Research Article

Comparison of the effectiveness of microsatellites and SNP panels for genetic identification, traceability and assessment of parentage in an inbred Angus herd

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Abstract

During the last decade, microsatellites (short tandem repeats or STRs) have been successfully used for animal genetic identification, traceability and paternity, although in recent year single nucleotide polymorphisms (SNPs) have been increasingly used for this purpose. An efficient SNP identification system requires a marker set with enough power to identify individuals and their parents. Genetic diagnostics generally include the analysis of related animals. In this work, the degree of information provided by SNPs for a consanguineous herd of cattle was compared with that provided by STRs. Thirty-six closely related Angus cattle were genotyped for 18 STRs and 116 SNPs. Cumulative SNPs exclusion power values (Q) for paternity and sample matching probability (MP) yielded values greater than 0.9998 and 4.32E^{-42}, respectively. Generally 2-3 SNPs per STR were needed to obtain an equivalent Q value. The MP showed that 24 SNPs were equivalent to the ISAG (International Society for Animal Genetics) minimal recommended set of 12 STRs (MP ~ 10^{-11}). These results provide valuable genetic data that support the consensus SNP panel for bovine genetic identification developed by the Parentage Recording Working Group of ICAR (International Committee for Animal Recording).

Keywords: microsatellite, single nucleotide polymorphism, exclusion probability, genetic identification, bovine.

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Introduction

DNA markers are becoming increasingly important in animal breeding and have been successfully used in bovine identification, in parentage testing and to establish relationships between two or more individuals (Glowatzki-Mullis *et al.*, 1995; Heyen *et al.*, 1997; Williams *et al.*, 1997; Heaton *et al.*, 2002). These markers have also been used to trace meat through the entire food chain (Arana *et al.*, 2002) because of the reliable and accurate traceability they provide based on matching genetic marker profiles (Dalvit *et al.*, 2007); the use of such markers has the potential to improve the rate of genetic progress (Van Eenennaam *et al.*, 2007).

Microsatellites or short tandem repeats (STRs) have been the genetic markers of choice for more than two de-

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cades. Despite being highly polymorphic, informative and interspersed throughout the entire genome (Baumung *et al.*, 2004; Tian *et al.*, 2007), the results obtained with STRs by different laboratories are not always comparable because of inconsistencies in allele size calling and errors in size determination. Furthermore, STRs are time consuming for trained personnel to analyze, even with the use of appropriate software or other automated methods for allele analysis (Vignal *et al.*, 2002). Recent advances in high-throughput DNA sequencing, computer software and bioinformatics have made the use of SNPs more popular (Heaton *et al.*, 2002). Although in terms of genetic information a biallelic marker may be considered as a step backwards, SNPs have some promising advantages, including greater abundance (Heaton *et al.*, 2005), genetic stability in mammals (Markovtsova *et al.*, 2000; Nielsen, 2000; Thomson *et al.*, 2000), simpler nomenclature and suitability to automated analysis and data interpretation (Wang *et al.*, 1998; Lindblad-Toh *et al.*, 2000). Furthermore, SNPs have been successfully used in the discovery of quantitative trait loci (QTL) and the association of genes with specific produc-

tive traits (Chen and Abecasis 2007; Wollstein *et al.*, 2007) and in the identification of individuals and breeds (Negrini *et al.*, 2008).

A prerequisite for the development of efficient SNP-based identification systems is the description of a minimal set with sufficient power to uniquely identify individuals and their parents in a variety of popular breeds and cross-bred populations (Heaton *et al.*, 2002), even though the information content in a SNP set may vary significantly between populations (Krawczak, 1999). Previous studies designed strategies to sample the entire genetic diversity in beef cattle or purebred populations and simulated populations of purebred gene frequencies have been used to estimate the resolution and sensitivity of these methods in identifying individuals and in parental analysis (Table S7) (Heaton *et al.*, 2002; Werner *et al.*, 2004; López Herráez *et al.*, 2005; Van Eenennaam *et al.*, 2007; Baruch and Weller, 2008; Karniol *et al.*, 2009; Allen *et al.*, 2010; Hara *et al.*, 2010a,b).

Most of the routine work done in livestock genetic laboratories includes the analysis of closely related animals (herdbook registry, half-sibs, etc.). Since high consanguinity is common in commercial ranches, additional markers are required to maintain the accuracy of the analysis (Pollak, 2005). In dealing with this problem, Anderson and Garza (2005) calculated the discriminatory power of SNPs in large scale parentage studies by considering the occurrence of related individuals among the members of putative mother-father-offspring trios. More recently, Fisher *et al.* (2009) used simulated and empirical data to evaluate the effectiveness of SNPs and STRs for parentage matching based on different degrees of relatedness.

Recently, the Parentage Recording Working Group of the ICAR (International Committee for Animal Recording) developed a cattle consensus panel of 99 SNPs, and a final ring test to certify laboratories around the world is underway. Considering this scenario, and the fact that there is considerably more experience in the use of microsatellites than SNPs (in terms of laboratory and statistical methods for analysis), the aim of this work was to compare the amount of information provided by microsatellites and SNPs within a consanguineous Angus herd.

Materials and Methods

Sample and DNA extraction

The study was done using 36 consanguineous Angus calves from a herd in Buenos Aires Province. This herd belongs to a typical commercial farm that produces, selects and sells bulls to breeding farms. The samples analyzed included half-sibs from six bulls that shared a grandfather and were obtained from the nucleus herd (consanguinity ~0.2). Figure S1 provides a schematic diagram of the breeding system used. DNA was extracted from blood using NucleoSpin Blood purification kits (Macherey-Nagel,

Düren, Germany), according to the manufacturer's instructions.

Genotyping

DNA genotyping was done with microsatellites and SNPs. The microsatellite markers used were *BM1818*, *BM1824*, *BM2113*, *BRR, CSRM60, CSSM66, ETH3*, *ETH10, ETH225, HAUT27, HEL1, INRA023, RM067*, *SPS115, TGLA53, TGLA122, TGLA126*, and *TGLA227*. These 18 STRs belong to the standard FAO panel (Van de Goor *et al.*, 2009) and/or to the standardized recommended list of the International Society for Animal Genetics (ISAG). A self-developed kit was used for PCR and the fragments were identified in an automatic MegaBACE 1000 DNA sequencer (GE Healthcare, USA). Allele sizes were standardized to the ISAG nomenclature. For SNP genotyping, 116 parentage SNPs from the Illumina BovineHD BeadChip were used (the list of SNPs is detailed in the Supplementary Material). This set comprised all SNPs included in the consensus panel for cattle identification developed by the Parentage Recording Working Group of ICAR (International Committee for Animal Recording). Genotypes with auto-calling < 85% were excluded from the analyses despite the fact that they were highly curated; 30 duplicates were included in the chip used. SNP genotyping was done using the genotyping services of GeneSeek Inc. (Lincoln, NE, USA).

Statistical analysis

Allele frequencies were determined by direct counting. ARLEQUIN 3.5 software (Schneider *et al.*, 2000) was used to estimate the levels of genetic variability through allelic diversity (n_a; total number of alleles, average number of alleles and number of alleles per locus) and the unbiased expected (h_e) and observed heterozygosity (h_o) for each locus and all loci. Hardy-Weinberg equilibrium (HWE) was estimated by F_{IS} using the exact test implemented in GENEPOP 4 (Rousset and Raymond, 1997; Rousset, 2007). The F_{IS} index was also used to estimate the degree of molecular consanguinity instead of pedigree consanguinity or kinship because the entire matrilineage was unavailable.

The match probability (MP) and exclusion power (Q) were estimated for cases involving two known parents, one known parent, missing parents and individual identification based on one (Q_1) and two (Q_2) marker exclusion criteria. These parameters were calculated for each marker and for the whole set as described by Weir (1996), using algorithms programmed with Visual Basic and implemented in Excel software (available upon request from the corresponding author).

Results

Thirty-six related animals were studied for 18 STRs and 116 SNPs. The animals belonged to a farm that uses artificial insemination (AI) and a natural multi-sire mating

system. The exclusion of data with an auto-calling < 85% resulted in 4144 genotypes (32 missing data), with an average of 35.72 successful genotype (range: 34-36) per locus. All of the SNPs analyzed were polymorphic ($n_a = 2$) while an STR n_a of 5.22 ± 1.35 (mean ± SD; range: 3-8) (Table 1). The minimum allele frequency (MAF) for SNPs was > 0.05 in 114 of the 116 SNP markers, the exceptions being the SNPs ARS-USMARC-Parent-EF034087-no-rs and ARS-USMARC-Parent-AY842472-rs29001941. The SNP h_e values ranged from 0.028 to 0.507, with an average value of 0.417 (Table 1). For STRs, the h_e values ranged from 0.255 to 0.816, with an average of 0.640 (Tables S1 and S2). In total, 133 HWE tests were done (115 for SNPs and 18 for STRs), nine of which (five for SNPs and four for STRs) showed significant deviations ($p < 0.05$) from theoretical proportions (Tables S1 and S2). The allele frequencies for SNPs and STRs are available from the corresponding author upon request.

Q was estimated for each SNP marker for the most common cases of genetic identification (two known parents, one known parent, missing parents and matching samples), while MP was calculated only for matching samples (Tables S3 and S4). As shown in Figure S2, the distribution of the number of SNPs based on their individual Q values yielded a logarithmic curve. In the case of matching samples, more than 50% of the SNPs had Q values > 0.60. When the genotypes of both parents were known, more than 50% of the SNPs had a Q value ≥ 0.17, while in the worst scenario (one known parent) this value was ≥ 0.10. In addition, Q was estimated for each whole set of markers by considering one and two mismatch criteria. The corresponding Q_1 and Q_2 values were > 0.999991 and > 0.9998 for SNPs and > 0.994 and > 0.957 for STRs, respectively; the MP values were $2.45E^{-42}$ and $3.0E^{-12}$ for SNPs and STRs, respectively (Table 2). Figures 1 and 2 and Tables S5 and S6 show the cumulative Q_1, Q_2 and MP values for all of the cases studied. These results show that it is necessary to
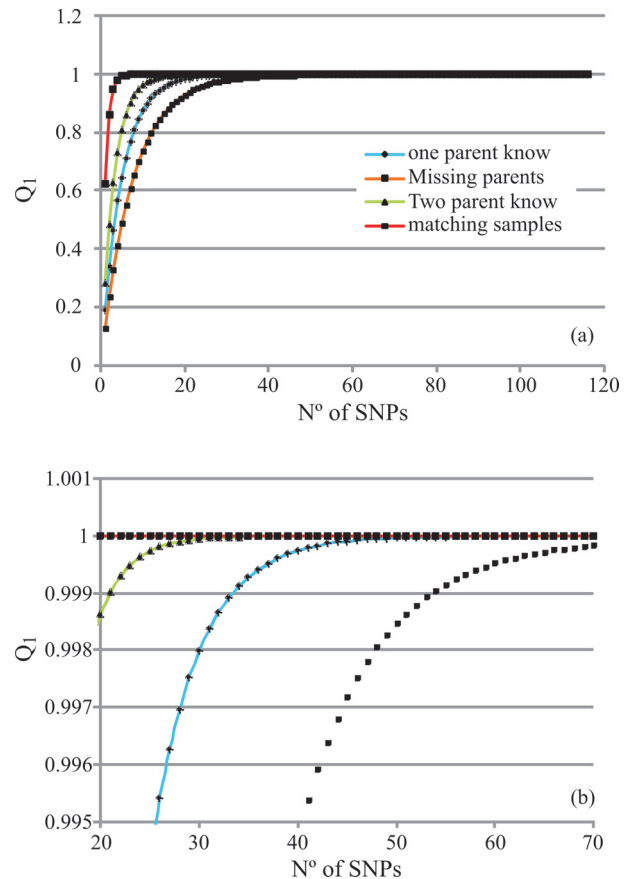

Figure 1 - Cumulative exclusion power (Q) calculated for SNPs considering (A) one (Q_1) mismatch criterion and (B) two mismatch criteria (Q_2) for cases of two known parents, one known parent, missing parents and matching samples. Markers are listed based on decreasing expected heterozygosity (h_e).

analyze between eight (matching samples scenario) and 55 (one known parent) SNPs to achieve a $Q_1 \geq 0.999$ [or cumulative non-exclusion power $(1 - Q) = 1.0E^{-4}$]. On the other hand, for STRs, three and more than 18 markers, re-

Table 1 - Average number of alleles (n_a), unbiased expected (h_e), standard deviation of n_a and h_e, range of n_a and h_e among loci and F_{IS} estimated for the SNP and STR sets of markers in Angus inbred cattle.

Marker type	n_a (range)	H_e (range)	F_{IS} p value
SNP	2 ± 0* (2)	0.417 ± 0.0098 (0.028-0.507)	< 0.001
STR	5.22 ± 1.35 (3-8)	0.640 ± 0.015 (0.255-0.816)	< 0.001

*Mean ± SD.

Table 2 - Non-exclusion power (1 - Q) estimated for the whole set of SNPs and STRs considering one (Q_1) and two (Q_2) mismatch criteria for the cases of two known parents, one known parent, missing parents and matching samples. MP - match probability calculated for matching samples.

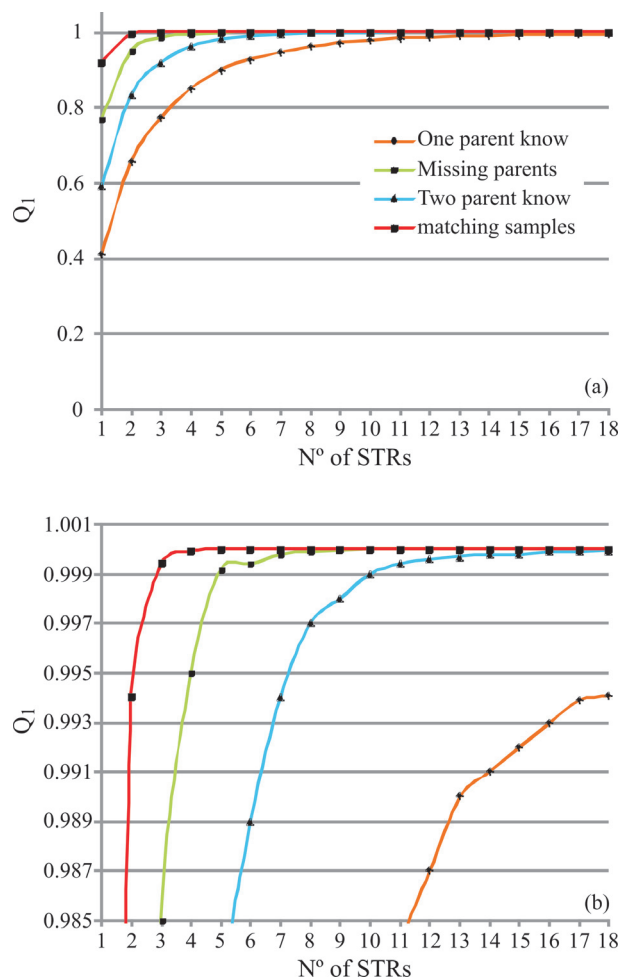| Locus type	N	Both parents		One parent		Missing parent		Matching samples		MP
		$1 - Q_1$	$1 - Q_2$	$1 - Q_1$	$1 - Q_2$	$1 - Q_1$	$1 - Q_2$	$1 - Q_1$	$1 - Q_2$	
SNPs	116	1.4E-09	3.2E-08	1.6E-05	2.1E-04	4.0E-15	1.6E-13	< 4.1E-15	< 4.1E-15	2.4E-42
STRs	18	6.0E-05	9.0E-04	5.9E-03	4.2E-02	1.0E-08	3.0E-06	3.0E-14	3.0E-12	2.6E-14

Figure 2 - Cumulative exclusion power (Q) calculated for STRs considering (A) one (Q_1) mismatch criterion and (B) two mismatch criteria (Q_2) for cases of two known parents, one known parent, missing parents and matching samples. Markers are listed based on decreasing expected heterozygosity (h_e).

spectively, are necessary. When using the $Q_2 \geq 0.999$ criterion, 10 (matching samples) and 79 (one known parent) SNPs are needed, whereas for STRs five and > 18, respectively, are required. Finally, in the population studied here, 24 SNPs or 11 STRs were necessary to obtain an $MP \geq 10^{-11}$.

The minimum number of markers recommended by the ISAG for bovine genetic identification is 12 STRs. In our work, around 24 SNPs were necessary to achieve an MP ($1.78E^{-11}$) equivalent to the standard marker set, and 31 SNPs (MP = $1.87E^{-14}$) were equivalent to the 18 STR set (Tables S5 and S6). For paternity testing, and when the two parents were known, 37 SNPs were needed for a Q value similar to the standard marker set. The resolution of more complex cases requires the use of additional markers. In these situations, such as one known parent or missing parents, around 39 and 49 SNPs are required, respectively, to obtain the same Q values as the 18 STRs (Figure 3).

Discussion

Unrelated animal sampling has been successfully used to determine breed genetic profiles in phylogeographic studies and to estimate general theoretical Q and MP values for DNA identification (traceability, parentage analysis, etc.). Several studies have evaluated and compared the Q and/or MP values obtained for STR and SNP sets (Table S7). Most of them used only representative (unrelated) purebred samples to determine the entire genetic diversity. For example, Heaton *et al.* (2002) analyzed three composite bovine beef groups to identify SNPs useful for animal identification and paternity testing. Werner *et al.* (2004) selected unrelated bulls belonging to three dairy or dual-purpose pure breeds to identify SNPs and estimate their respective allelic frequencies. López Herráez *et al.* (2005) genotyped Galloway animals from different farms and used STRs and SNPs to compare the Q values in the identification of individuals and parental analysis. More recently, Karniol *et al.* (2009) evaluated the statistical power of the 25-plex assay in traceability (identity control) and parentage testing by genotyping unrelated animals from six cattle breeds.

These common approaches do not take into account population structure and consanguinity. Furthermore, most of the routine genotyping of livestock done in genetic laboratories consists of the analysis of highly related pedigree animals rather than unrelated animals from beef breeding or dairy farms. In this framework, a marker set should have enough exclusion power to resolve any possible situation, including cases of paternity with multi-putative consanguineous sires. In view of this scenario, and considering that there is generally much more experience in the use of STRs compared with SNPs, in this work we examined the amount of information obtained with SNP and STR markers for paternity testing and genetic identification within a consanguineous commercial Angus herd.

Almost all of the SNPs examined were polymorphic, with a mean MAF of 0.328, while more than 50% of the SNPs had a high Q value because both alleles had balanced gene frequencies. These findings were not unexpected given that SNPs from the Illumina BovineHD BeadChip were validated in Angus breeds and showed a high rate of polymorphic loci (573,437 out of 770,000). Comparison of the mean MAF values for the parentage subset of 116 SNPs showed that our inbred population gave a similar result in the Illumina test to that of the Red Angus (MAF = 0.327) and Angus (MAF = 0.346) samples used to validate the chips (ftp.illumina.com). These values ranked in the upper third distribution among 29 breeds (MAF = 0.135 to 0.395), as reported by the manufacturer. The average MAF of the parentage subset was greater than those reported for the entire SNP panel (0.13-0.27), perhaps because this subset had been carefully selected and highly curated for this purpose.

The comparison of the two types of markers showed that, in the case of matching samples, two SNPs were nec-
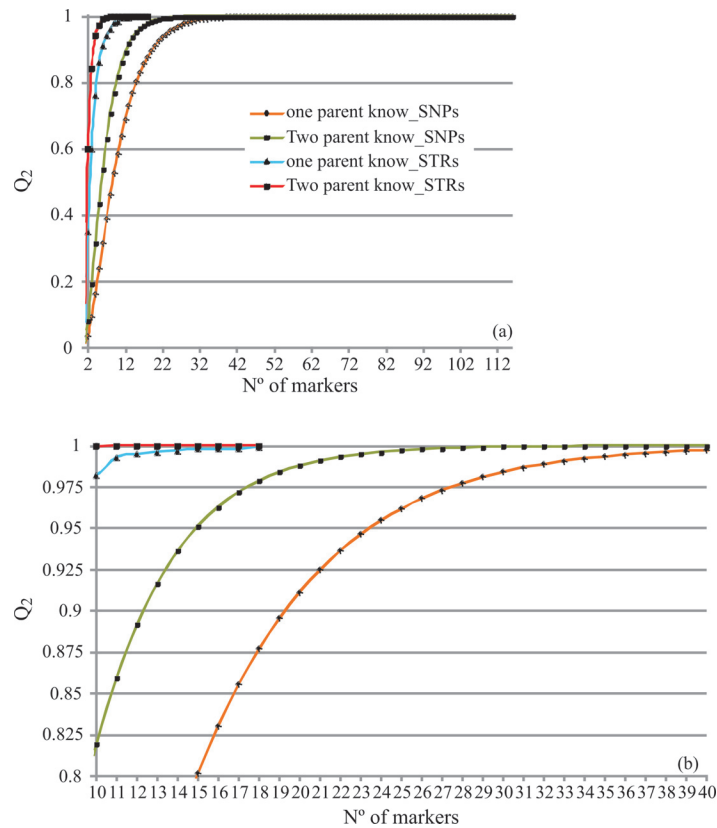
Figure 3 - Comparison of the cumulative exclusion power (Q) curves calculated for SNPs and STRs considering two mismatch criteria (Q_2) for cases of two known parents and matching samples. Markers are listed based on decreasing expected heterozygosity (h_e).

essary to provide the same statistical power as one STR (five STRs and 10 SNPs for a $Q_2 \geq 0.999$). In the parentage analysis, 2.55 SNPs had a Q value equivalent to one STR when both parents were known and the two exclusion (Q_2) criteria were used. In this case, 18 STRs and 46 SNPs were required to reach a $Q_2 \geq 0.999$. The SNP/STR ratios obtained here were similar to those reported by others using unrelated animals. For example, Werner *et al.* (2004) observed that 37 SNPs provided the same power as a typical, commonly used microsatellite set, whereas Weller *et al.* (2006) reported a ratio of 2-2.25 (25 SNPs were equivalent to 11 microsatellites with five alleles) using simulated data. More recently, Fisher *et al.* (2009), based on an analysis of simulated data and data from a test Jersey herd, indicated that 40 SNPs (with a mean MAF of 0.35, similar to that observed here) would be at least as effective for parentage matching as the 14 STR panel currently used for parentage testing in New Zealand dairy animals.

With regard to the MP, our results agreed with previously published data in that 25 SNPs were equivalent to 11-12 STRs (MP $\sim 10^{-11}$) (Table S7), sufficient to resolve simple cases of genetic identification. However, in routine work, more markers (17-18) are usually needed to resolve complicated cases such as parentage analysis with one known parent and multiple, closely related putative sires. As shown in Table S7, an MP value of 10^{-13} to 10^{-15} can be obtained by analyzing 17-18 STRs in a purebred breed, whereas 29-34 SNPs were required to reach an equivalent MP in our inbreeding Angus population. Interestingly, by using 12 and 18 STRs we achieved MP values of 10^{-11} and 10^{-14}, similar to that obtained with 24 and 31 SNPs, respectively.

Recently, Baldo *et al.* (2010) showed that in beef traceability $\sim 25\%$ more microsatellite markers were needed to identify consanguineous animals *vs.* unrelated animals. In contrast, our results show that, in this same context, the number of SNPs needed to provide the same Q in consanguineous samples and in the Illumina reference samples would be similar. The difference between these two studies can be explained by the fact that biallelic SNP markers are less affected by consanguinity than multiallelic STRs. In this sense, consanguinity affects the number of alleles first and then gene diversity, thereby easily purging rare STR alleles.

In conclusion, our results show that approximately twice as many SNP markers were needed to provide the same effectiveness as STRs for genetic identification and parentage analysis in a consanguineous Angus herd. This ratio is similar to previously reported values and provides evidence that biallelic SNPs are apparently less affected by consanguinity and population structure than STRs. International collaborations by the ISAG and ICAR have sought to

select and validate SNPs that can be used in a standard panel for genetic identification in cattle. The results described here provide genetic information that supports the consensus SNP panel developed by the Parentage Recording Working Group of ICAR.

Acknowledgments

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Internet Resources

International Society for Animal Genetics, http://www.isag.org.uk (March 30, 2012).

Illumina BovineHD BeadChip, http://www.illumina.com/Documents//products/datasheets/datasheet_bovineHD.pdf (March 30, 2012).

Supplementary Material

The following online material is available for this article:
- Figure S1 - Schematic diagram of the breeding system used.
- Figure S2 - Distribution of the SNP exclusion power.
- Table S1 - Alleles observed per SNP.
- Table S2 - Alleles observed per STR.
- Table S3 - Exclusion power (Q) estimated for each SNP.
- Table S4 - Exclusion power (Q) estimated for each STR.
- Table S5 - Cumulative non-exclusion power (1 - Q) calculated for SNPs.
- Table S6 - Cumulative non-exclusion power (1 - Q) calculated for STRs.
- Table S7 - Match probability values obtained in recent studies.

This material is available as part of the online article from http://www.scielo.br/gmb.

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