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DNA fingerprinting analysis of Booroola pedigrees: a search for linkage to the Booroola gene

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Abstract. Seven minisatellite probes from a variety of sources were used to analyse 11 paternal half-sib families in which the Booroola gene was segregating. A total of 402 bands that showed segregation in the pedigrees were examined for linkage to the Booroola gene. None of the bands showed segregation with the Booroola gene. The most likely evidence for a linked band was produced by the HaRas HVR probe in Family 902 ($\theta = 0.0$; LOD 2.3). The conclusion, however, is that the minisatellite probes used in this study could not be used as markers for the Booroola gene. The study highlighted problems associated with the use of minisatellite probes in linkage studies in half-sib families. The complex banding patterns found on fingerprinting gels was a major source of scoring error. In a few cases both of the sire's alleles could be identified at a particular locus, but in most cases only one of the alleles could be identified. For the most part, the bands had to be treated as dominant alleles. The contribution of dam alleles to the banding pattern could only be estimated. There was an indication that minisatellite loci in sheep are clustered in particular regions of the sheep genome as the rate at which bands segregated with each other was higher than one would expect from loci randomly distributed throughout the genome.

Key words: DNA fingerprinting – Multilocus minisatellite probes – Sheep genetics – Booroola (Fec^B mutation) – Genetic linkage analysis

Introduction

The Booroola gene (Fec^B), first identified in Merino sheep from New South Wales, Australia (Piper and Bindon 1982), increases ovulation rate in sheep. Ewes carrying the Fec^B mutation display differences in pituitary and ovarian function both during development and as adults (Fleming et al. 1992; McNatty et al. 1987; Montgomery et al. 1989). The Fec^B mutation has been significantly excluded from linkage to the α- and β-subunits of FSH (Montgomery et al. 1992), α-inhibin, βA-inhibin and follistatin (G. W. Montgomery, personal communication). A range of polymorphic blood protein markers have also been excluded from linkage to the Booroola gene (Tate et al. 1992; Nguyen et al. 1992).

Minisatellites or VNTRs (variable number tandem repeats) are usually GC rich, short 9- to 64-bp sequences that are repeated in tandem (Jeffreys et al. 1985A; Nakamura et al. 1987; Wyman and White 1980). The number of repeats in tandem shows allelic variation thought to be brought about initially by mis-alignment and crossover at meiosis. The frequency of this event has been estimated at approximately 10^{-2}–10^{-4} per kilobase of DNA per generation (Jeffreys et al. 1985A), which is stable enough to follow the inheritance of bands from either parent.

The applications of DNA fingerprinting in forensics (Gill et al. 1985), immigration law (Jeffreys et al. 1985B), paternity testing, transplant screening, ecological genetics (Pemberton et al. 1992), segregation analysis with disease (Jeffreys et al. 1986) or production traits (Georges et al. 1990) and gene mapping (Wells et al. 1989) are far reaching and well documented. In this paper we demonstrate the application of DNA fingerprinting to linkage studies in sheep using a variety of minisatellite probes to examine linkage to the Booroola gene.

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Materials and methods

DNA fingerprinting

A heparinised blood sample was taken from each animal, and the DNA was purified from the white blood cells (Montgomery and Sise 1990) and digested with restriction endonucleases *Alu*I and *Hae*III. The digested DNA was loaded onto a 0.7% agarose gel and electrophoresed in TBE buffer for 40 h at 55 V (Crawford and Buchanan 1990). The dimensions of the agarose gels were 250 mm × 200 mm (BRL Model H4) using a 20-well comb. The DNA in the gel was transferred to Hybond N+ membrane according to the manufacturer's instructions (Amersham, UK). The membrane was prehybridised for a minimum of 30 min in 7% SDS, 1% BSA, 1% dextran sulphate, 1 m*M* EDTA, 0.263 *M* phosphate buffer pH 7.2 at 63 °C. The membranes were hybridised at 63 °C overnight in the same prehybridisation buffer containing a radioactively labelled heat-denatured probe, and then the were washed consecutively in 2 × SSC + 0.1% SDS at 63 °C for 1, 15 and 30 min before being blotted dry, wrapped in polyethylene film and autoradiographed using Kodak XAR film with intensifying screens at −70 °C.

Fingerprinting probes

A total of seven DNA fingerprinting probes were used in this study (see Table 1). Of these six were typical fingerprinting probes containing GC-rich tandem repeats between 15 and 28 bp in length: four were derived from the human genome and two from viruses. The seventh probe contained a dinucleotide repeat derived from the sheep genome. The probes were all radioactively labelled using the random priming method (Feinberg and Vogelstein 1983).

In scoring each probe/pedigree combination for linkage the gel was independently scored by two individuals. The sires' alleles (bands) to be scored were identified first, and then the progeny were scored for the presence or absence of each of the sires' alleles. Sire bands were chosen for scoring if they were considered readable across the entire gel and showed segregation, i.e. the band was not found in all offspring.

Sheep pedigrees and phenotype assignment

Half-sib pedigrees, each containing a ram heterozygous for the Booroola gene (B+) and his daughters, were used in the segregation study. All of the mothers were wild type (++) at the Booroola locus so that the daughters were either B+ or ++. A description of the pedigrees used in this study is found in Table 2. Assignment of the daughters' Booroola genotype as either B+ or ++ was made on the basis of ovulation rate measurements.

The ovulation rate was measured by counting the number of corpora lutea on the ovaries by laparoscopic examination. Three or four examinations over 2 years were made for each daughter. Genotypes were assigned using a more stringent version of the phenotype criteria of Davis et al. (1982). Daughters were classified B+ if two or more observations of three corpora lutea, or one or more of more than three were recorded. Daughters were classified as ++ if there was at least one observation of a single corpus luteum and if there were no observations of three or more corpora lutea over at least three examinations. Daughters in which the observations fell outside these criteria were not assigned or used in the linkage analysis. These are the same pedigrees used by Tate et al. (1992) in excluding blood protein markers from linkage with the Booroola gene.

Estimation of allele frequencies in dams

By considering the excess of bands present over those absent in the daughters, we could calculate an estimate of the probability that a dam contributed the allele: if the allele frequency in the dams is p then the probability that the daughter does not have the band is (1-p)/2. Therefore, p is estimated by the number of bands present minus the number of bands absent divided by the total number of bands scored.

Linkage analyses

Linkage of the minisatellite markers with the Booroola gene was tested using the methods of Dodds et al. (1993) for dominant markers in half-sib families where the marker types of the dams are unknown. This method allows for the possibility that a daughter may have received the band of interest from her dam. Linkage between pairs of markers was analysed in a similar way. The probabilities of the band patterns were found which allowed the likelihood to be written as a function of the recombination fraction and the dam's allele frequency at the two loci being analysed. The LOD score was calculated as the difference be-

Table 2. Half-sib pedigrees used for DNA fingerprinting analysis and linkage analysis to the Booroola gene

Family number	Sire number	Genotype of daughters[a]		
		++	B+	Total
901	82/0173	8	22	30
902	82/0161	11	20	31
903	85/0109	13	7	20
904	86/0367	6	8	14
905	86/0026	7	5	12
906	86/0041	8	6	14
907	86/0402	8	7	15
908	86/0037	9	5	14
909	83/0008	6	3	9
961	84/0006	4	7	11
962	86/0213	4	7	11

[a] The Booroola genotypes of 70 additional daughters couldn't be assigned

Table 1. Probes used in DNA fingerprinting analysis

Name	Origin	Repeat sequence	Reference
α-Globin HVR	Human	AACAGCGACACGGGGGG	Wyman and White 1980
M13	Bacteriophage	GAGGGTGGXGGXTCT	Vassart et al. 1987
HaRas HVR	Human	GGGGGAGTGTGGCGTCCCCTGGAGAGAA	Capon et al. 1983
ORF	Parapox virus	CTCCCTGACTCCCGA	Crawford et al. 1991
pUCJ	Human	GGAGGTGGGCAGGAAG	Georges et al. 1988
pV4	Sheep	$(GT)_{10}G_{10}TGGAT(GT)_4GG(GT)_4$	Buchanan and Crawford 1992
Insulin HVR	Human	ACAGGGGTGTGGGG	Bell et al. 1982

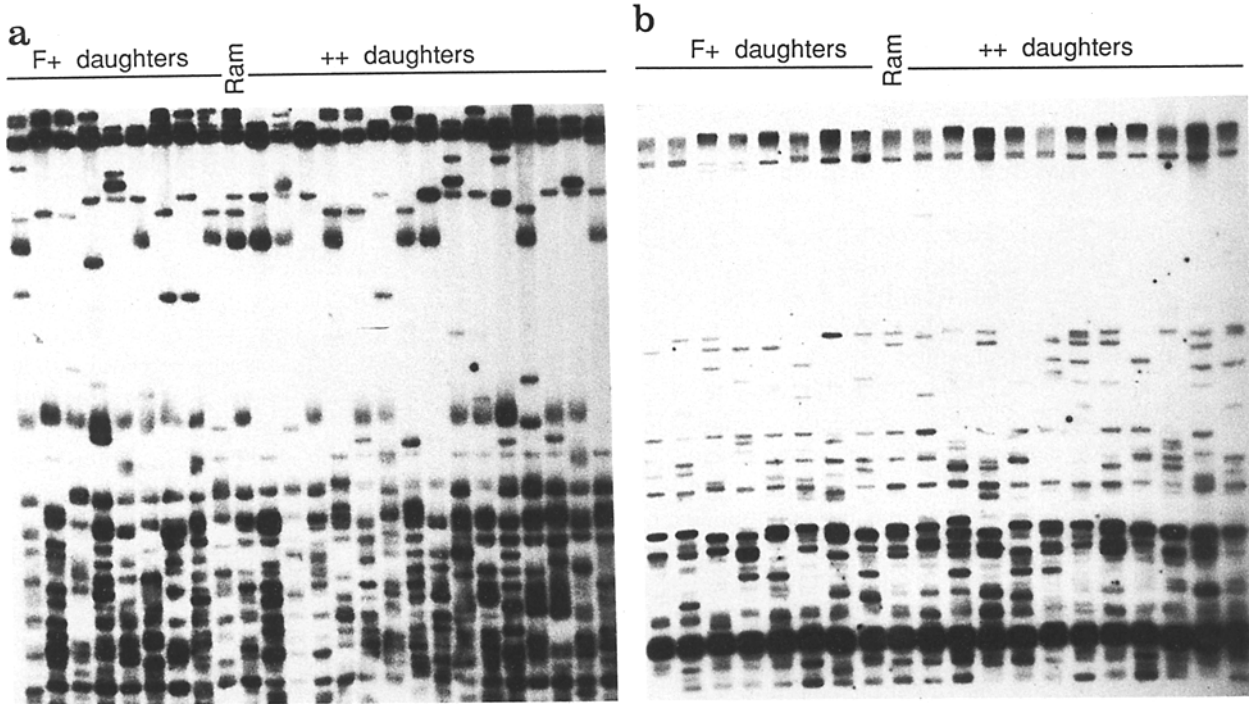

Fig. 1 a, b. Fingerprinting results from two half-sib pedigrees in which the rams are heterozygous for the Booroola gene (Fec^B). *Panel a* contains DNA of animals from Family 903 probed with M13 and *Panel b*, Family 907 probed with Insulin HVR. The *arrowheads* on the left-hand side of panel A indicate two bands in this pedigree that are allelic

Table 3. Comparison of probe usefulness

	α-Globin	M13	HaRas	ORF	pUCJ	pV4	Insulin
Average number of bands scored/pedigree	3.4	6.0	7.3	3.5	4.7	5.6	7.5
Percentage mismatches[a]	3.4	7.2	9.0	8.8	17.0	9.9	8.4

[a] Each autoradiograph was independently analysed by two scores. The number of scoreable bands found in the sire's pattern was first agreed upon by both scorers then each daughter's fingerprint was analysed for the presence or absence of ech of the sire's bands. The results from the two individuals were then compared and where the interpretation differed (i.e. one individual scored a band as being present and the other individual scored it as absent or vice versa), a mismatch was noted

tween the $\log_{10}$ likelihood maximised over the three of these parameters and the $\log_{10}$ likelihood with the recombination fraction set at 0.5 and maximised over the dam's allele frequencies.

Markers identified with the same probe were not analysed for linkage, but bands which were always present or absent together were assumed to be the same allele, while band pairs present in any daughter were assumed to be different alleles at the same locus. These reduced the total set of bands under investigation.

Results

Two examples of our fingerprinting gels are given in Fig. 1. Occasionally, we were able to see both alleles at a locus (see arrowheads in Fig. 1 A), but in the great majority of cases we made the assumption that the other allele was not visible. Absence of a band implied that the other allele had been inherited. The probes varied in the number of bands that could be scored (Table 3). The Insulin HVR probe was the most informative with an average of 7.5 bands scored per pedigree (range = 4–12) and α-globin was the least informative (average = 3.4 scored bands; range = 0–9).

Two major difficulties arose in scoring. Sometimes faint bands were visible to some scorers but not to others. Bands with very slightly altered positions required a subjective decision about whether it was to be scored as the sire's band or as a non-scored maternal band. To gain some insight into what the error rate might be, we compared the 8,946 individual assignments given by two independent scorers (see Table 3). Depending on the probe, the rate at which the assignments disagreed (mismatches) varied from 3.4% (α-globin) to 17% (pUCJ). To remain

consistent, we chose the results from one scorer only when we analysed the bands for linkage to the Booroola gene.

In linkage studies it is crucial that pedigree information is correct. As a check of our pedigree records we analysed all of the daughters to determine what proportion of the sire's bands could be identified in their fingerprinting pattern. One would expect that each daughter would receive 50% of the sire's bands, and may also receive copies of these bands from their dams. The majority of daughters had more than 50% of their sire's alleles, but a few individuals stood out. An example of this is provided by Family 906 (Table 4). Daughter 7 received 32% of the sire's bands, whereas the remaining daughters all received more than 50% of the sire's bands. While these data do not completely exclude this individual from the pedigree, it suggests that the ram may not be the sire of this individual. This individual was subsequently excluded from the pedigree using a highly polymorphic microsatellite (data not shown). Within the families that have been genotyped extensively by highly polymorphic single locus probes (Families 901–909), 6 out of 9 individuals with at most 40% of their sire's bands have been excluded from the pedigree whereas only 1 of the remaining 203 individuals with more than 50% of their sire's bands was excluded. Family 961, which has not been genotyped with microsatellites, also had 2 daughters that received less than 40% of their sire's bands. Given our experience with the other families, there was a high probability that these were not correctly assigned to the pedigree, and they were also excluded from the analysis.

Another feature of the data was that there were often bands which were absent for only those individuals who were eventually excluded. This meant that 7 bands needed to be removed from the list of segregating bands. From the remaining data the frequency of the sire bands in the dams was estimated to be 0.23 (SE 0.01) on average. This is close to the figure of 0.2 reported in cattle by Georges et al. (1990).

Despite DNA fingerprinting 251 individuals with seven different multilocus minisatellite probes, the aim of this study, which was to find a DNA fingerprinting band linked to the Booroola gene, was not achieved. Not one of the 399 segregating sire bands that was identified in the pedigrees by any of the probes showed significant linkage to the Booroola gene. The strongest linkage obtained was with a band produced by the HaRas HVR probe in

Table 4. Band sharing between sire and putative offspring in Family 906

Probe used	Number of sires bands scored	Daughter number																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
pV4	5	3	3	2	4	3	2	2	3	3	3	3	3	3	2	3	1	1	3	3
pUCJ	7	3	5	5	4	3	4	3	6	6	3	4	5	4	5	6	4	5	5	6
HaRas	8	7	5	7	5	6	6	2	5	5	6	6	5	5	5	6	4	6	5	6
Insulin	6	3	5	5	2	5	3	2	3	5	6	4	3	4	4	4	5	5	3	6
α-Globin	4	1	1	3	1	3	3	0	2	2	2	3	3	2	3	2	3	3	2	1
M13	8	5	7	7	7	7	6	3	6	5	5	6	5	7	5	6	6	6	7	6
Total	38	22	26	29	23	27	24	12	25	26	25	26	24	25	24	27	23	26	25	28

[a] Unlikely to be part of the family as only 32% of the sire's bands were found in this daughter

Table 5. Number of bands scored[a] for each probe in each family

Family number	α-Globin	M13	HaRas	ORF	pUCJ	pV4	Insulin	Total
901	4	3	6	5	5	6	4	33
902	7	4	7	4	4	6	5	37
903	0	5	7	3	4	5	6	30
904	0	5	10	6	6	7	8	42
905	0	4	7	3	4	4	6	28
906	4	7	8	0	7	5	5	36
907	4	3	5	3	0	6	9	30
908	5	9	8	1	7	7	7	44
909	0	9	7	4	3	3	10	36
961	9	3	5	6	5	7	12	47
962	3	0	9	3	7	5	9	36
Total sires bands scored for linkage								399

[a] A band was chosen for scoring if it was considered readable across the entire gel and showed segregation, i.e., not found in all offspring

Family 902, which showed no recombinants and a LOD score of 2.3. Table 5 lists the numbers of sire's bands scored for each probe in each family.

DNA fingerprinting patterns for many domestic animal species, including sheep, are less variable than for humans (Jeffreys et al. 1985A). As a further source of variation, we explored the possibility of using a variety of enzymes on the same pedigree. It was found, however, that despite using different enzymes the same probe often gave similar patterns especially in the high-molecular-weight region of the gel where often the most readable and informative bands occur. An example of this is shown in Fig. 2, where the high-molecular-weight regions of two fingerprinting gels of the same 19 individuals are shown. The gels differ only in the use of two different restriction enzymes with different recognition sites, *Hinf*I (G/ANTC) and *Alu*I (AG/CT). Although not identical, the high degree of similarity between the patterns suggested that we were analysing the same loci, indicating that changing enzymes does not necessarily change the loci that are observed on the fingerprinting gel. As a result of this finding we used a double digest of *Alu*I and *Hae*III for all of the DNA fingerprinting gels of Booroola pedigrees.

As well as looking for linkage between bands and the Booroola gene, we also examined our pedigrees for linkage among bands. Evidence from humans indicates that minisatellite loci are clustered in regions near the telomeres (Royle et al. 1988), whereas evidence from mice and cattle shows no such clustering. If minisatellite loci were clustered in sheep, one would expect linkage between bands to be higher than if they were randomly distributed throughout the genome.

To estimate how often we might expect significant linkage from randomly spaced markers, some simulations were performed. It was assumed that with the allele frequencies in the dams averaging 0.226, linkages up to 10 c*M* for families 901 and 902 and linkages up to 5 c*M* in the other families could be detected. For each family the simulations generated 1,000 sets of markers randomly placed on chromosomes whose lengths were those of sheep chromosomes (26 pairs of autosomes with a total length 27 M, Chapman and Bruere 1977). For each family, the number of markers simulated was the same as the number we had scored in that family (see Table 5). The number of pairs of simulated markers within 10 c*M* (for Families 901 and 902) or 5 c*M* (all other families) was noted. Over all of the families the expected number of linkages was found to be 22.5 (SE 4.7) compared with the observed number, 43. This result suggests that the alleles identified by these seven minisatellite probes may be clustered in the sheep genome. We recognise, however, that the standard error given may be an underestimate, as we have simplified the effect of several sources of variation (e.g. dam's allele frequency at each locus, number of daughters scored within a particular family, non-identification of all allelic or same locus bands for a probe, scoring errors); and therefore, the observed number of linkages may not be as extreme as it appears.

Discussion

This study has highlighted some of the problems associated with the use of minisatellite markers in linkage studies, has allowed us to audit the parentage information of our half-sib pedigrees and has given us insight into the distribution of minisatellite elements in the sheep genome.

Multilocus DNA fingerprinting probes have two main advantages over restriction fragment length polymorphism (RFLP) markers. The fingerprinting probes are multilocus so that more than one locus can be analysed in a single experiment. In our case, an average of five loci could be analysed per gel run. Minisatellite loci are also highly polymorphic, and as a result most loci are heterozygous in the sire thereby allowing segregation to be observed.

These features can cause difficulties when it comes to analysing the DNA fingerprinting gel. The first difficulty is that all analysis has to be conducted within a pedigree because the locus analysed in one pedigree cannot be identified in the next, thus preventing the combining of LOD scores across the pedigrees. Therefore, marker loci

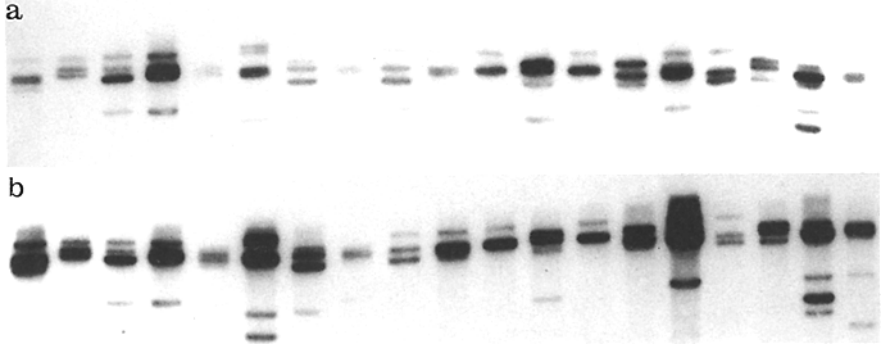

Fig. 2a, b. Fingerprinting results from the same animals using different restriction enzymes. Genomic DNA from animals from Family 902 (first 18 daughters and the sire) was cut with either *Alu*I (*Panel a*) or *Hinf*I (*Panel b*) and probed using the M13 minisatellite repeat. Only the high-molecular-weight region of the fingerprinting results (15–20 kbp) are shown in each panel

must be close to the Booroola gene if genetic linkage is to be detected in small families. In our two small pedigrees, even with no recombinants, a LOD score of 3.0 or greater was not possible. In our largest pedigree, any marker that was greater than 16 c*M* from the Booroola gene would not be expected to show significant linkage even if the sire's band was not present in the dams. Had we been able to identify the most strongly linked band (Haras HVR band 4 in Family 902) in other pedigrees, we may have been able to confirm that it was linked to the Booroola gene. Another example of this problem was the genetic linkage to the bovine muscular hypertrophy gene obtained by Georges et al. (1990) where a LOD score of 2.4 to this gene was obtained in a single pedigree, but this could not be combined with information from other pedigrees.

The second problem is that often only one allele is identified, and therefore markers have to be treated as being dominant. The third problem is the potential errors in scoring for the presence or absence of a band. To some extent this is dependent on the quality of the DNA fingerprinting gel, as this methodology is technically very demanding. We believe our fingerprinting gels were of an acceptable standard, yet two independent and well-practiced scorers could not agree on the presence or absence of a band in about 8% of the cases. A solution to this problem that does not involve replication of the technically demanding experiments is not readily apparent. In using the results obtained from fingerprinting gels it is important that this source of error is recognised.

Once linkage to a particular major gene such as Booroola has been achieved, the chromosome location is required. Some DNA sequence not repeated many times in the genome is necessary for this. For this reason a linked RFLP probe or a microsatellite with its unique primer pair is better than a multilocus minisatellite probe. The only information one has about a linked minisatellite band is that it contains a widely distributed genomic repeat. Although some minisatellite loci have been cloned, it is a very difficult exercise which is preferable to avoid.

Because of the disadvantages associated with minisatellite probes we have now switched to searching for linkage to the Booroola gene with microsatellites. These markers offer the advantage of being both highly polymorphic yet identifiable as a single unique locus thereby allowing LOD scores to be combined across pedigrees and providing a unique site for in situ hybridisations to identify the chromosomal origin of any linked marker.

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