

Y-Chromosomal Profile and Mitochondrial DNA of the Chevalier Bayard (1476?-1524)

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Abstract

Objective: We report the results of Y-chromosomal profile and mtDNA (mitochondrial DNA) of the Chevalier Bayard (1476?-1524). **Methods:** His genomic DNA was extracted from a tooth of his mandible. His Y-STRs profile was obtained using the AmFirst identifier PCR amplification kit. The mtDNA genomic sequence intervals for *HVR1* and *HVR2* were amplified by PCR, with specific primers. **Results:** We obtained the complete STR (Short Tandem Repeats) profile, based on fourteen STRs (DYS19, DYS385.a, DYS389.I and .b, DYS390, DYS391, DYS392, DYS393, DYS438, DYS439, DYS448, DYS456 and DYS458 and Y-GATA-H4). The deduced Y-STRs profile corresponds to the sub-clade S21 of the major European haplogroup **R1b-M269** (the “Germanic” haplotype). There are six mutations (16093C, 16211T and 16519C in the *HVR1* sequence, 263G, 309.1C and 315.1C in the *HVR2* sequence) in the mtDNA of Bayard. The 263G mutation determines the **H** mtDNA haplogroup and the 16211T suggests the **H5** sub-clade of the **H** haplogroup (a sub-clade found at >8% frequency in France, at the periphery of the Alpine arch region). This sub-clade **H5** (subsequently assimilated to the **H10e** haplotype) is that (with a perfect match) of a modern living male related (to 32 generations) to the Bayard maternal ascendance. The Bayard mtDNA haplotype was found once only in a database of 100 South-German mtDNA control sequences. **Conclusions:** The resulting **R1b-M269** Y haplogroup established confirms the Germanic origin of the Bayard ancestors, suggested by genealogic studies concerning his paternal ascendance. The result concerning the mtDNA **H10e** haplotype found in the modern living male related to Bayard by matrilinear ascendance establishes that the DNA tooth is well of him, with a 99% of chance.

Keywords

The Chevalier Bayard, Tooth, Genomic DNA, Y-STRs Profile, mtDNA Mutations

1. Introduction

The Chevalier Bayard (1476?-1524)—named Pierre (III) du Terrail—is well known in French history as “le chevalier sans peur et sans reproche”. He is unanimously considered as the last true knight in shining armor, the last flower of the late Middle Ages, and the epitome of chivalry before the modern world took over [1].

As a soldier, Bayard was one of the most skilful commanders of his time. He served under three successive French kings: Charles VIII (with whom he participated to the conquest of the kingdom of Naples), Louis XII (with whom he acted to the conquest of Genoa) and François Ier. On the accession of François Ier in 1515, Bayard was made lieutenant-general (governor) of Dauphiné (a French region at this time); after the victory of Marignan, to which his valour largely contributed, he had the honour of being conferred knighthood from his youthful sovereign.

When the war broke out again between François Ier and Charles Quint (the Holy Roman Emperor), Bayard held Mézières against an army of 3500 men, and after six weeks compelled the imperial generals to raise the siege. This stubborn resistance saved central France from invasion. The parliament thanked Bayard as the saviour of his country and the king made him (in 1521) a knight of the order of Saint Michel.

In 1524, Bayard was sent to Italy with the Admiral Bonnivet, who had been defeated at Robecco and wounded in a combat. During the retreat of the French army Bayard repulsed the foremost pursuers, but in guarding the rear at the passage of the Sesia, was mortally wounded at Rovasenda (April 30, 1524) by an arquebuse ball which pierced his armor.

We do not know exactly when Bayard was born (between 1473 and 1476) but he was very probably born at Château Bayard (near Pontcharra, Isère), in Dauphiné.

Bayard was the second son (the third-born child of a kinship of eight children) of Aymon du Terrail (1458-1490), the second Lord de Bayard, and Hélène Alleman de Laval (born before 1436-died after 1504); we ignore the exact date of their marriage.

Bayard’s cranium is at present kept in the Dauphiné Museum of Grenoble. We have reconstituted the whole Bayard cranium (Lucotte, unpublished) from his upper, lateral and posterior parts, his mandible and most of his osseous facial part. Detailed examination of the reconstituted cranium establishes that it is the skull of a Caucasian male, aged from 45 to 50 years; some observed particularities of the mandible (brachygnathy, elevated corpus, squared and non-protruding chin) correspond to those depicted on the portraits of Bayard.

A molar tooth was extracted from this mandible. Genomic DNA obtained from this tooth permits us to study the Y-chromosomal profile and the mtDNA (mitochondrial DNA) of Bayard, in a similar way to that recently explored [2] for King Richard III of England.

2. The Sample

We extracted a tooth from the mandible articulated to the cranium. This incomplete cranium, presumed as the Bayard's skull, is stored in the Dauphiné Museum (Grenoble). This tooth (**Figure 1**) is the first molar located at the left side of the mandible (the tooth number 36 according to the Nomenclature Dentaire Internationale). The second root basis of that tooth was saved, and the interior of the canal of the crown was abraded with a dentist drill. The recuperated powder was sterilized, and then used for DNA extraction.

3. Methods

The dentine powder was washed with 15% HCl, rinsed with UV-treated ddH₂O, and dried under an UV lamp for 15 min.

The sterilized powder was introduced in 15 ml tubes (Costar), and DNA was extracted according to a modified silica-based protocol [3]. Briefly, 2 ml of an undiluted commercial guanidine thiocyanate solution (DNAzol®) was added to the tube and incubated at room temperature for 3 days; after that, the supernatant was passed through a silica column (QIAquick®, Qiagen).



Figure 1. The tooth extracted from the mandible (lingual view). E: enamel, R1: the first (broken) tooth' root; R2: the second (sawed along the line) tooth root.

All staff involved in the sampling wore protective clothing, sterile gloves and facemasks, to prevent exogenous contamination. DNA extraction and purification were performed according to our previously published protocol [4], in a dedicated laboratory.

We amplified from the genomic DNA extracted 14 Y-chromosomal short tandem repeats (Y-STRs) by using the AmFirst Identifier PCR amplification kit (Amp FIRSTLY filer™, Applied Biosystems), according to the instructions given by the Company; this amplification kit is specially adapted to the study of ancient DNA (a-DNA). The fifteen STRs studied are the followings: DYS19 (=DYS394), DYS385.a, DYS389.I and .b (DYS389.b = DYS389.II *minus* DYS389.I), DYS390 (=DYS708), DYS391, DYS392, DYS393 (=DYS395), DYS438, DYS439 (=Y-GATA-A4), DYS448, DYS456, DYS458, and DYS635 (=Y-GATA-C4); Y-GATA-H4 was detected in an independent PCR (Polymerase Chain) reaction. To detect the long STR alleles, we proceeded to two successive essays, with various degrees of stringency.

We predict, starting from the allele values, the corresponding Y haplogroup using the Whit Atey's Haplogroup Predictor [5].

From the genomic DNA extracted, we studied also the mtDNA. The mtDNA genomic sequence intervals for *HVR1* and *HVR2* (Hypervariable regions 1 and 2) were amplified by PCR with primers F15971 and R16610 and with primers L15 and H484, respectively. For each PCR, the DNA extract from the tooth root specimen was amplified by PCR in a 12.5 µl reaction mixture: 2 mM MgCl₂, 50 mM KCl, 10 mM Tris/HCl pH = 9, 0.1% Triton X-100, 0.2 mM each dNTP, 0.1 µM each primer, and 2.5 U of DNA polymerase (Ampli Taq Gold; Applied Biosystems). The amplification was carried out with an initial denaturation step at 95°C for 6 min., followed by 35 cycles at 95°C for 1 min., 55°C for 1 min., and 72°C for 1 min.

PCR products were purified from agarose gel (QIA-Quick PCR purification kit; Qiagen). Both strands of all the amplified mtDNA fragments eluted from agarose gel slides were directly sequenced (Big Dye Terminator Cycle Sequencing kit; Applied Biosystems) and separated (ABI PRISM 3130 Genetic Analyzer; Applied Biosystem).

The sequences obtained were aligned against the Revised Cambridge Reference Sequence [6], to identify the presence of polymorphic sites. Seqscape software (Applied Biosystems) and Clustal analysis were used for pairwise alignment.

The laboratory performed DNA typing under strict precautions, following previously published criteria for ancient DNA authentication [7].

4. Results

A quantity of about 100 ng of a total genomic DNA was obtained from the dental powder.

Preliminary experiments on the genomic DNA extracted established that it contains sequences of the amelogenin human gene, which show two peaks cor-

responding to the two X and Y chromosomes. Consequently, the individual under study is truly a XY male.

Table 1 gives the allelic Y-STRs profile obtained. All these allele values were confirmed in a second PCR essay; we were not able to obtain the allele value corresponding to DYS635 (probably the longest).

The predicted Y haplogroup using the Haplogroup Predictor is **I-M223**.

We obtained DNA sequences (from 16,025 to 16,555 and from 67 to 369, respectively) of the *HVR1* (16,024 16,569) and *HVR2* (1-576) segments of the mtDNA. Three mutations (16093C, 16221T and 16519C) are present in the *HVR1* sequence, and three also (263G, 309.1C and 315.1C) in the *HVR2* sequence. The same results were obtained in a replication study.

5. Discussion

In the present study we obtain, with genomic DNA extracted from one of his tooth, the Y-STRs profile (coming from his father) and the mtDNA sequence (coming from his mother) of Bayard.

The predicted Y-haplogroup **I-M223** is equivalent to **I2a2a**, previously known as **I2b1** of haplogroup I [8]. In fact one of us (G.L.) established that this haplogroup corresponds to the sub-clade S21/U106 of the major haplogroup **R1b-M269** [9]. In current European populations, this sub-clade shows a peak of S21 frequencies centred on Germany and surrounding areas (**Figure 2**); because of these particularities, it was named the “Germanic” Y-haplotype.

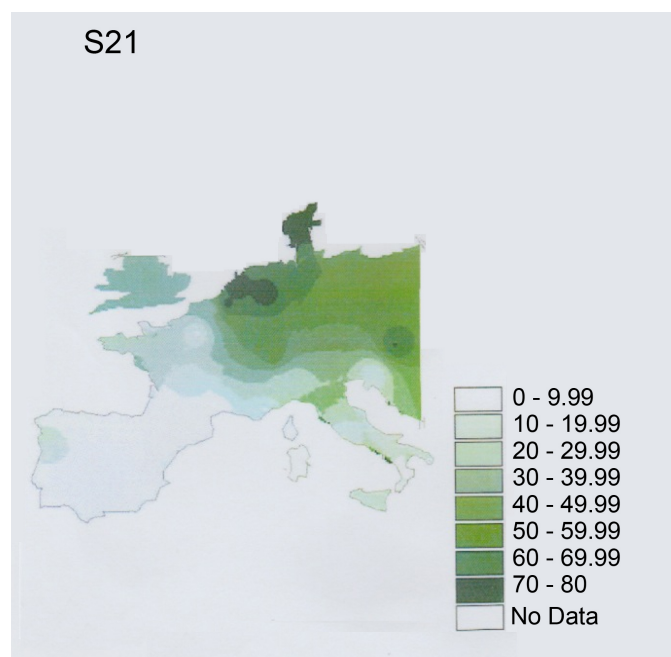
Table 2 summarizes what we know about the real paternal Bayard ancestry [10]. Bayard’s father, Aymon du Terrail, was the second Lord de Bayard. His father, Pierre said “le Jeune” (1421-1460) was the first Lord de Bayard; his

Table 1. Y-chromosomal STR data analysis.

Numbers	Y-STRs	Allele values
1	DYS19	16
2	DYS385.a	14
3	DYS389.I	14
4	DYS389.b	18
5	DYS390	24
6	DYS391	10
7	DYS392	12
8	DYS393	14
9	DYS438	10
10	DYS439	12
11	DYS448	20
12	DYS456	15
13	DYS458	16
14	DYS635	?
15	Y-GATA-H4	11

Table 2. Bayard's paternal ancestry.

Generations	Bayard paternal ancestry	Names	Birth- and death rates	Titles
0	Chevalier Bayard	Pierre (III) du Terrail	1476?-1524	third Lord de Bayard
1	Bayard's father	Aymon (or Amon) du Terrail	1458-1490	second Lord de Bayard
2	Bayard's grand-father	Pierre II (junior) du Terrail	1421-1460	first Lord de Bayard
3	Bayard's aïeul	Pierre I (senior) Terrail	1387-1433/34	
4	Bayard's bisaïeul	Pierre Terrail	?-1387	

**Figure 2.** Isofrequency map of R-S21 in West-Europe (from Lucotte, 2015). Isofrequency lines indicate the artificial limits (of the areas with various nuances of green) between decreasing S21 values from the peak.

grand-father, Pierre said “le Vieux”, was born in 1387 and died in 1433/34. We do not know the birth date of the ancestor Pierre Terrail, but he probably died in 1387. Nothing is known with certainty concerning Bayard's remote paternal ancestors.

Some past biographers spread various legendary accounts about Bayard's paternal ancestry [11]. But it is generally admitted that the House of de Terrail (“Terra alii” means stranger, in latin language) is very ancient in Dauphiné, and that they come from Germany (“at the time when the Emperors possessed the Dauphiné”). This explains why Bayard's Y-STRs profile corresponds to the Germanic Y-haplotype S21/U106.

The only-known Bayard descendant is an (illegitimate) daughter: Jeanne (1501-

1580), who married in 1525 (one year after Bayard's death) to François II de Bocsozel (1483-1532); they have four sons: Pierre, Jehan, Piraud and Soffrey, but the break in the Bayard paternal transmission line (with Jeanne) do not permit us to compare their Y-STRs profiles (and those of their further male descendants) to that of Bayard.

Concerning now Bayard's mtDNA haplogroup, the *HVR2* sequence mutation 263G defines the mtDNA haplogroup **H**; it is the most commonly found mtDNA haplogroup in Europe [12]. The *HVR1* sequence mutation 16221T indicates (because of the absences of both 456T and 16304C mutations) the **H5** sub-clade of **H** [13].

The Eupedia map [14] of sub-clade **H5** shows a remarkable concentration (that can attain >8%) of **H5** frequencies (in West-Europe) at the near-periphery of the Alpine arch (in Slovenia, Austria, Switzerland and in the south-eastern part of France).

Bayard inherited his mtDNA haplotype from his mother Hélène Alleman de Laval. Now the Dauphiné region-from which Hélène came from-is located at the Western part of the Alpine arch periphery (an area with the maximal concentration of **H5** frequencies). But, as for other European nobility [2], the female mobility of Hélène's family tends to be higher than the general population.

J. C. Parisot de Bayard, who funded this study, was able to identify a modern descendant of Bayard's family (Figure 3). This subject (named P. R.) is a living male individual born near the town of Annecy (in Savoy), 32 generations removed from Bayard (from his mother Hélène Alleman du Terrail) on the female line.

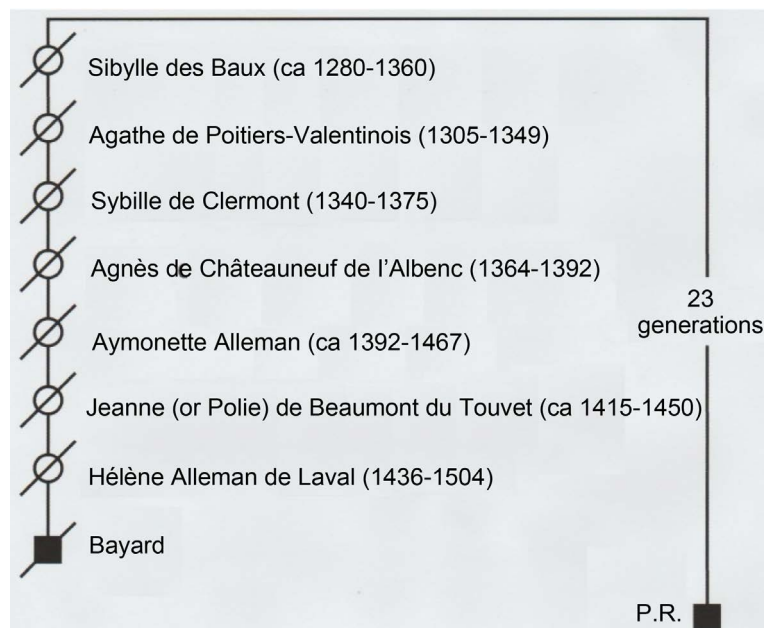


Figure 3. Genealogical links between Bayard and a modern-day relative (P. R.) who participated in this study. Genealogical information links P. R. (who descended from Bayard's mother) and Bayard through a female-only line (ca: circa).

The mtDNA analysis (repeated twice) of P.R. shows a perfect match (he had the three *HVR1* mutations 16093C, 16221T and 16519C, and the three other *HVR2* mutations 263G, 309.1C and 315.1C) between his mtDNA haplotype and that of Bayard; this is consistent with this subject being a matrilineal relative-in a similar form that it was found in [2]-at the genealogical time depth considered.

In contrast to false paternity, false-maternity is much less likely [2]; but historical records of female-line lineages are usually more difficult to track over multiple generations, due to the change of women's surnames after marriage. In the case reported here, the family tree concerns noble families (often better recorded) tracing down from Bayard to the beginning of the 13th century.

Because of the maximal value of >8% observed frequency of the sub-clade **H5** in the geographic region considered, we considered at first that there is less than about 10% of probability that the mtDNA match between P.R. and Bayard could have occurred by chance. But that is certainly an overestimate, because Bayard's mtDNA haplotype (Table 3) is only one of those constituting haplogroup **H5** considered as a whole. To note that the attribution adopted here to consider Bayard's mtDNA haplogroup as being of the sub-clade **H** (usually determined by the two supplementary mutations 16304C and 456T) is entirely due to the presence in it of the 16221T mutation; this mutation is generally considered, together with the 16085T and 16106A mutations, as a typical "Alpine mutation" [15].

Next we investigated more precisely the probability that Bayard's mtDNA haplogroup had occurred by chance, by tempting to find it in three databases of complete mtDNA control sequences concerning subjects originating from geographic regions located in the North periphery of the Alpine arch. These three databases are: 1/a first database [16] concerning 104 Slovenians and 144 Bosnians; 2/a second database [17] concerning 273 unrelated West-Eurians from Austria; 3/a third database [18] concerning one hundred of samples that were collected from native German speakers in the middle of Southern Germany (in the region of Ulm city, that is located between Lake Constance and the Swabian Alps).

The only perfect match we found is for the UL1A8 subject of South-Germany (Table 4) of the third database; he is nomenclatured under the mtDNA haplogroup **H*** (the paragroup). So, for this geographic region, we found Bayard's

Table 3. Bayard's mtDNA haplotype.

HVR sequences	Mutations	Comments
1	16093C	this variant appeared in about 5% of most haplogroups, but most commonly in K
	16221T	indicates the H5 sub-clade of H
	16519C	corresponds to a hotspot; it appears in almost every haplogroup, in over half of them
2	263G	determinates the H haplogroup
	309.1C	is one of the most recurrent mutation
	315.1C	most members of H also have this mutation

Table 4. Results of the research to find the Bayard mtDNA haplotype in three databases of mtDNA control sequences.

Populations	Samples	Bayard mtDNA haplotype						Attributed haplogroups	%
		16093C	16221T	16519C	263G	309.1C	315.1C		
1. Slovenia and Bosnia	Number 45 in the list	+	+	?	+	+	+	H	1/248
2. Switzerland	F1E3	+	-	+	+	+	+	H*	1/273
3. South-Germany	UL1A8	+	+	+	+	+	+	H*	1/100

+ indicates presence of the mutation; -: their absence; ?: uncertain.

mtDNA haplotype at a frequency of 1/100.

The subject number 47 (a Slovenian) of the first database is of a mtDNA haplogroup very similar to that of Bayard's (but he had 150T as a supplementary mutation in the *HVR2* sequence); the reason why he had not 16519C is that the second primer of the PCR reaction used for *HVR1* sequence covers until 16400 only. The nearest mtDNA haplotype we found in the second database is that of the Swiss f1E3 subject (but he had 16271C as a supplementary mutation in the *HVR1* sequence); the fact that he had not 16221T is possibly related to the event that this variant could be a phantom mutation [19], that is a systematic artefacts generated in the course of the sequencing process itself.

A synthetic study [20] concerned an analysis of 1350 mtDNA haplotypes belonging to **H**, originating from Central Europe: Austria (**H** samples = 973), Germany (=31), Hungary (=71), Macedonia (=100), Romania (=124), and from Dubaï (=51). The prevalence of sub-clades **H1**, **H5**, **H6** and **H10** (defined by the 16093C and 16221T mutations), **H13**, **H14**, **H15**, **H16**, **H17** and **H21** was consistent across Europe; the **H10** sub-clade particularly concerns 44 samples (3.3% of the total), but manifests hardly and genetic heterogeneity.

Today [21] the 16221T mutation defines the **H10e** type. Various sub-types of **H10e** are characterized by some specific mutations (Table 5). We had the opportunity to examine 56 mitogenomes (complete mtDNA sequences) belonging to **H10e** for the presence of the Bayard mtDNA haplotype: three **H10e1** sequences (among 9), four **H10e1a** (among 6), three **H10e2** (among 4) and one **H10e3a** (among 2) contained it.

Among the thirty five mitogenomes examined, twelve of them (Table 6) are of the Bayard mtDNA haplogroup: three subjects from Denmark, three from UK, two from England, one from Wales, one from France (he is not P.R.) and two from USA (who revendicate remote Anglo-Saxon ancestries).

6. Conclusion

In conclusion, it is the first time that the DNA of the Chevalier Bayard is studied (for paternal and maternal ancestries). His Y-STRs profile shows that he belongs to the Germanic S21/U106 Y haplogroup sub-clade. His mtDNA haplogroup,

Table 5. Characteristic mutations of the **H10e** haplogroup type and of four sub-types found in the collection of 56 mitogenomes bearing the Bayard mtDNA haplotype.

Type	Mutations	Numbers found
H10e	16221T	35
Sub-types		
H10e1	13830C	9
H10e1a	16266T	6
H10e2	14602G	4
H10e3a	961C	2

Table 6. Characterisations of the twelve **H10e** mitogenomes (on 35) of the Bayard mtDNA haplotype.

Numbers (on 12)	Numbers (on 35)	GenBank ID	Geographic origins
1	7	KF161474	Denmark
2	26	JX153333	Denmark
3	29	KF161060	Denmark
4	11	JQ701809	UK
5	21	JQ705324	UK
6	24	JQ705702	UK
7	14	JQ703082	England
8	18	JQ704209	England
9	17	JQ704082	Wales
10	5	HQ662520	France
11	3	GU569076	USA
12	4	HM101252	USA

found again in a living male individual removed from 32 generations on the female line of Bayard ancestry, is of the **H5** sub-clade further precised as being the **H10e** type. The Bayard mtDNA haplotype is found at an approximate percentage of 1/100 in the geographic region located at the periphery of the Alpine arch. We now move towards phenotypical DNA markers concerning his skin, eyes and hair pigmentation and his nose and chin forms, in order to compare them to the corresponding characters observable on Bayard's portraits.

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Conflict of Interest

The authors declare no conflict of interest.

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