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Reconstruction of the Lineage Y Chromosome Haplotype of Napoléon the First

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Abstract: As part of the Napoléon I Genome (NIG) project we have reconstructed, based on more than one hundred Y-STRs (Y-short tandem repeats), the complete Y-haplotype of the non-recombinant part of the Y-chromosome (NRY) of French Emperor Napoléon I (1769-1821). We already knew the allelic values at Y-markers of the Y-chromosome of Napoléon I, but only for the palindromic STR YCAIIa and b and for the non-palindromic Y-STR DYS19. The present reconstruction aims to compare the allelic values at Y-STRs of the DNA of Charles Napoléon (C.N.), the living 4th generation descendant of Jérôme Bonaparte (Napoléon I's youngest brother), with those of Alexandre Colonna Walewski (A.C.W.), the living 4th generation descendant of Count Alexandre Walewski (the son born of the union between Napoléon I and Countess Maria Walewska). We have previously established that Napoléon I, C.N. and A.C.W. are of the same Y-haplogroup E1b1b1b2a1. The allelic values for C.N. and A.C.W. are the same for ninety-three other non-palindromic markers (belonging to ninety different STRs) and for thirty-eight other palindromic markers (belonging to fifteen different STRs); these values then constitute those deduced in the reconstruction of the allelic values of the STR markers of the Napoléon I's Y-haplotype. Four non-palindromic STRs and two palindromic STRs have different allelic values in C.N. and A.C.W.; we have deduced the allelic value of Napoléon I for one (DYS454), and the probable allelic values for two (Y-GATA-C4 and DYS712) of these non-palindromic variable STRs. To sum up, we have established, by reconstruction of the lineage, the allelic values of the markers of Napoléon I's Y-haplotype for a total of one-hundred and thirty-three different Y-STR markers.

Keywords: Y-chromosome haplotype ; Napoléon the First ; short tandem repeats

Review

The genetic identification of old biological specimens is limited to the analysis of short and degraded DNA fragments, but the development and application of comprehensive DNA testing for identification of historical samples is of considerable interest. These sorts of studies, for those concerning French dynasties, include the analysis of the heart of Louis XVII, the son of Louis XVI King of France [1] and the genetic analysis of the presumptive blood of Louis XVI [2].

One of us have recently [3] described the finding of a rare variant (16184 C>T) in the sequence of the hypervariable segment (HVS1) of mitochondrial DNA (mtDNA) extracted from two preserved hairs conserved in the Vivant Denon reliquary; these hairs were authenticated as belonging to French Emperor Napoléon I (Napoléon Bonaparte; 1769-1821). More recently [4] our group have described a first reconstruction of the Napoléon I's Y-haplogroup based on the genomic DNA of his indirect descendant Charles Napoléon. DNA of Napoléon I was extracted from two islands of follicular sheaths located at the basis of two of his beard hairs, also conserved in the Vivant Denon reliquary. The Y-haplogroup of Napoléon I, determined by the study of ten NRY-SNPs (non-recombinant Y-single nucleotide polymer-phisms) is now designated as M123+, M34+, and L791 and L792+, a new nomenclature precising the previous denomination of the E1b1b1c1* paragroup keeping with a less recent agreement concerning the use of binary polymorphisms to reshape and increase resolution of the human Y chromosomal haplogroup tree [5]. The ten SNPs used consecutively for this initial determination were: M125, M174, M33, M35, M78, M81, M123, M34, M84 and M290. The haplogroup, being $M84^-$, cannot be $M136^+$. Further studies on SNP markers have shown that it is $L792^+$ (and $L791^+$); but probably all other members of cluster D are also L792. All $L792^+$ subjects tested are $V23^-$ (http://www.familytreedna.com/public/e3b/default.aspx?section=ysnp). So, according to the more recent datas obtained on the subject (http://www.isogg.org/tree/ISOGGhapgrE.html; http://www.isogg.org/tree/ISOGG_YDNA_SNP_Index.html; http://www.isogg.org/tree/ISOGG_YDNA_SNP_IndexSource.html), the new designation of E1b1b1c1* is now E1b1b1b2a1.

Because of the little quantity (about 50 ng) of DNA, that we used mainly in SNPs determinations, obtained

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from Napoléon I's beard hairs, we previously tested it for three Y-STRs (Y-short tandem repeats = Y-microsatellites) only: DYS19 (=DYS394), and YCAIIa and b (with allelic values of 13, 19 and 22, respectively). That constitutes the real Napoléon I haplotype for these three loci. Computed with the Whit Athey's haplogroup predictor program [6], these three values considered together estimate that Napoléon I corresponds (with a probability value = 76.5%) to a subject belonging to the previously described Y-haplogroup cluster E1b1b (http://fr.wikipedia.org/wiki/Haplogroupe_E#E1b1b1_.28E-M35.29).

In order to reconstruct Napoléon I's Y-haplotype, we chose to study the NRY-DNA of the current indirect male descendant of his family, Prince Charles Napoléon (C.N.), the present head of family of the Napoléon I dynasty (Figure 1). The C.N. buccal smear DNA was previously genotyped for the first 37 genetic markers of the Family Tree DNA (FTDNA) kit, in order to determine his Y-STR profile. These markers are, in order of their use: DYS393 (= DYS395), DYS390, DYS19 (= DYS394), DYS391, DYS385a and b, DYS426, DYS388, DYS439 (= Y-GATA-A4), DYS389i, DYS392, DYS389ii, DYS458 DYS459a and b, DYS455, DYS454 (= DYS639), DYS447, DYS437 (= DYS457), DYS448, DYS449, DYS464a, b, c, and d, DYS460 (=Y-GATA-A7.1), Y-GATA-H4, YCAIIa and b, DYS456, DYS607, DYS576, DYS570, DYS724 (= CDY)a and b, DYS442 and DYS438. Results showed that the allelic values for DYS19 and for YCAIIa and b are the same for C.N. and for Napoléon I. Computed with the Whit Athey's haplogroup predictor program, this profile is highly indicative (99.9%) of the previous E1b1b1c1* (named now $M34^{+}m84^{-}$) paragroup (allelic values at DYS19 = 13, and at DYS464a = 14, b = 15, c = 16 and d = 17 being discriminant in the establish-ment of this Y-paragroup), present at relatively high frequencies in some populations (http://fr.wikipedia.org/wiki/Haplogroupe_E#E1b1b1c_Y-DNA). But an aberrant value of DYS454 = 7 was obtained for C.N., DYS454 (= DYS639) being the least varying Y-STR marker commonly used in genealogical DNA testing [7].

To obtain a better coverage of the NRY-DNA part of C.N., we used the FTDNA Y-DNA111 kit. These 111 markers (numbered 1 to 111 in Table 1) correspond to 101 different Y-STRs, ninety-nine of them being DSYns (D stands for DNA, Y stands for Y-chromosome, S corresponds to a unique segment of the STR and n is the STR number) and two of them (DYF395S1 and DYF406S1) are DYFns (F corresponds to a segment that has multiple copies on the Y-chromosome). To these 111 markers we added to the study those of another DYSn (DYS725) and of seven other DYFns (in order DYF371X, DYF385, DYF397, DYF399X, DYF401, DYF408 and DYF411).

A total number of seventeen STRs studied (DYS413 in the palindrome P8; YCAII and DYF395S1 in P5; DYF411 and DYS385 in P4; a first DYF397 in P3; DYS464X and a first DYS725 in P2; the second DYF397, DYF401, DYF459, DYF385, CDY, DYF371X, DYF408, DYF399X and the second DYS725 in P1) are located in the palindromic region of the Y-chromosome. Among them, nine (in order: DYS385, DYS413, DYS459, CDY, YCAII, DYF385, DYF395S1, DYF401 and DYF411) are two copy STRs. Only one (DYF399X) is a three-copy STR and seven (in order: DYS464X, two DYS725s, DYF371X, two DYF397s and DYF408) are four-copy STRs.

Table 1 indicates the allelic values for 136 markers of the non-recombinant part of the Y-chromosome of C.N., markers belonging to a total number of 109 Y-STRs.

Prince Charles Napoléon, born in 1950, is the elder son of Louis-Napoléon-Jérôme Bonaparte (1914-1997), the "Napoléon Prince". Charles Napoléon is the 4^{th} generation descendant of Jérôme Bonaparte (1784-1860), the "King of Westphalie", the Napoléon I's youngest brother. To compare the allelic values for the 136 markers of C.N. with those of a direct descendant of Napoléon I, we studied the same 109 Y-STRs of Alexandre Colonna Walewski (A.C.W.). Alexandre Colonna Walewski, born in 1934, is called "the 5^{th} count" (Figure 1); Alexandre Colonna is the 5^{th} generation descendant of "Count Alexandre Walewski" (1810-1868), the son born of the union between Napoléon I and Countess Maria Walewska (1786-1817).

The allelic values for the 136 markers of A.C.W. are shown in Table 1. As for C.N., results show that the allelic values for DYS19 and for YCAIIa and b are the same as for A.C.W. This shows that alleles at these three markers have remained unchanged for five/six successive male generations.

On the other hand, the allelic values for A.C.W. are the same as those of C.N. for 93 markers other than DYS19, these markers belonging to 90 different DYSns (listed on Table 2). Because they are identical in A.C.W. and C.N., we can reasonably infer that the 94 allelic values of the above markers correspond to those of Napoléon I (because they have also remained unchanged for 5/6 generations of remote ancestry).

The allelic values are different in A.C.W. and C.N. for four (4%) DYSns markers (Table 1): for DYS454

the allele value = 11 for A.C.W., being = 7 for C.N.; for DYS481 the allele value = 28 for A.C.W. and = 27 for C.N.; for Y-GATA-C4 the allele value = 21 for A.C.W. and = 22 for C.N.; and for DYS712 the allele value = 25 for A.C.W. and = 23 for C.N.

The allelic values for A.C.W. are also the same as those of C.N. for 38 markers belonging to 15 palindromic STRs (listed on Table 2) other than YCAII1 and 2. The corresponding 40 allelic values for those markers must reasonably be the deduced values for Napoléon I. The allelic values are different in A.C.W. and C.N. for two (4.8%) palindromic markers (Table 1): for CDYa the allele value = 34 for A.C.W. and = 35 for C.N., and for DYF397.2 the allele value = 13 for A.C.W. and = 14 for C.N.

Table 3 shows the allelic ranges and modal class for the four non-palindromic variable Y-STRs DYS454, Y-GATA-C4, DYS712 and DYS481. Table 1 shows that for DYS454, A.C.W. had the modal allelic class value of 11 whereas C.N. had the minor allele value = 7. The most parsimonious interpretation is to admit that allele 11 at this marker is the ancestral form – that of Napoléon I - the allele value of 7 representing the derived one, which happened during one of the five generations separating C.N. from the father of Napoléon I, Charles-Marie Buonaparte (Figure 1). Variant 7 in the Jérôme line is probably due to a multistep deletion, a rare event which often results in a much more stable allele [G. Henson, personal communication]. It is very uniquely that the 7 allele would mutate into any of the lines which carry it, because the modal value of 11 itself is known as one of the most stable [7] of the marker set.

Things are less clear for the Y-GATA-C4 marker, where the modal allelic value is 23: neither the allele value = 22 of C.N. nor the allele value = 21 of A.C.W. (the two differing by one repeat only) correspond to the modal value. But because allele 21 is the best represented class of alleles in the distribution [8] after the 23, we suppose that it corresponds to the deduced allelic value of Napoléon I for the Y-GATA-C4 marker.

Things are also less clear for the newly discovered DYS712 marker, possibly the fastest mutator [K. Norved, personal communication] among the markers of the FTDNA111 kit: neither the allele value = 23 of C.N. nor the allele value = 25 of A.C.W. (but the two differing by two repeats) correspond to the modal value = 22 for this marker. But because allele 23 is the best represented class of alleles in the distribution after the 22, we suppose that it corresponds to the deduced allelic value of Napoléon I for this DYS712 marker. According to this hypothesis the allelic value = 25 of A.C.W. has appeared during one of the five generations separating A.C;W; from Napoléon I.

An ambiguity remains for the determination of the deduced allelic value for Napoléon I at the DYS481 marker. Both the 27 (that of C.N.) and the 28 (that of A.C.W.) alleles (the two differing by one repeat only) are located at the superior edge of the distribution of values in the European population [9], the modal value being 23. Because allele 27 is absent in the European distribution of reference, we suppose (but there is no formal proof at all for that) that the Napoléon I allele could be the 28.

Predicted values for mutation rates [10] range from 3.60×10^{-4} mutations per generation for DYS645 to 9.64×10^{-3} for DYS449 (the average being 2.12×10^{-3}, SD = 1.58×10^{-3}). All of three variable non-palindromic markers for which we have data (Table 3] had mutation rate estimates above this average; the 6.94×10^{-3} estimated value for DYS481 is the most elevated one among them, but it does not go out of the superior value of the mutation rate predicted values.

CDY (= DYS724), the first variable palindromic STR found by comparing C.N. to A.C.W., is a two-copy STR, with allelic values of 35-36 for C.N. and of 34-36 for A.C.W. Like DYS459 and DYS464, CDY is located on palindrome P1. We have considered in a first time that the difference between C.N. and A.C.W. at the duplicated STR marker CDY as an example of recombinational loss of heterozygosity (recLOH): first we could have alleles 35-36 for C.N., and after the recombination we have alleles 34-36 for A.C.W. [G. Haines, personal communication]. Consequently, the deduced CDYa allele value for Napoléon I could be the 35. CDY is an expressed gene located on the Y chromosome. So, differences reported here for CDY between C.N. and A.C.W. could be of possible functional significance.

Similar possible conclusions to that for CDY could be reached for DYF397 (a trinucleotide repeat, with two alleles on P3 and two alleles on P1), the second variable palindromic STR: for this STR the allelic values = 13-14-14-14 for C.N. and = 13-13-14-14 for A.C.W. The DYF397.2 allele = 14 of C.N. could be the first form, and the DYF397.2 allele = 13 of A.C.W. could be the derived one. In this hypothesis, highly speculative, the deduced DYF397.2 allele value of Napoléon I could be 14.

In fact, as the differences between Napoléon I's line and Jérôme's line are only one step on each of the two markers CDY and DYF397 and because there is no difference on any of the other palindromic

markers studied, the most likely cause of change is a single step mutation (not recombination) for each of these two markers; but it remains that the ancestral values can't be known for sure for either CDY or DYF397.

In conclusion, we have reconstructed the Y-haplotype of Napoléon I, based on more than one hundred Y-short tandem repeats. We already know, directly, his allelic values for the palindromic STR markers YCAIIa and b, and for the non-palindromic STR DYS19. New results we obtained that are presentated in this synthesis concerns: 1/ the determination of the two supplementary Y-SNP markers L792 and L791 in the genomic DNA of Napoléon I; 2/ the increase in the number of Y-STR studied up to 136 markers for Charles Napoléon, an indirect descendant of Napoléon I; 3/ the complete study of the 136 Y-STR markers for Alexandre colonna Walewski, a direct descendant of Napoléon I. We now know, after comparing Y-STRs of Charles Napoléon and Alexandre Colonna Walewski, the deduced – because they are identical in both cases – allelic values of Napoléon I for ninety-three other non-palindromic markers (belonging to ninety different STRs), and for thirty-eight other palindromic markers (belonging to fifteen different STRs). Four non-palindromic STRs are variable between Charles Napoléon and Alexandre Colonna Walewski, and we have deduced the more probable allelic values of Napoléon I for three of them (DYS454, Y-GATA-C4 and DYS712); ambiguity remains for the determination of the deduced allelic values of Napoléon I for the other variable non-palindromic STR DYS481. The possible deduced allelic value of Napoléon I for the variable palindromic marker CDYa is 35, and an ambiguity remains for the determination of the deduced allelic value for the other variable palindromic marker DYF397.2. So we have now a complete "formula" of allelic values of the Napoléon I Y-chromosome non-recombinant part, for a total of one hundred and thirty-three markers. Figure 2 depicts the results we obtain for ninety-five of them, whose chromosomal locations of the corresponding Y-STRs are known [11]. As for King Louis XVI [2], we have obtained a formula, concerning however mainly deduced alleles from lineage, of the Y-chromosome haplotype of Emperor Napoléon I. Knowledge of this Y-chromosome formula should permit a very precise genetic identification of Napoléon I's remains (bones, teeth, hair's bulbs, tendons, skin…). It should also be possible to compare the Y-chromosome of Napoléon I to those (to be established) of his son, the Duke of Reichstadt (1811-1832) and of his other brothers (allele 7 of DYS454 being characteristic of the Jérôme line): Joseph (1769-1844), Lucien (1775-1840) and Louis (1778-1846).

We have now involved in the construction of a geographic map of E-M34 (http://www.haplozone.net/wiki/index.php?title=E-M34) frequencies (that remains the terminal SNP marker of the E1b1b1b2a1 haplogroup differentiation), in order to determinate the distant locations of the paternal origin of Napoléon I ancestry.

List of abbreviations

A. C.W.: Alexandre Colonna Walewski ; C.N.: Charles Napoléon ; DYF: multiple segment DNA from the Y-chromosome ; DYS: unique segment DNA from the Y-chromosome ; FTDNA: Family Tree DNA ; HVS: hypervariable segment ; mtDNA: mitochondrial DNA ; NRY: non-recombinant part of the Y-chromosome ; P: palindrome ; SNP: single nucleotide polymorphism ; STR: short tandem repeats ; Y: Y-chromosome.

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Competing interests

The authors declare that they have no competing interests.

Authors contributions

GL Conceived of the study, and assumed his design and coordination; he drafts the manuscript, JM participated in the recruitment of genomic DNA samples; PH carried out the molecular genetic studies. All authors read and approved the final manuscript.

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Table 1. Allelic values at 109 Y-STRs (numbers refer to the 111 markers of the FTDNA Y-DNA111 kit) for Charles Napoléon (C.N.) and Alexandre Colonna Walewski (A.C.W.) NRY-DNAs. This list of DYS follows approximately (minus: DYS443, DYS453, DYS508, DYS573, DYS612, DYS614 and DYS626; plus: DYS492, DYS510, DYS511, DYS513, DYS537, DYS552, DYS561, DYS568, DYS587, DYS590, DYS593, DYS617, DYS640, DYS650, DYS712 and DYS715) the Familipedia list of DYS markers (http://familypedia.wikia.com/wiki/List_of_DYS_markers). Asterisks indicate the six differential markers between C.N. and A.C.W.

		Allelic values 644444474444448			
Numbers	**Y-STRs**	**Napoléon I**	**C.N.**	**A.C.W.**	**Napoléon I (deduced)**
3	**DYS19 = DYS394**	**13**	13	13	**13** (direct determination)
5	**DYS385.a** (palindromic)		16	16	**16**
6	**.b**		16	16	**16**
8	**DYS388**		12	12	**12**
10	**DYS389.i**		14	14	**14**
12	**.ii**[1]		31	31	**31**
2	**DYS390 = DYS708**		24	24	**24**
4	**DYS391**		10	10	**10**
11	**DYS392** (located in the untranslated region of the transcription unit TTTY10)		11	11	**11**
1	**DYS393 = DYS395**		14	14	**14**
49	**DYS413**[2]**.a** (palindromic)		22	22	**22**
50	**.b**		22	22	**22**
48	**DYS425**[3] (one copy of DYF371)		0	0	**0**
7	**DYS426 = DYS483**		11	11	**11**
109	**DYS434**		9	9	**9**
111	**DYS435**		11	11	**11**
55	**DYS436**		12	12	**12**
19	**DYS437 = DYS457**		14	14	**14**
37	**DYS438** (located in the untranslated region of the USP9 Y gene)		10	10	**10**

9	**DYS439 = Y-GATA-A4**		12	12	**12**
91	**DYS441**		14	14	**14**
36	**DYS442**		12	12	**12**
57	**DYS444 = DYS542**		11	11	**11**
88	**DYS445**		11	11	**11**
60	**DYS446**		12	12	**12**
18	**DYS447**		21	21	**21**
20	**DYS448** (located in the P3 loop)		20	20	**20**
21	**DYS449**		28	28	**28**
56	**DYS450**		7	7	**7**
87	**DYS452**		30	30	**30**
17	**DYS454* = DYS639**		7	11	**11**
16	**DYS455** (located in the intron 2 of the TBL1 Y gene)		11	11	**11**
30	**DYS456**		15	15	**15**
13	**DYS458**		16	16	**16**
14	**DYS459.a** (palindromic)		9	9	**9**
15	**.b**		9	9	**9**
26	**DYS460 = Y-GATA-A7.1**		10	10	**10**
110	**DYS461 = Y-GATA-A7.2**		11	11	**11**
86	**DYS462**		12	12	**12**
90	**DYS463**		18	18	**18**
22	**DYS464X^{4}.a** (palindromic)		14g	14	**14**
23	**.b**		15g	15	**15**
24	**.c**		16g	16	**16**
25	**.d**		17g	17	**17**
45	**DYS472**		8	8	**8**
58	**DYS481***		27	28	**28 or 27**

69	**DYS485**		15	15	**15**
63	**DYS487 = DYS698**		14	14	**14**
54	**DYS490**		12	12	**12**
66	**DYS492 = DYS604**		10	10	**10**
81	**DYS494**		9	9	**9**
71	**DYS495**		15	15	**15**
107	**DYS497**		14	14	**14**
99	**DYS504 = DYS660**		16	16	**16**
76	**DYS505**		13	13	**13**
108	**DYS510**		17	17	**17**
47	**DYS511**		10	10	**10**
100	**DYS513 = DYS605**		12	12	**12**
59	**DYS520 = DYS654**		18	18	**18**
80	**DYS522**		12	12	**12**
93	**DYS525**		11	11	**11**
38	**DYS531 = DYS600**		10	10	**10**
97	**DYS532**		11	11	**11**
82	**DYS533**		11	11	**11**
55	**DYS534**		15	15	**15**
43	**DYS537**		12	12	**12**
72	**DYS540**		11	11	**11**
78	**DYS549**		12	12	**12**
102	**DYS552**		25	25	**25**
77	**DYS556**		12	12	**12**
51	**DYS557**		21	21	**21**
101	**DYS561**		15	15	**15**
67	**DYS565**		11	11	**11**
62	**DYS568**		12	12	**12**

33	**DYS570** (located in the untranslated region of the TBL1 Y gene)		19	19	**19**
64	**DYS572**		11	11	**11**
84	**DYS575**		8	8	**8**
32	**DYS576**		18	18	**18**
39	**DYS578**		8	8	**8**
105	**DYS587**		22	22	**22**
79	**DYS589**		11	11	**11**
42	**DYS590**		7	7	**7**
95	**DYS593**		16	16	**16**
52	**DYS594**		11	11	**11**
31	**DYS607**		12	12	**12**
61	**DYS617**		13	13	**13**
70	**DYS632**		8	8	**8**
104	**DYS635* = Y-GATA-C4**		22	21	**21 ?**
83	**DYS636**		11	11	**11**
85	**DYS638**		11	11	**11**
65	**DYS640 = DYS606**		13	13	**13**
44	**DYS641**		11	11	**11**
106	**DYS643**		12	12	**12**
96	**DYS650**		18	18	**18**
68	**DYS710**		31	31	**31**
94	**DYS712***		23	25	**23?**
73	**DYS714**		24	24	**24**
98	**DYS715**		23	23	**23**
74	**DYS716**		28	28	**28**
75	**DYS717**		19	19	**19**
34 35	**DYS724 = CDY.a*** (palindromic) = gene **.b**		35 36	34 36	**35 or 34** **36**

	DYS725[5].1 (palindromic; in duplicate) **.2** **.3** **.4**		29 30 30 32	29 30 30 32	**29** **30** **30** **32**
103	**DYS726**		15	15	**15**
89	**Y-GATA-A10**		12	12	**12**
27	**Y-GATA-H4**		11	11	**11**
92	**Y-GGAAT-1B07**		13	13	**13**
28 29	**YCAII.a** (palindromic) **.b**	**19** **22**	19 22	19 22	**19** (direct determination) **22** (direct determination)
	DYF371X.1 (palindromic) **.2** **.3** **.4**		10c 10c 13c 13c	10c 10c 13c 13c	**10c** **10c** **13c** **13c**
	DYF385[6].1 (palindromic) **.2**		10 10	10 10	**10** **10**
40 41	**DYF395S1.a** (palindromic) **.b**		15 15	15 15	**15** **15**
	DYF397.1 (palindromic; in duplicate) **.2*** **.3** **.4**		13 14 14 14	13 13 14 14	**13** **14 or 13** **14** **14**
	DYF399X.1 (palindromic) **.2** **.3**		20t 22.1t 24c	20t 22.1tt 24c	**20t** **22.1t** **24c**
	DYF401[7].1 **.2**	(palindromic; DYS527 is another names for DYF401)	10.1 15	10.1 15	**10.1** **15**

46	**DYF406S1**		10	10	**10**
	DYF408.1 (palindromic) **.2** **.3** **.4**		188 188 14 14	188 188 14 14	**188** **188** **14** **14**
	DYF411 .1 (palindromic) **.2**		11 12	11 12	**11** **12**

1. DYS389ii refers to the total length of DYS389.
2. DYS413 is a two-copy STR, DYS413a and b (like DYS459, CDY and YCAII).
3. DYS425 is a part of DYF31; null (=0) 425 allele observed is assigned to the predictive value of 12 within the FTDNA's system.
4. For the multi-copy marker DYS464, the letters are reported in alphabetic order, from the lowest to the highest order: a = 14, b = 15, c = 16, d = 17.
5. For the multi-copy marker DYS725 (as for the other multi-copy markers DYSF371X, DYF397, DYF399X and DYF408), the numbers are reported here in the lowest to highest order.
6. DYF385 is a two-copy STR, numbered here 1 and 2.
7. DYF401 is also a two-copy STR (like DYF411), numbered here 1 and 2; for these two STRs, numbers are reported from the lowest to highest order.

Table 2. A comprehensive list of Y-STR allelic values common to C.N. and A.C.W.

Non-palindromic markers

In order: DYS385a = 16; DYS388 = 12; DYS389i = 14, ii = 31; DYS390 = 24; DYS391 = 10; DYS392 = 11; DYS393 = 14; DYS413a = 22, b = 22; DYS425 = 0 (null allele); DYS426 = 11; DYS434 = 9; DYS435 = 11; DYS436 = 12; DYS437 = 14; DYS438 = 10; Y-GATA-A4 = 12; DYS441 = 14; DYS442 = 12; DYS444 = 11; DYS445 = 11; DYS446 = 12; DYS447 = 21; DYS448 = 20; DYS449 = 28; DYS450 = 7; DYS452 = 30; DYS455 = 11; DYS456 = 15; DYS458 = 16; Y-GATA-A7.1 = 10; Y-GATA-A7.2 = 11; DYS462 = 12; DYS463 = 18; DYS472 = 8; DYS485 = 15; DYS487 = 14; DYS490 = 12; DYS492 = 10; DYS494 = 9; DYS495 = 15; DYS497 = 14; DYS504 = 16; DYS505 = 13; DYS510 = 17; DYS511 = 10, DYS513 = 12; DYS520 = 18; DYS522 = 12; DYS525 = 11; DYS531 = 10; DYS532 = 11; DYS533 = 11; DYS534 = 15; DYS537 = 12; DYS540 = 11; DYS549 = 12; DYS552 = 25; DYS556 = 12; DYS557 = 21; DYS561 = 15; DYS565 = 11; DYS568 = 12; DYS570 = 19; DYS572 = 11; DYS575 = 8; DYS576 = 18; DYS578 = 8; DYS587 = 22; DYS589 = 11; DYS590 = 7; DYS593 = 16; DYS594 = 11; DYS607 = 12; DYS617 = 13; DYS632 = 8; FYS636 = 11; DYS638 = 11; DYS640 = 13; DYS641 = 11; DYS643 = 12; DYS650 = 18; DYS710 = 31; DYS714 = 24; DYS715 = 23; DYS716 = 28; DYS717 = 19; DYS726 = 15; Y-GATA-A10 = 12; Y-GATA-H4 = 11; and Y-GGAAT-1B07 = 13.

Palindromic markers

In order: DYS385a = 16, b = 16; DYS413a = 22, b = 22; DYS459a = 9, b = 9; DYS464Xa = 14g, b = 15g, c = 16g, d = 17g; CDYb = 36; DYS7251.1 = 29, .2 = 30, .3 = 30, .4 = 32; DYF371X.1 = 10c, .2 = 10c, .3 = 13c, .4 = 13c; DYF385.1 = 10, .2 = 10; DYF395S1.a = 15, b = 15; DYF397.1 = 13, .3 = 14, .4 = 14; DYF399X.1 = 20t, .2 = 22.1t, .3 = 24c; DYF401.1 = 10.1, .2 = 15; DYF406S1 = 10; DYF408.1 = 188, .2 = 188, .3 = 14, .4 = 14; and DYF411.1 = 11, .2 = 12.

Table 3. Allelic ranges, modal class and Napoléon I deduced alleles for the four non-palindromic variable Y-STRs.

Y-STRs	Allele ranges	Modal class	Mutation rate estimates	References	Napoléon I deduced alleles
DYS454	6-15	11	2.18×10^{-3}	[12]	**11**
Y-GATA-C4	17-27	23	2.83×10^{-3}	[8]	**21 ?**
DYS712	18-30	22	-	[13]	**23 ?**
DYS481	19-28	23	6.94×10^{-3}	[9]	**28 , or 27**

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Figure 1. Simplified representation of the masculine descent of Jérôme, and of the Walewski direct masculine descent of Napoléon I. Present Charles Napoléon and Alexandre Colonna Walewski are framed.

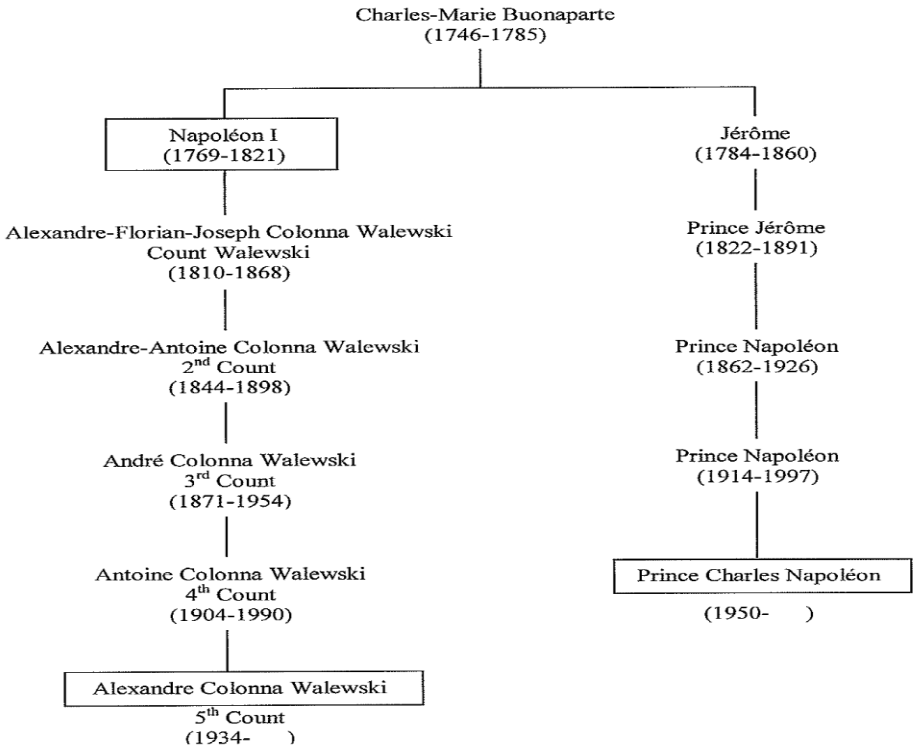

Figure 2. Allele values corresponding to Napoléon I for 95 markers whose precise chromosomal locations are known [11] for the corresponding Y-STRs. The boxes demarcate loci that are present in different chromosomal segments. Asterisks indicate five out the six of the variable markers between C.N. and A.C.W.