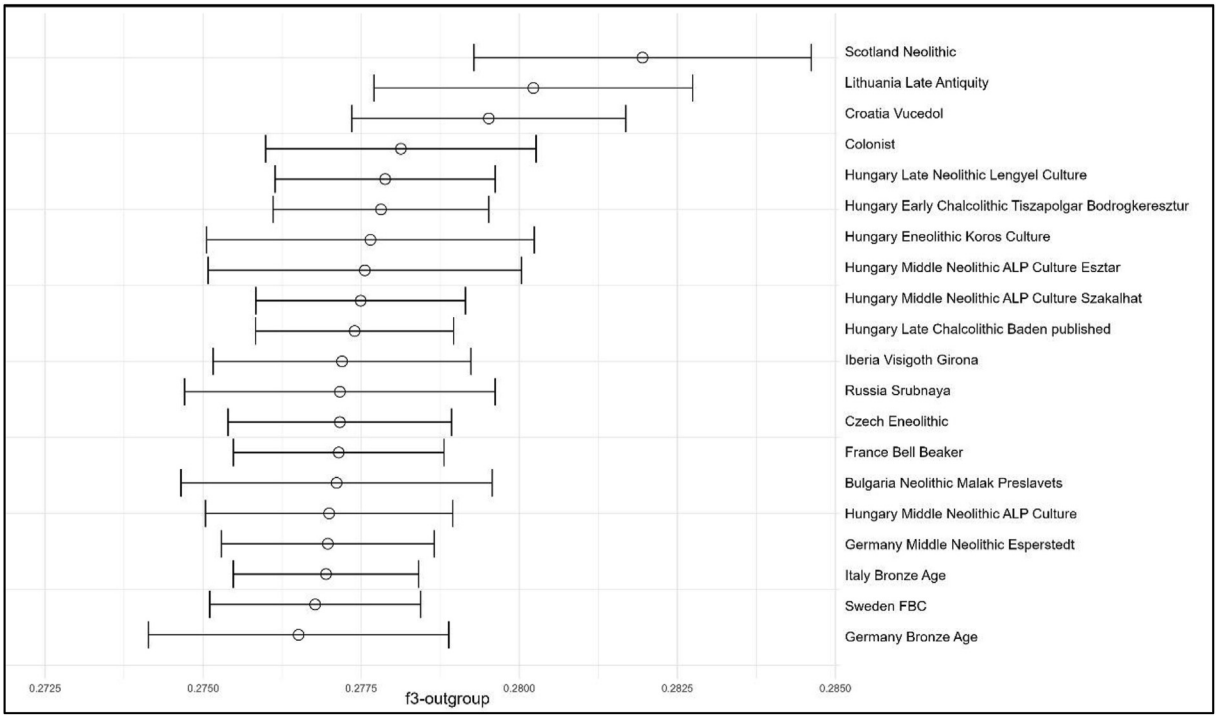

Figure 4. f3 outgroup statistics in the from f3 (Mbuti; Johannes Corvinus, Y).

nevertheless they are clustered closest due to the similar proportion of their major components, compared to other individuals with identical components in different proportions. At the population level the Corvinus genome clustered with populations from northern Italy, Spain, Basques, France, Croatians and Hungarians (Figure 3c). The genome of the medieval Corvinus show the greatest similarity to the genomes of today's southern European and Carpathian Basin populations, but we can also find individuals with similar genome compositions in the Eastern European steppe.

According to f3-outgroup statistics the Corvinus' genomes have the highest shared drift with Neolithic European samples, Hungarian Neolithic samples Lengyel, Bodrogkeszetúr, Kőrös, ALP appearing in the top list. This clearly shows that the majority genome components of the Corvinus were present in the Carpathian Basin thousands of years ago, which is in agreement with Admixture results (Figure 4).

Next to its Neolithic heritage, conspicuously, the genome of Johannes Corvinus's son, Christophorus Corvinus, has outstanding shared drift with a sample from the Croatian Copper Age Vucedol culture (Supplementary Material), which is in line with a higher Mediterranean heritage, received from the mother, also seen on PCA and supported by historical data.

4. Conclusion

We have successfully identified the DNA profile of the last two male members of the renowned Central European Hunyadi family, who have an ancient Neolithic genetic heritage at the genomic level. The Y-chromosomal E1b1b1a1b1a6a1c ~ (E-BY4281) haplogroup, which characterizes the Hunyadi family, will provide clues for the attempt to identify the remains of Matthias Hunyadi, among the remains from the ossarium adjacent to the site of the destroyed basilica at Székesfehérvár, Hungary.

Declarations

Author contribution statement

Endre Neparáczki: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Luca Kis, Zoltán Maróti, Pamjav Horolma: Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Bence Kovács: Performed the experiments; Analyzed and interpreted the data.

Balázs Tihanyi, Péter L. Nagy, Kitti Maár, Gergely I. B. Varga, Oszkár Schütz, Eszter Dudás: Analyzed and interpreted the data.

Vesna Pascuttini-Juraga, Ivančica Peharda, László Tamás Vizi, Gábor Horváth-Lugossy: Contributed reagents, materials, analysis tools or data.

Attila Gyenesei: Performed the experiments.

Miklós Makoldi: Performed the experiments; Wrote the paper.

Éva Teiszler, Tibor Török: Analyzed and interpreted the data; Wrote the paper.

Miklós Kásler: Performed the experiments; Wrote the paper.

Funding statement

Dr. Endre Neparáczki and Luca Kis were supported by Nemzeti Kutatási Fejlesztési és Innovációs Hivatal [TUDFO/5157-1/2019-ITM; TKP2020-NKA-23 & K 125561].

Data availability statement

Data associated with this study has been deposited at European Nucleotide Archive (http://www.ebi.ac.uk/ena) under the accession number PRJEB47418.

Declaration of interest's statement

The authors declare the following conflict of interests: Péter L. Nagy is sole owner of Praxis Genomics LLC was not directly involved in the design and execution of the experiments of the manuscript. This affiliation does not alter our adherence to Heliyon policies on sharing data and materials. All other authors have no conflict to declare.

Additional information

Supplementary content related to this article has been published online at https://doi.org/10.1016/j.heliyon.2022.e11731.

Acknowledgements

János Dezső, the director of Liszt Institute – Hungarian Culture Center in Zagreb, help with communication. Ivica Cujzek Parish of Varaždin, Diocesan Representative, conducting worthy and ethical research. For assistance to Péter Urbán and Gálik Bence during the sequencing. We are also grateful to Szabolcs Tóth for his administrative work.

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