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REVIEW

Y chromosome STR typing in crime casework

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Abstract Since the beginning of the nineties the field of forensic Y chromosome analysis has been successfully developed to become commonplace in laboratories working in crime casework all over the world. The ability to identify male-specific DNA renders highly variable Y-chromosomal polymorphisms, the STR sequences, an invaluable addition to the standard panel of autosomal loci used in forensic genetics. The male-specificity makes the Y chromosome especially useful in cases of male/female cell admixture, namely in sexual assault cases. On the other hand, the haploidy and patrilineal inheritance complicates the interpretation of a Y-STR match, because male relatives share for several generations an identical Y-STR profile. Since paternal relatives tend to live in the geographic and cultural territory of their ancestors, the Y chromosome analysis has a potential to make inferences on the population of origin of a given DNA profile. This review addresses the fields of application of Y chromosome haplotyping, the interpretation of results, databasing efforts and population genetics aspects.

Keywords Y chromosome · Y-STR · Crime casework · Haplotyping · DNA mixture analysis · Match probability · Population genetics · Population databases · Intelligence information

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Introduction

Haplotyping of the human Y chromosome by use of STR markers or Y-STR haplotyping is a method used to detect and differentiate male DNA. The methodology was developed in parallel with the autosomal STR analysis for human identification purposes and evaluated in a very similar way for forensic analysis. Shortly after the characterization and evaluation of the first Y-chromosomal STR polymorphism its usefulness in crime casework was demonstrated when a mixed stain from a vaginal swab of a raped and murdered female victim was resolved by Y-STR analysis and a falsely convicted male was excluded [1, 2]. Unambiguous detection of the male component in DNA mixtures with a high female background is still the main field of application of forensic Y-STR haplotyping. Y-STRs in combination with autosomal STRs will thus be employed preferentially in sexual assault cases. Furthermore, the method has proved useful in reconstructing paternal relationship e.g., in mass disaster investigations [3] and Y-STRs as well as Y-SNPs can provide intelligence information on the ethnic origin of a male DNA donor [4]. The principal weakness of Y chromosome STR analysis is that even when a crime sample matches the Y-STR profile of a suspect, patrilineal relatives of the suspect cannot be excluded as being the donor of the stain. Hence, in contrast to autosomal STRs, access to reference databases representing the variance and relatedness of haplotypes within local populations is of crucial importance for interpreting a Y-STR match. The different nature of underlying population structure also implies that a combination of the information obtained from lineage genetic markers, such as the Y-chromosome (or mitochondrial DNA) with data resulting from meiotically recombining loci (autosomes) into a single likelihood ratio is generally inconsistent and should be avoided [5].

Similarly to autosomal STRs, forensically suitable Y-STRs have been selected from a range of candidate sequences. Mostly tetrameric repeats were the markers of choice with an average repeat number between 10 and 30 producing short amplicons in the PCR. The power of discrimination must be reasonably high in all major metapopulations and the mutation rate reasonably low (Table 1). The selected markers must be unambiguously Y-specific and male-specific. Based on these requirements a core set of STR markers (termed minimal haplotype or minHt) has been chosen and proposed for practical use [6]. Currently a panel of up to 17 thoroughly evaluated markers (Table 1) in practical use is gaining support through recommendations of the DNA commission of the ISFG (International Society of Forensic Genetics) [7, 8]. Commercially available Y-STR kits contain between 9 and 17 loci, all of which consist of the recommended core STRs. Other Y-STR loci are being screened and evaluated aiming to extend the core marker sets [9–12].

The Y-STR haplotyping method has been validated and standardized between labs [6, 13, 14] and is now widely used in forensic applications. The intent is not for Y-STR loci to replace any of the core autosomal loci but to provide a separate tool contributing otherwise unavailable information in a number of scenarios:

- For mixed stains where the proportion of female DNA is higher than the male DNA present (which is frequently observed in vaginal swabs collected after sexual intercourse)
- For cases of alleged sexual assault where tests for seminal fluid or sperm are negative
- For sexual assault cases where the evidence in question is positive for semen, but no DNA foreign to the victim can be detected, or potential male alleles are below the threshold for autosomal STR detection
- For sexual assault cases where the evidence in question is amylase-positive and a male/female mixture is expected (e.g., traces of kisses or bites)
- For cases with very old semen stains, where the majority of sperm cells are suspected to be degraded and differential lysis is unsuccessful or risky
- For sexual assault cases where a large number of semen or other stains have to be screened
- For cases where the number of male donors in a stain needs to be determined
- For cases where the evidence in question is expected to include cells of a male perpetrator (e.g., female fingernail hyponychium where male biological material may accumulate after violent attacks)
- For cases where the patrilinear relationship of a stain donor needs to be determined
- For cases where the stain donor's population of origin needs to be inferred

Application of Y-STR haplotyping for DNA mixture analysis

One problem connected with the application of PCR for DNA typing is the failure to amplify the minor component

Table 1 Characteristics of forensic core set Y-STRs

Locus	Allelic range	Mutation rate (CIL)*	*h* (all)	*h* (African)	*h* (East Asian)	*h* (European)
DYS19	10–19	0.0027 (0.0018–0.0038)	0.7313	0.7235	0.6886	0.7059
DYS389I	9–17	0.0028 (0.0018–0.0040)	0.6155	0.5447	0.6487	0.5358
DYS389II	24–35	0.0031 (0.0021–0.0044)	0.7543	0.7408	0.7595	0.7305
DYS390	12–29	0.0022 (0.0014–0.0032)	0.7453	0.6160	0.7132	0.7268
DYS391	5–16	0.0030 (0.0021–0.0042)	0.5179	0.3951	0.4044	0.5366
DYS392	4–20	0.0006 (0.0002–0.0013)	0.6803	0.3567	0.7332	0.5879
DYS393	7–18	0.0010 (0.0005–0.0018)	0.5773	0.6225	0.6586	0.4341
DYS385ab	6–28	0.0021 (0.0015–0.0029)	0.9425	0.9487	0.9714	0.8764
DYS438	7–18	0.0006 (0.0002–0.0015)	0.6863	0.5285	0.5602	0.7118
DYS439	5–19	0.0056 (0.0040–0.0077)	0.7065	0.6330	0.6700	0.7166
DYS437	4–18	0.0013 (0.0006–0.0025)	0.5276	0.3696	0.4495	0.6135
DYS448	15–24	0.0006 (0.0001–0.0020)	0.7349	0.6314	0.7247	0.6551
DYS456	10–23	0.0044 (0.0025–0.0073)	0.6815	0.6119	0.6730	0.7138
DYS458	11–24	0.0071 (0.0045–0.0105)	0.8147	0.7266	0.8163	0.7787
DYS635	16–29	0.0039 (0.0023–0.0063)	0.7986	0.7037	0.7755	0.7056
YGATAH4	8–22	0.0031 (0.0017–0.0052)	0.6256	0.5967	0.6105	0.6628

h haplotype diversity

* Data from [37], with 95% confidence interval limits

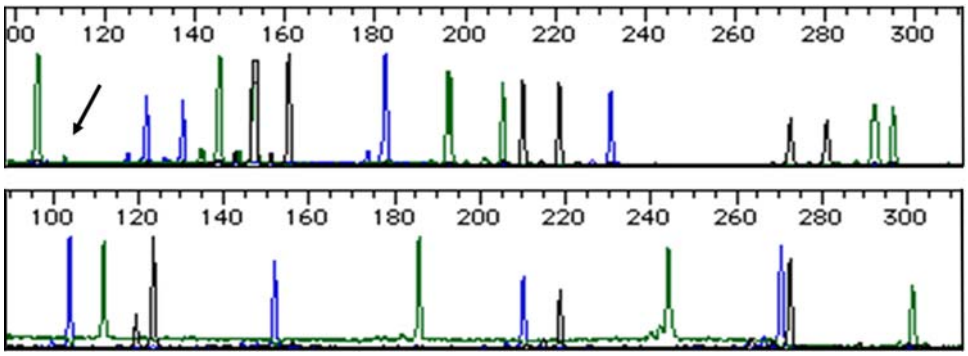

Fig. 1 Autosomal (above) vs. Y-chromosomal STR analysis (below) of a female/male mixed stain (fingernail scrapings) from a homicide crime scene. The *AMEL-Y* peak in the autosomal analysis is marked with an arrow. The male Y-STR profile is 14 (DYS19), 12 (DYS389I), 28 (DYS389II), 25 (DYS390), 11 (DYS391), 11 (DYS392), 13 (DYS393), 14,14 (DYS385ab), 15 (DYS437), 11 (DYS438), 11 (DYS439). The YHRD search for this profile excluding loci DYS437, DYS438, DYS439 is shown in Fig. 2

in DNA mixtures with very unequal ratios of heterogeneous DNA. Allelic dropout, masking or suppression of the amplicons of the minor component is mainly caused by the accumulation of PCR products from alleles of the major component [15]. The minor component is generally undetectable below a ratio of 1:25–1:50 for autosomal mixtures [16] (see also Fig. 1). This diagnostic gap can be closed or reduced by Y-STR typing especially in mixtures with a minor male component and a high female background, a typical situation found in vaginal swabs examined after alleged sexual assault. Quantitation of non-differentially extracted vaginal swabs routinely showed DNA amounts >1000 ng with the majority stemming from the female DNA [17].

During the last 10 years a series of studies on non-probative samples with very unequal ratios of male and female DNA have been published. Prinz et al. [17] showed in model experiments that the minor male component in male/female mixtures could be detected up to a ratio of 1:4000 by a small Y-STR tetraplex and 0.4 ng male DNA as the minor component. Other authors report on successful typing in ratios up to 1:3000 with 1 ng male DNA amplified in a triplex [18] or 1:600 (0.5 ng male DNA) with a hexaplex [19]. Performance of Y-STR typing in mixtures is influenced by the design of the multiplex PCR, its sensitivity limit and the concentration of the minor component. Currently the multiplex kits on the market include between 9 and 17 Y-STR markers, with detection limits below 0.1 ng DNA. As an example, analyses with the PowerPlex®Y system (12 markers) revealed clear results with artificial blood stains on cotton (18 cells per PCR), and partial profiles (65% drop out of markers) with only two cells [20]. In parallel to experimental mixture studies, Y-STR analyses of casework-related samples have been reviewed in a number of articles. Sibille et al. [21] report on positive Y-STR results in approximately one-third of their re-tested sexual assault cases where the swabs were initially characterized as "negative" for semen. In another systematic study Dekairelle and Hoste [22] reported a 48% success rate for Y-STR haplotype analysis for PSA (prostate-specific antigen) positive differentially extracted swabs which did not show a result using autosomal STRs.

It has to be emphasized that the method of differential lysis [23] widely used to separate sperm nuclei from vaginal cellular debris in vaginal swabs is still important for producing an autosomal DNA profile from the sperm. Nevertheless, various types of non-sperm cells left by a perpetrator (e.g., epithelial, salivary cells, leucocytes) cannot be detected by this technique. Shewale et al. [24] analysed post-vasectomized azoospermic semen samples for Y-STRs and observed a wide variation in the yield of extracted DNA from 12.5 to 1,000 ng attributed to epithelial cells and/or leukocytes. Differential extractions also tend to fail or be ineffective in cases with aged and degraded sperm DNA or low numbers of sperm. In a retrial request case Honda et al. [25] tested 25 year old vaginal swabs from two murder and rape cases by Y-STR testing without prior differential lysis and matched the stains to each other and the defendant. Furthermore mixtures with male cells other than sperm cannot be resolved by differential lysis. This concerns, for example, cases with saliva evidence in sexual assault cases [17] or with fingernail scrapings of a female victim when the assailant is male [26]. Y-STR typing in these scenarios is especially helpful. Figure 1 shows a typical example of a mixed STR profile generated with both an autosomal and a Y-chromosomal multiplex PCR reaction from fingernail scrapings of the victim. Whereas the male component is weakly amplified in the autosomal analysis, the Y-STR multiplex PCR applied for the same stain generates strong and unequivocally interpretable allelic peaks from the perpetrator despite the high female background.

Therefore, the presence of Y-chromosomal DNA in cases with negative cytology can provide evidence of

sexual contact independently of ejaculation, sperm cell count, differential lysis success, or proportion of female cells in the extract and could thus be used to corroborate the testimony of the sexual assault female victims. Even after long delays (2–8 days) between sexual assault and medical examination swabs can be successfully typed for Y-STRs [21]. In cases where autosomal STRs have failed, Y-STR analysis may provide crucial evidence for investigators [27, 28]. In the USA alone, there are about 180,000 sexual assault samples that have not yet been processed. Similar backlogs also exist in many other countries. The case of the US citizen A.B. Butler Jr. clearly demonstrates the benefit of this method. He was imprisoned in Texas for 16 years for having supposedly raped a woman. The evidence was not tested until 1999 but the autosomal STR analysis did not yield conclusive results. Instead the results of Y chromosome testing excluded Butler as the source of the semen from the rape kit. Butler was released in January 2000 [29].

Interpretation of Y-chromosomal STR profiling results

In principle, the three possible interpretations of a diploid DNA profiling result also apply to Y-STR haplotypes, including matches (or inclusions), exclusions, and inconclusive outcomes. However, since DNA profiles based upon Y-STRs are not individual-specific but lineage-specific, the significance of matches differs somewhat from that of autosomal markers. Owing to the lack of recombination, the major part of the Y-chromosome (including all STRs currently used in forensic genetics) represents, in effect, a single locus. Therefore, the "product rule" of autosomal markers cannot be applied to estimate the population frequency of a Y-STR haplotype, and large reference databases have to be used for this purpose instead (Table 2). Haplotype frequencies observed in, or extrapolated from, these databases usually range between 10^{-3} and 10^{-5}, so that the power of discrimination of Y-STRs is low compared to that of autosomal STRs.

Two approaches are currently available for evaluating the probability of a coincidental match between two Y-STR haplotypes:

- The counting method [7], and
- The "haplotype surveying" method [30, 31].

The latter is a Bayesian approach that attempts to extract more information from the structure of Y-STR haplotype databases than does the counting method. For the frequency of a haplotype in question, the surveying method yields a ß-type posterior distribution, the mean of which is a robust estimator of the haplotype frequency [30, 31]. This posterior distribution is obtained by extrapolation from the structure and frequency of all other haplotypes in the database. It makes use of the fact that the frequency of a haplotype is positively correlated with the combined frequency, in the same population, of all "neighbouring" haplotypes that are only a small number of mutational steps away. Since the haplotype in question is not included in the estimation process, it does not even have to be present in the database itself. In terms of match probabilities, correctly taking the suspect haplotype into account [31], the results obtained with either the counting or the surveying method are in strong agreement for frequent haplotypes (>0.1% in a reference population). For rare haplotypes, the discrepancies are slightly more pronounced since the size of the database represents a lower limit to the prior frequency estimates that can be obtained via the counting method. This notwithstanding, until more adequately sampled regional databases are available that reflect the population-wide spectrum of Y-STR haplotypes in sufficient detail, the counting method appears to represent the most simple and easily defensible method of interpreting Y-STR forensic evidence.

For cases with more than one haploid profile detectable in a stain (e.g., in the case of a gang rape) a likelihood

Table 2 Online available Y-STR haplotypes reference databases

Supplier	Name of the database	Y-STR markers	Number of haplotypes (April 2009)	URL
Institute of Legal Medicine and Forensic Sciences, Berlin, Germany	YHRD	17	72.055	yhrd.org
National Center for Forensic Science, Orlando, USA	US Y-STR Database	17	17,216	usystrdatabase.org
Promega Corporation, Madison, USA	PowerPlex Y Haplotype Database	12	4,004	promega.com/techserv/tools/pplexy
Applied Biosystems Inc, Foster City, USA	YFiler Haplotype Database	17	3,561	appliedbiosystems.com/yfilerdatabase

calculation for varying numbers of known and unknown male contributors has been devised [32]. A prerequisite for such calculations is again the use of large Y-STR haplotype population databases in order to retrieve frequencies of the haplotype profiles detected in the trace.

Due to intense international collaboration such a large quality-assessed database is only a mouse-click away. The Online Y Chromosome Haplotype Reference Database (URL: www.yhrd.org) represents the largest repository for Y-chromosomal haplotypes to-date. Current release 28 of the database from March 27, 2009 contains 72,055 haplotypes from 538 populations sampled worldwide [33–35]. Both above described methods to interprete haplotype profiles, the counting method (with 95% confidence intervals attached to the average frequency estimate) as well as the haplotype frequency extrapolation method (so far limited to Europe) are implemented in the search/calculate tool at www.yhrd.org.

For the generation of realistic haplotype frequency estimates, however, the structure of the respective reference population databases is critical. Due to the effects of the socially instituted practice of patrilocality in many societies, the number of male relatives not distinguishable by haplotyping could be high in a local population. Therefore, the priority for population sampling should not be sample size alone but should also include a good representation of the spectrum of population-specific haplotypes. The particular sensitivity of Y-chromosome specific genetic markers to population differentiation [33–36] demands appropriate sampling strategies. Sampling records should include information on the birthplace of the father or grandfather, on the language group and, where informative and appropriate, on family names and patronyms, demographic history, religious affiliation, and kinship system (especially in traditional societies). When sampled properly, even populations such as the Europeans, formerly regarded as sufficiently homogeneous for the purpose of forensic genetics, appear genetically subdivided into distinct Y chromosomal clusters formed and maintained by recent demographic events [36]. Intense efforts by the forensic genetic community are therefore currently under way to increase the sample sizes for populations shown to be, in fact, genetically homogeneous entities. The progress of these efforts can be monitored: the YHRD with monthly updates of its haplotype and population counts allows for online haplotype searches via the menu "Search Haplotype". For this search algorithm (providing population-specific average frequencies plus confidence intervals) the worldwide sampled haplotypes in the database were assigned to hierarchical levels of geographically and linguistically predefined metapopulations comprising regional samples with genetic connectivity (e.g., the Eurasian, the European, and the Western European metapopulation). The assignment of discrete regional samples to metapopulations (groups of samples interconnected by gene flow and migration) has been confirmed by genetic differentiation tests [35]. A mere traditional classification of haplotype data based on nationality was also implemented in the YHRD. Currently, 63 such national databases can be searched from "A" as in Albania to "V" as in Vietnam.

Y-STR haplotyping can provide useful information where paternal relatedness is an issue in criminal cases. Detlaff-Kakol and Pawlowski [28] describe an imposing case where the Y-STR typing of a large population was used to identify the offender. DNA profiles obtained from semen stains left at the scenes of crime gave information that one and the same man had committed all of the rapes. The Y-chromosome haplotype (nine loci) obtained was used for the elimination process of a large number of suspects. One man was found who had an identical DNA profile in all Y-chromosome STR loci analysed and possessed common alleles in nine out of 10 autosomal loci, strongly suggesting that the real rapist and the typed man were closely related males. Analysis of reference DNA obtained from the man's brother revealed an identical autosomal STR profile to that identified at the crime scenes. Cases like this with Y-STRs providing information on paternal relatedness of tested persons are expected to become more frequent with the routine application of Y-chromosome typing in forensic casework.

The genetic relationship between men within a population can pose problems if a match has to be evaluated. In the casework example mentioned earlier a clear Y-chromosomal but no autosomal profile was retrieved from the fingernail scrapings of the female victim (Fig. 1). The following mass screening (558 males) led to a man matching the evidence by the entire 11 core set Y-STR loci. The YHRD search among 63,369 9-loci haplotypes (release 25) clearly pointed to the man who left the trace being of African descent, since all six matching haplotypes stemmed from African, African-Caribbean or African-American populations and no match occurred in any other population sample (Fig. 2). The average frequency in all Africans was 1.9×10^{-3}, the frequency in Eurasians 9.8×10^{-5}, and in East Asians 2.5×10^{-4}. The evidence and the person were further typed for another set of Y-STR markers and finally one mismatch (among 21 markers) has been detected. This result led to the exclusion of the man from being the donor of the stain. A year later a suspect whose DNA matched the full 21 loci profile was arrested and confessed the crime. The ethnic background of this man was Afro-Caribbean. The implications of this case are two-fold: First, the 11-locus core set must inevitably be extended in some cases by additional highly informative STR loci to confirm or exclude a match [9–12]. Second, in certain cases Y-STR haplotype analysis and use of refined

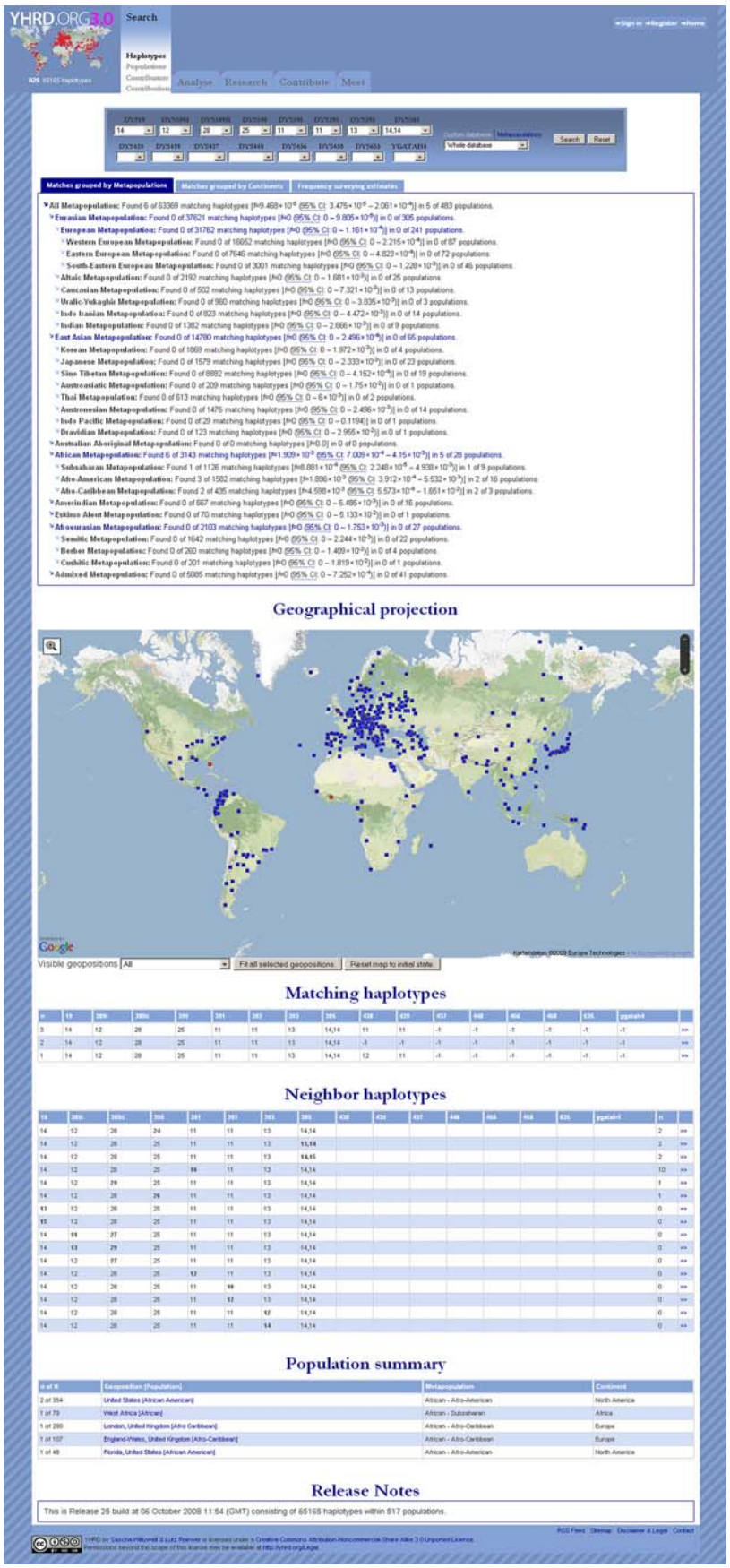

Fig. 2 YHRD search for the 9-locus minimal haplotype profile (minHt) amplified from the evidence (see Fig. 1 for the electropherogram). Note the exclusive occurrence of the profile in African populations

population databases allows inferences to be made on the population of origin.

As Y-STR haplotyping becomes more widespread due to the availability of commercial kits and suitable population databases, the potential of Y-linked markers to indicate the population origin of a male person will become more useful. Not only distant metapopulations as African, or European isolates such as Finns, Sami or Roma, but even more recently diverged neighbouring populations such as the Eastern Slavic or Romance-speaking Europeans possess different modal Y-STR haplotypes [36]. This information can prove useful in tracing the paternal population of origin of a stain donor in non-suspect cases or in cases where decomposed bodies or skeletal remains need to be identified.

Key points

1. Y-STR haplotyping is method to detect and differentiate male DNA. Y-STRs are an invaluable addition to the standard panel of autosomal loci used for DNA profiling, especially in crime cases with mixture samples.
2. The haploidy and patrilineal inheritance complicates the interpretation of Y-STR haplotype matches, because male relatives share for several generations an identical Y-STR profile. For the assessment of match probabilities large structured databases are necessary in order to estimate the extent of haplotype sharing in a reference population. The most conservative and easily defensible approach to report a Y haplotype match is the counting method which deserves a large database of worldwide sampled populations. For this purpose the Y-STR Haplotype Reference Database (YHRD) has been established.
3. Since paternal relatives tend to live in the geographical and cultural territory of their ancestors, the Y chromosome analysis has a potential to make inference on the population of origin of a given Y chromosomal profile.
4. Currently a panel of validated Y-STR markers is used by crime labs. In cases, where other than Y chromosome information is not available, this core marker set must inevitably be extended by additional highly informative loci to confirm or exclude a match.

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