

# Extensive genomic conservation of cattle microsatellite heterozygosity in sheep

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## Summary

We report the evaluation of 1036 bovine microsatellite primer pairs for their suitability as linkage markers in sheep. Approximately 58% (605/1036) of bovine primer pairs amplified a locus in sheep. Sixty-seven per cent (409/605) of amplified loci were detected as polymorphic. Marker heterozygosity, allele number and range of allele sizes were significantly lower in sheep than cattle sampled in this study. However, median fragment size was similar. These data suggest that high-resolution comparative linkage maps between closely related species can be constructed relatively efficiently.

*Keywords:* heterozygosity, microsatellite, ovine

## Introduction

The significant homology of chromosomal banding structures between cattle, sheep and goats suggests a homologous genetic structure and karyotype (Hayes *et al.* 1991; Hediger *et al.* 1991; Ansari *et al.* 1993) that simplifies synteny mapping (Ansari *et al.* 1994; Pearce *et al.* 1995). Genome conservation extends to microsatellite (ms) loci among *bovid* and *caprid* species (Moore *et al.* 1991, 1992; Crawford *et al.* 1995; Vaiman *et al.* 1996). These tandemly repeated, highly polymorphic, single-locus DNA sequences (Weber 1990) are well distributed over numerous mammalian genomes (Hamada *et al.* 1982; Tautz 1989; Weber & May 1989), and are readily adaptable to polymerase chain reaction (PCR) systems (Weber & May 1989). Microsatellites are currently the marker of choice for establishing linkage maps (Dietrich *et al.* 1994; Barendse *et al.* 1994; Bishop *et al.* 1994; Crawford *et al.* 1995; Hudson *et al.* 1995), estimating genetic diversity (Takezaki & Nei 1996) and studying evolutionary relationships (reviewed in Beattie 1996). Primer pairs developed for ms loci derived from cattle and sheep

have recently been reciprocally assigned to linkage groups on homologous chromosomes within each species (Barendse *et al.* 1994; Bishop *et al.* 1994; Crawford *et al.* 1995; Barendse *et al.* 1997; Kappes *et al.* 1997a).

However, the use of a comparative linkage strategy to provide a robust estimate of genome coverage, determine (genetic) breakpoints about syntenic regions and improve the resolution around a quantitative trait locus (QTL) (Georges *et al.* 1993; Cockett *et al.* 1994; Charlier *et al.* 1995) is currently hampered by the limited number of ms informative across species (Moore *et al.* 1991, 1994; Pepin *et al.* 1995; Kemp *et al.* 1995; Crawford *et al.* 1995).

We report the evaluation of 1036 primer pairs for bovine ms for their suitability as (linkage) markers in sheep. This total includes 82 bovine primer pairs previously screened across several sheep populations (Moore *et al.* 1994; Vaiman *et al.* 1994a,b; Kemp *et al.* 1995). All sequences have been deposited in either the GenBank or USDA-ARS-MARC (Keele *et al.* 1994) databases.

## Materials and methods

### Microsatellites

Bovine ms were screened across ovine DNA, irrespective of whether they had been previously described to amplify sheep DNA, to eliminate any bias in sampling. It was presumed that all published primer pairs were originally selected based on a minimum repeat length of approximately 12 dinucleotides.

### Animals

DNA was isolated from eight F<sub>1</sub> rams, representing two different pedigrees, designed to maximize marker heterozygosity for construction of a sheep linkage map. Four rams were paternal half-sibs with a common Texel sire and different Coopworth dams; these rams were sires of the three generation International Mapping Flock (IMF) (Crawford *et al.* 1995). The remaining four rams were produced from reciprocal matings of Romanov and Rambouillet sheep (two rams) and the product of Romanov × Suffolk matings (two

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Accepted 17 April 1997

rams). Bovine DNA samples included the two F<sub>1</sub> sires and eight F<sub>1</sub> dams of the four-way *Bos taurus*-cross reference population (Bishop *et al.* 1994).

#### PCR conditions and analysis

DNA was extracted from white blood cells as previously described (Miller *et al.* 1988). Primer pairs were initially tested for amplification using a PTC-100 thermocycler (MJ Research, Inc., Watertown, MA) without incorporation of radioisotope (Bishop *et al.* 1994). Approximately half of the primer pairs (494; 47.6%) were tested at a single annealing reaction. The remaining primer pairs (542) were screened over several annealing reactions. In general, PCR reactions (12 µl) contained 100 ng template DNA, buffer (50 mM KCl, 1.5 mM MgCl<sub>2</sub>, 10 mM Tris HCl; pH 9.0), 30 mM of each dNTP (unlabelled), 0.04 mM primer pairs and 0.35 units *Taq* DNA polymerase.

All amplifications included an initial denaturing step of 3 min at 94°C; this was followed by 30 cycles of 1 min at 94°C, 1 min at the annealing temperature and 1 min at 72°C. Final extension was for 4 min at 72°C. Amplification products were electrophoresed (40 V/cm) in 3% agarose and visualized after staining with ethidium bromide (1.5 µg/ml) against a standard set of markers. Radioisotope was directly incorporated into the PCR product by addition of 0.1 µCi (3000 Ci/mmol) [ $\alpha$ -<sup>32</sup>P]dATP and 3 mM unlabelled dATP, under identical conditions. Reaction products were electrophoresed on 7% denaturing polyacrylamide gels with a standard M13mp18 ladder and visualized as described (Bishop *et al.* 1994). References for each ms are listed in Table 1 and the MARC bovine database (<http://sol.marc.usda.gov>, Keele *et al.* 1994). Number of alleles, median fragment size, range of allele sizes and heterozygosity are listed for each ms in Table 1. Percentage heterozygosity was calculated because the number of unrelated animals was not deemed adequate for the use of allele frequency. A paired *t*-test was conducted on the data set of 551 bovine-derived microsatellites that produced genotypes with cattle and sheep DNA. The difference between bovine and ovine values for each marker was analysed, taking into account the positive covariance between species to improve precision of the estimate. The null hypothesis therefore tested the equality of species means for each characteristic. Rejection of the null hypothesis indicated that the mean values for species were significantly different.

## Results and discussion

A total of 1036 primer pairs of bovine origin were screened across cattle and sheep genomic DNA. Table 1 identifies each bovine primer pair that amplified a product in sheep and details individual marker PCR conditions and heterozygosity. Bovine primer pairs that did not amplify sheep DNA under the limited conditions tested in this study are listed on the World Wide Web (<http://sol.marc.usda.gov/>). Six hundred and five bovine primer pairs amplified a single locus in sheep. Four hundred and nine of these amplified more than one allele among the eight sires. The remaining 196 that amplified a product amplified only one allele. Overall ms heterozygosity, excluding genotypes contributing null alleles identified by segregation, was 45.3% (Table 2). Table 2 summarizes allele number, range of allele sizes, median fragment size and heterozygosity of bovine-derived ms in cattle and sheep. Mean allele number, range and heterozygosity were significantly lower in sheep compared with F<sub>1</sub> *Bos taurus* sires and dams of a four-way-cross population (Bishop *et al.* 1994) genotyped for the same ms. Median fragment size was not different, however ( $P = 0.08$ ).

Recent analyses (Moore *et al.* 1994; Kemp *et al.* 1995; Crawford *et al.* 1995) suggest that about 68% (276/406) of primer pairs for bovine ms amplify a product from ovine DNA. Approximately 67% (range 63–73%) of primers amplifying a product were polymorphic, e.g.  $\geq 2$  alleles (Moore *et al.* 1994; Kemp *et al.* 1995; Crawford *et al.* 1995). However, the number of informative ms is likely to be overestimated because about 66% (133/202) of the bovine primers polymorphic in sheep were preselected in the Crawford *et al.* (1995) study on the basis of an allele number  $> 2.0$  in cattle. Sixty-seven per cent (409/605) of bovine primers amplifying a single locus in sheep were polymorphic (40% overall, 409/1036) in the present study. These results extend previous observations on the relative usefulness of bovine primers across closely related *bovidae* species to a larger number of primers. Our estimate of the percentage of bovine primers yielding polymorphic loci in sheep is conservative as only one set of amplification conditions was tried on a significant proportion of primers. Vaiman *et al.* (1996) reported that 34% (165/472) of bovine primer pairs yielded a polymorphic ms in goat under a single standardized condition, a value similar to our observation of approximately 40% polymorphic. Sixty-nine of the 165 ( $\approx 42\%$ ) bovine ms that were polymorphic in goat (Vaiman *et al.* 1996) were present and informative in sheep in this study.

**Table 1.** Polymerase chain reaction (PCR) conditions and heterozygosity of bovine primer pairs amplifying a product in sheep

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
2HF3B	USDA-MARC database, GenBank acc. no. L25287	58	7	1.00	145–173
ACIGP	GenBank acc. no. X03642	50	1	0.00	333
ADCY2	Lipkin <i>et al.</i> (1989)	56	4	1.00	186–204
AGLA13	Georges & Massey (1992)	50	1	0.00	189
AGLA17	Georges & Massey (1992)	56	1	0.00	207
AGLA227	Georges & Massey (1992)	58	1	0.00	141
AGLA232	Georges & Massey (1992)	58	2	0.25	170–172
AGLA233	Georges & Massey (1992)	50	1	0.00	229
AGLA269	Georges & Massey (1992)	56	9	0.75	228–274
AGLA280	Georges & Massey (1992)	60	3	0.38	153–157
AGLA285	Georges & Massey (1992)	56	5	1.00	130–138
AGLA29	Georges & Massey (1992)	58	7	0.63	166–198
AR028	Avraham <i>et al.</i> (1993)	54	2	0.67	246–256
BL1009	Smith <i>et al.</i> (1997)	58	5	0.75	167–181
BL1022	Smith <i>et al.</i> (1997)	58	2	0.25	82–84
BL1023	Primer pair sequences in USDA-MARC database	52	2	0.13	56–76
BL1080	Smith <i>et al.</i> (1997)	58	9	0.75	129–221
BL1095	Smith <i>et al.</i> (1997)	58	2	0.38	163–179
BL1103	Smith <i>et al.</i> (1997)	58	1	0.00	96
BL1134	Smith <i>et al.</i> (1997)	58	2	0.43	98–128
BL25	Bishop <i>et al.</i> (1994)	58	2	0.00	188–190
BL26	Smith <i>et al.</i> (1997)	58	1	0.00	125
BL28	Bishop <i>et al.</i> (1994)	54	1	0.00	100
BL37	Bishop <i>et al.</i> (1994)	56	1	0.00	222
BL4	Smith <i>et al.</i> (1997)	56	7	0.75	151–167
BL41	Bishop <i>et al.</i> (1994)	58	3	0.67	244–254
BL42	Bishop <i>et al.</i> (1994)	56	3	0.25	230–234
BL45	Primer pair sequences in USDA-MARC database	56	1	0.00	120
BL50	Bishop <i>et al.</i> (1994)	58	5	0.38	217–237
BL6	Grosz <i>et al.</i> (1997)	50	7	0.71	170–194
BM103	Bishop <i>et al.</i> (1994)	56	1	0.00	144
BM121	Bishop <i>et al.</i> (1994)	58	7	0.83	178–216
BM1225	Bishop <i>et al.</i> (1994)	56	3	1.00	249–257
BM1227	Bishop <i>et al.</i> (1994)	58	4	1.00	126–156
BM143	Bishop <i>et al.</i> (1994)	58	4	1.00	102–128
BM148	Bishop <i>et al.</i> (1994)	56	2	0.14	94–96
BM1508	Stone <i>et al.</i> (1995)	54	1	0.00	109
BM1520	Stone <i>et al.</i> (1997)	56	2	0.13	184–186
BM1557	Stone <i>et al.</i> (1995)	50	1	0.00	152
BM1577	Stone <i>et al.</i> (1997)	58	4	0.63	161–169
BM1608	Primer pair sequences in USDA-MARC database	58	1	0.00	125
BM17132	Stone <i>et al.</i> (1995)	56	4	0.25	81–87
BM1818	Bishop <i>et al.</i> (1994)	58	2	1.00	258–284
BM1826	Primer pair sequences in USDA-MARC database	56	1	0.00	70
BM1831	Primer pair sequences in USDA-MARC database	56	3	0.75	326–332
BM1832	Stone <i>et al.</i> (1995)	58	1	0.00	137
BM1834	Stone <i>et al.</i> (1995)	60	1	0.00	169
BM1838	Primer pair sequences in USDA-MARC database	58	1	0.00	168
BM1857	Bishop <i>et al.</i> (1994)	56	1	0.00	130
BM1861	Stone <i>et al.</i> (1995)	58	3	1.00	96–106
BM1862	Bishop <i>et al.</i> (1994)	56	2	0.50	191–192

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BM18620V	Primer pair sequences in USDA-MARC database	56	2	0.80	110–111
BM1864	Stone <i>et al.</i> (1995)	58	1	0.00	113
BM189	Primer pair sequences in USDA-MARC database	50	1	0.00	363
BM1904	Primer pair sequences in USDA-MARC database	56	1	0.00	213
BM1905	Bishop <i>et al.</i> (1994)	54	2	0.50	173–175
BM2023	Primer pair sequences in USDA-MARC database	58	2	0.50	118–144
BM203	Bishop <i>et al.</i> (1994)	58	6	0.83	215–239
BM2113	Sunden <i>et al.</i> (1993)	56	3	1.00	148–152
BM226	Bishop <i>et al.</i> (1994)	50	2	1.00	130–140
BM2504	Bishop <i>et al.</i> (1994)	56	3	1.00	135–145
BM2515	Bishop <i>et al.</i> (1994)	56	1	0.00	129
BM2607	Bishop <i>et al.</i> (1994)	58	1	0.00	118
BM2613	Bishop <i>et al.</i> (1994)	60	6	0.57	144–158
BM2814	Stone <i>et al.</i> (1995)	58	5	1.00	184–192
BM2830	Bishop <i>et al.</i> (1994)	56	3	0.63	121–129
BM2901	Stone <i>et al.</i> (1995)	56	3	0.13	110–132
BM2934	Bishop <i>et al.</i> (1994)	56	7	1.00	100–126
BM3010	Stone <i>et al.</i> (1995)	60	1	0.00	120
BM3011	Stone <i>et al.</i> (1995)	50	4	0.29	118–132
BM3020	Stone <i>et al.</i> (1995)	56	3	0.75	169–175
BM3026	Stone <i>et al.</i> (1995)	50	1	0.00	111
BM3033	Stone <i>et al.</i> (1995)	56	4	1.00	127–143
BM310	Bishop <i>et al.</i> (1994)	54	1	0.00	114
BM315	Bishop <i>et al.</i> (1994)	54	1	0.00	111
BM3205	Bishop <i>et al.</i> (1994)	54	5	0.50	207–219
BM321	Bishop <i>et al.</i> (1994)	54	1	0.00	170
BM3212	Primer pair sequences in USDA-MARC database	56	5	1.00	182–190
BM3215	Stone <i>et al.</i> (1995)	58	5	0.75	129–171
BM3406	Stone <i>et al.</i> (1995)	58	2	0.50	111–115
BM3412	Stone <i>et al.</i> (1995)	54	6	0.88	130–148
BM3501	Stone <i>et al.</i> (1995)	58	7	0.83	186–200
BM3507	Bishop <i>et al.</i> (1994)	54	1	0.00	192
BM3509	Stone <i>et al.</i> (1995)	54	5	0.63	135–149
BM3627	Bishop <i>et al.</i> (1994)	50	3	0.25	103–115
BM4002	Primer pair sequences in USDA-MARC database	56	1	0.00	104
BM4005	Bishop <i>et al.</i> (1994)	58	4	0.75	122–136
BM4006	Bishop <i>et al.</i> (1994)	54	5	0.88	101–133
BM4025	Bishop <i>et al.</i> (1994)	54	4	1.00	140–160
BM4102	Bishop <i>et al.</i> (1994)	54	1	0.00	181
BM4129	Stone <i>et al.</i> (1995)	56	3	0.50	72–80
BM4208	Bishop <i>et al.</i> (1994)	58	2	1.00	182–192
BM4215	Primer pair sequences in USDA-MARC database	54	1	0.00	87
BM4301	Stone <i>et al.</i> (1995)	58	3	0.50	135–151
BM4305	Bishop <i>et al.</i> (1994)	58	1	0.00	132
BM4307	Bishop <i>et al.</i> (1994)	56	1	0.00	164
BM4321	Bishop <i>et al.</i> (1994)	56	1	0.00	99
BM4439	Bishop <i>et al.</i> (1994)	54	2	0.38	218–221
BM4509	Stone <i>et al.</i> (1995)	58	2	0.75	121–122
BM4621	Bishop <i>et al.</i> (1994)	56	4	1.00	135–157
BM5004	Bishop <i>et al.</i> (1994)	54	2	0.25	104–108
BM6026	Bishop <i>et al.</i> (1994)	54	1	0.00	140

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BM603	Primer pair sequences in USDA-MARC database	54	1	0-00	91
BM6041	Bishop <i>et al.</i> (1994)	56	3	1-00	127-139
BM6121	Bishop <i>et al.</i> (1994)	54	2	0-13	130-152
BM6302	Stone <i>et al.</i> (1995)	56	3	0-38	217-227
BM6404	Bishop <i>et al.</i> (1994)	58	3	0-50	133-145
BM6433	Stone <i>et al.</i> (1995)	56	3	0-88	91-94
BM6436	Bishop <i>et al.</i> (1994)	56	1	0-00	191
BM6447	Primer pair sequences in USDA-MARC database	54	3	0-50	192-198
BM6458	Bishop <i>et al.</i> (1994)	58	1	0-00	112
BM6465	Stone <i>et al.</i> (1995)	58	7	1-00	119-133
BM6466	Stone <i>et al.</i> (1995)	56	4	1-00	103-155
BM6506	Bishop <i>et al.</i> (1994)	58	3	1-00	192-202
BM6507	Stone <i>et al.</i> (1995)	52	2	0-33	143-149
BM6526	Bishop <i>et al.</i> (1994)	56	3	1-00	161-169
BM7109	Bishop <i>et al.</i> (1994)	54	4	1-00	174-194
BM7113	Primer pair sequences in USDA-MARC database	58	1	0-00	92
BM713	Bishop <i>et al.</i> (1994)	58	1	0-00	109
BM7136	Stone <i>et al.</i> (1995)	54	5	1-00	102-124
BM7144	Stone <i>et al.</i> (1995)	56	4	1-00	173-189
BM7145	Stone <i>et al.</i> (1997)	56	2	0-38	119-125
BM716	Bishop <i>et al.</i> (1994)	54	1	0-00	115
BM7160	Stone <i>et al.</i> (1995)	54	1	0-00	162
BM7165	Stone <i>et al.</i> (1995)	56	4	0-75	219-233
BM717	Primer pair sequences in USDA-MARC database	54	1	0-00	124
BM720	Bishop <i>et al.</i> (1994)	54	3	0-29	201-221
BM7207	Stone <i>et al.</i> (1995)	58	1	0-00	106
BM7208	Stone <i>et al.</i> (1997)	58	1	0-00	146
BM7213	Stone <i>et al.</i> (1995)	54	2	0-38	122-124
BM7225	Stone <i>et al.</i> (1995)	50	1	0-00	94
BM7228	Stone <i>et al.</i> (1995)	54	1	0-00	113
BM7234	Stone <i>et al.</i> (1995)	58	2	0-63	105-109
BM7237	Stone <i>et al.</i> (1995)	58	6	0-63	110-122
BM7241	Kappes <i>et al.</i> (1997a)	60	6	0-38	105-125
BM7243	Primer pair sequences in USDA-MARC database	56	6	0-88	140-158
BM7247	Bishop <i>et al.</i> (1994)	54	4	0-38	105-122
BM733	Bishop <i>et al.</i> (1994)	54	1	0-00	161
BM737	Stone <i>et al.</i> (1995)	54	4	1-00	119-125
BM741	Bishop <i>et al.</i> (1994)	54	1	0-00	156
BM746	Bishop <i>et al.</i> (1994)	56	5	0-63	163-173
BM757	Bishop <i>et al.</i> (1994)	58	5	1-00	179-186
BM804	Bishop <i>et al.</i> (1994)	54	1	0-00	161
BM81124	Stone <i>et al.</i> (1995)	54	6	1-00	183-213
BM8118	Stone <i>et al.</i> (1995)	56	3	0-38	138-142
BM8124	Stone <i>et al.</i> (1995)	58	4	0-50	113-120
BM8125	Bishop <i>et al.</i> (1994)	58	4	0-75	116-122
BM8129	Stone <i>et al.</i> (1995)	54	1	0-00	143
BM8139	Stone <i>et al.</i> (1995)	48	1	0-00	91
BM8151	Stone <i>et al.</i> (1995)	56	2	0-50	121-125
BM8217	Primer pair sequences in USDA-MARC database	50	2	0-50	240-246
BM8225	Stone <i>et al.</i> (1995)	58	3	0-13	141-145
BM8230	Stone <i>et al.</i> (1995)	58	3	1-00	99-109
BM8246	Stone <i>et al.</i> (1995)	58	6	0-75	172-186
BM8247	Stone <i>et al.</i> (1995)	58	1	0-00	131

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BM827	Bishop <i>et al.</i> (1994)	58	3	0.25	216–224
BM856	Stone <i>et al.</i> (1995)	54	6	1.00	169–189
BM861	Bishop <i>et al.</i> (1994)	60	1	0.00	163
BM888	Bishop <i>et al.</i> (1994)	54	1	0.00	104
BM9058	Stone <i>et al.</i> (1995)	54	6	0.88	127–145
BM9065	Stone <i>et al.</i> (1995)	52	1	0.00	159
BM9138	Stone <i>et al.</i> (1995)	52	1	0.00	162
BM9202	Stone <i>et al.</i> (1995)	54	1	0.00	81
BM9208	Stone <i>et al.</i> (1995)	58	1	0.00	119
BM9248	Stone <i>et al.</i> (1995)	60	6	1.00	244–308
BM9284	Stone <i>et al.</i> (1995)	58	1	0.00	112
BM9289	Stone <i>et al.</i> (1995)	50	2	0.13	93–97
BMB1227OV	Primer pair sequences in USDA-MARC database	58	2	0.50	108–114
BMC1222	Bishop <i>et al.</i> (1994)	56	8	0.88	307–322
BMC2208	Kappes <i>et al.</i> (1997b)	60	2	0.50	153–157
BMC2228	Kappes <i>et al.</i> (1997b)	50	4	0.88	169–179
BMC3221	Kappes <i>et al.</i> (1997b)	56	3	0.50	121–129
BMC5221	Bishop <i>et al.</i> (1994)	56	7	0.86	181–217
BMC5227	Kappes <i>et al.</i> (1997)	58	1	0.00	151
BMC6004	Kappes <i>et al.</i> (1997)	58	3	0.25	269–277
BMCR17A	Primer pair sequences in USDA-MARC database	58	1	0.00	149
BMS1004	Stone <i>et al.</i> (1995)	58	9	1.00	153–183
BMS1008	Stone <i>et al.</i> (1995)	54	2	1.00	167–171
BMS1022	Primer pair sequences in USDA-MARC database	58	2	0.75	90–92
BMS1048	Stone <i>et al.</i> (1995)	58	2	0.13	106–112
BMS107	Primer pair sequences in USDA-MARC database	54	1	0.00	176
BMS1074	Stone <i>et al.</i> (1995)	60	1	0.00	143
BMS108	Stone <i>et al.</i> (1995)	54	5	0.67	90–112
BMS109	Stone <i>et al.</i> (1995)	56	3	0.75	114–122
BMS1101	Stone <i>et al.</i> (1995)	58	1	0.00	156
BMS1120	Stone <i>et al.</i> (1995)	58	3	0.25	114–126
BMS1126	Stone <i>et al.</i> (1995)	60	5	0.88	165–177
BMS1145	Stone <i>et al.</i> (1995)	50	2	0.13	145–153
BMS1148	Stone <i>et al.</i> (1995)	50	6	0.75	153–173
BMS1172	Stone <i>et al.</i> (1995)	58	4	0.57	95–113
BMS1185	Stone <i>et al.</i> (1995)	58	2	0.25	117–125
BMS119	Stone <i>et al.</i> (1995)	54	2	0.38	105–107
BMS1192	Stone <i>et al.</i> (1995)	58	1	0.00	132
BMS1195	Primer pair sequences in USDA-MARC database	60	1	0.00	202
BMS1231	Stone <i>et al.</i> (1995)	56	1	0.00	77
BMS1232	Stone <i>et al.</i> (1995)	56	4	1.00	127–161
BMS1237	Stone <i>et al.</i> (1995)	58	4	0.50	163–171
BMS1241	Primer pair sequences in USDA-MARC database	58	1	0.00	133
BMS1242	Stone <i>et al.</i> (1995)	56	6	0.38	150–172
BMS1247	Stone <i>et al.</i> (1995)	56	2	0.25	116–124
BMS1248	Stone <i>et al.</i> (1995)	58	4	0.50	132–144
BMS1282	Stone <i>et al.</i> (1995)	58	1	0.00	129
BMS1290	Stone <i>et al.</i> (1995)	58	5	0.57	130–156
BMS1296	Stone <i>et al.</i> (1995)	58	1	0.00	127
BMS130	Stone <i>et al.</i> (1995)	60	1	0.00	124
BMS1300	Stone <i>et al.</i> (1995)	58	1	0.00	149
BMS1304	Stone <i>et al.</i> (1995)	54	5	1.00	126–166
BMS1315	Stone <i>et al.</i> (1995)	60	1	0.00	193

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BMS1316	Stone <i>et al.</i> (1995)	58	7	0.63	102–122
BMS1318	Stone <i>et al.</i> (1995)	58	4	0.38	139–149
BMS1332	Stone <i>et al.</i> (1995)	60	5	0.67	137–149
BMS1341	Stone <i>et al.</i> (1995)	56	9	1.00	115–137
BMS1350	Stone <i>et al.</i> (1995)	58	8	0.88	124–144
BMS1353	Stone <i>et al.</i> (1995)	58	1	0.00	89
BMS1355	Stone <i>et al.</i> (1995)	58	5	0.50	149–155
BMS1373	Stone <i>et al.</i> (1995)	58	2	0.13	98–100
BMS1383	Primer pair sequences in USDA-MARC database	56	1	0.00	202
BMS1385	Stone <i>et al.</i> (1995)	58	2	0.38	70–72
BMS14	Stone <i>et al.</i> (1995)	50	1	0.00	192
BMS1451	Primer pair sequences in USDA-MARC database	58	1	0.00	93
BMS1471	Primer pair sequences in USDA-MARC database	58	1	0.00	132
BMS1494	Stone <i>et al.</i> (1995)	58	2	0.13	227–237
BMS1525	Primer pair sequences in USDA-MARC database	58	1	0.00	123
BMS1561	Primer pair sequences in USDA-MARC database	60	3	0.25	135–147
BMS1580	Stone <i>et al.</i> (1997)	58	1	0.00	121
BMS1591	Stone <i>et al.</i> (1995)	58	8	0.88	96–120
BMS1612	Stone <i>et al.</i> (1995)	58	2	0.00	84–86
BMS1616	Stone <i>et al.</i> (1995)	58	3	1.00	92–108
BMS1617	Stone <i>et al.</i> (1995)	54	4	0.43	163–169
BMS1620	Stone <i>et al.</i> (1995)	58	3	1.00	86–104
BMS1636	Stone <i>et al.</i> (1995)	58	5	1.00	116–126
BMS1660	Stone <i>et al.</i> (1995)	58	5	0.75	143–153
BMS1669	Stone <i>et al.</i> (1997)	56	3	0.63	109–113
BMS1678	Stone <i>et al.</i> (1995)	58	7	0.88	153–173
BMS1694	Stone <i>et al.</i> (1995)	58	6	0.75	103–135
BMS1701	Primer pair sequences in USDA-MARC database	60	1	0.00	126
BMS1714	Stone <i>et al.</i> (1995)	58	4	0.75	130–140
BMS1717	Primer pair sequences in USDA-MARC database	50	1	0.00	80
BMS1724	Stone <i>et al.</i> (1995)	58	7	1.00	164–182
BMS1732	Primer pair sequences in USDA-MARC database	58	1	0.00	79
BMS1758	Stone <i>et al.</i> (1995)	62	1	0.00	134
BMS1779	Stone <i>et al.</i> (1996)	56	6	0.86	105–123
BMS1782	Stone <i>et al.</i> (1995)	58	4	1.00	88–106
BMS1787	Stone <i>et al.</i> (1997)	58	8	0.88	152–188
BMS1788	Stone <i>et al.</i> (1995)	58	8	1.00	105–116
BMS1789	Stone <i>et al.</i> (1995)	58	2	0.25	119–121
BMS1820	Stone <i>et al.</i> (1995)	58	4	1.00	111–117
BMS1878	Stone <i>et al.</i> (1996)	54	2	0.29	125–126
BMS1915	Stone <i>et al.</i> (1995)	52	2	1.00	84–94
BMS1926	Stone <i>et al.</i> (1995)	56	1	0.00	115
BMS1932	Stone <i>et al.</i> (1995)	56	2	0.25	64–70
BMS1943	Stone <i>et al.</i> (1997)	56	1	0.00	125
BMS1948	Stone <i>et al.</i> (1995)	58	3	0.14	88–92
BMS1953	Stone <i>et al.</i> (1995)	56	2	0.25	134–136
BMS1967	Stone <i>et al.</i> (1995)	58	2	0.50	112–114
BMS1987	Stone <i>et al.</i> (1995)	58	1	0.00	109
BMS2	Stone <i>et al.</i> (1995)	54	2	0.38	127–129
BMS2053	Stone <i>et al.</i> (1995)	58	1	0.00	134
BMS2055	Stone <i>et al.</i> (1995)	58	4	0.38	152–166

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BMS2060	Stone <i>et al.</i> (1997)	56	1	0.00	75
BMS2072	Stone <i>et al.</i> (1995)	58	4	1.00	167–173
BMS2076	Stone <i>et al.</i> (1996)	60	7	0.63	144–174
BMS2079	Stone <i>et al.</i> (1995)	58	3	0.50	116–120
BMS2095	Stone <i>et al.</i> (1995)	56	1	0.00	68
BMS2104	Stone <i>et al.</i> (1995)	58	3	0.38	145–148
BMS2131	Stone <i>et al.</i> (1997)	58	4	0.88	104–110
BMS2137	Stone <i>et al.</i> (1995)	58	1	0.00	111
BMS2145	Stone <i>et al.</i> (1995)	58	2	0.38	147–151
BMS2152	Stone <i>et al.</i> (1995)	58	1	0.00	121
BMS2168	Stone <i>et al.</i> (1997)	58	4	0.88	147–169
BMS2196	Stone <i>et al.</i> (1995)	58	5	0.67	100–126
BMS2200	Stone <i>et al.</i> (1995)	58	7	0.60	81–111
BMS2213	Stone <i>et al.</i> (1995)	58	7	1.00	127–147
BMS2258	Primer pair sequences in USDA-MARC database	58	5	0.75	131–139
BMS2263	Stone <i>et al.</i> (1995)	58	7	0.88	145–175
BMS2270	Stone <i>et al.</i> (1997)	58	3	0.38	94–100
BMS2319	Stone <i>et al.</i> (1996)	58	5	0.43	114–158
BMS2321	Stone <i>et al.</i> (1997)	58	4	0.88	144–168
BMS2346	Primer pair sequences in USDA-MARC database	54	1	0.00	102
BMS2352	Primer pair sequences in USDA-MARC database	54	1	0.00	147
BMS2355	Stone <i>et al.</i> (1997)	58	6	0.63	126–158
BMS2361	Stone <i>et al.</i> (1997)	58	8	0.75	106–132
BMS2377	Stone <i>et al.</i> (1997)	58	5	0.63	128–148
BMS2389	Stone <i>et al.</i> (1996)	56	1	0.00	107
BMS2460	Stone <i>et al.</i> (1997)	56	4	0.88	63–69
BMS2466	Stone <i>et al.</i> (1997)	58	3	0.88	80–84
BMS2503	Stone <i>et al.</i> (1997)	58	1	0.00	125
BMS2519	Stone <i>et al.</i> (1996)	56	1	0.00	97
BMS2526	Stone <i>et al.</i> (1997)	58	4	0.63	154–162
BMS2567	Stone <i>et al.</i> (1997)	58	1	0.00	131
BMS2569	Stone <i>et al.</i> (1997)	58	5	0.75	168–178
BMS2572	Stone <i>et al.</i> (1997)	58	6	0.75	115–129
BMS2573	Stone <i>et al.</i> (1997)	56	1	0.00	106
BMS2598	Stone <i>et al.</i> (1996)	58	2	0.57	117–119
BMS2614	Stone <i>et al.</i> (1997)	58	4	1.00	107–121
BMS2626	Stone <i>et al.</i> (1997)	58	3	0.63	161–165
BMS2641	Stone <i>et al.</i> (1997)	58	4	0.38	180–186
BMS2658	Stone <i>et al.</i> (1997)	58	2	0.25	113–114
BMS2721	Stone <i>et al.</i> (1996)	58	7	0.88	145–171
BMS2742	Stone <i>et al.</i> (1996)	58	7	0.67	120–148
BMS2780	Stone <i>et al.</i> (1997)	58	8	0.88	250–276
BMS2812	Stone <i>et al.</i> (1996)	56	4	0.50	98–104
BMS2815	Stone <i>et al.</i> (1996)	56	3	0.75	101–111
BMS2833	Stone <i>et al.</i> (1997)	58	8	0.88	117–149
BMS2840	Stone <i>et al.</i> (1996)	52	2	0.50	249–259
BMS2842	Stone <i>et al.</i> (1996)	58	2	0.50	116–118
BMS2843	Primer pair sequences in USDA-MARC database	58	3	0.86	231–237
BMS2891	Stone <i>et al.</i> (1997)	58	1	0.00	62
BMS2914	Stone <i>et al.</i> (1997)	58	1	0.00	94
BMS3002	Stone <i>et al.</i> (1997)	58	1	0.00	114
BMS3006	Primer pair sequences in USDA-MARC database	58	1	0.00	159
BMS3011	Primer pair sequences in USDA-MARC database	58	1	0.00	141



Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BMS3034	Stone <i>et al.</i> (1995)	56	1	0-00	171
BMS332	Stone <i>et al.</i> (1995)	58	8	0-88	137-157
BMS340	Primer pair sequences in USDA-MARC database	50	7	0-75	225-265
BMS345	Stone <i>et al.</i> (1995)	58	2	0-13	106-120
BMS346	Stone <i>et al.</i> (1995)	58	1	0-00	109
BMS356	Stone <i>et al.</i> (1995)	58	2	0-38	98-100
BMS357	Stone <i>et al.</i> (1995)	58	4	0-50	111-116
BMS360	Stone <i>et al.</i> (1995)	58	7	0-63	104-128
BMS362	Stone <i>et al.</i> (1995)	54	2	0-38	119-120
BMS381	Stone <i>et al.</i> (1996)	52	2	0-25	115-121
BMS382	Stone <i>et al.</i> (1995)	54	1	0-00	155
BMS390	Stone <i>et al.</i> (1995)	58	2	0-25	118-120
BMS397	Stone <i>et al.</i> (1995)	58	4	1-00	126-140
BMS4000	Sonstegard <i>et al.</i> (1997b)	56	6	0-88	135-159
BMS4001	Sonstegard <i>et al.</i> (1997b)	58	4	0-75	117-147
BMS4004	Sonstegard <i>et al.</i> (1997b)	58	1	0-00	154
BMS4008	Primer pair sequences in USDA-MARC database	58	5	0-71	159-181
BMS4011	Sonstegard <i>et al.</i> (1997b)	58	2	0-13	197-199
BMS4018	Primer pair sequences in USDA-MARC database	54	1	0-00	95
BMS4045	Sonstegard <i>et al.</i> (1997b)	58	4	0-63	120-124
BMS418	Primer pair sequences in USDA-MARC database	50	1	0-00	327
BMS419	Stone <i>et al.</i> (1995)	54	4	0-63	276-284
BMS424	Stone <i>et al.</i> (1995)	50	6	0-75	118-132
BMS430	Primer pair sequences in USDA-MARC database	52	1	0-00	121
BMS431	Stone <i>et al.</i> (1995)	64	4	0-75	149-155
BMS434	Stone <i>et al.</i> (1995)	54	5	0-71	119-139
BMS460	Stone <i>et al.</i> (1995)	58	7	0-75	120-138
BMS462	Stone <i>et al.</i> (1995)	62	2	0-00	123-125
BMS466	Stone <i>et al.</i> (1995)	54	1	0-00	86
BMS468	Stone <i>et al.</i> (1995)	58	2	0-00	117-121
BMS482	Stone <i>et al.</i> (1995)	56	7	0-88	167-225
BMS483	Stone <i>et al.</i> (1995)	58	2	0-38	88-89
BMS490	Stone <i>et al.</i> (1995)	54	1	0-00	137
BMS499	Stone <i>et al.</i> (1995)	48	1	0-00	102
BMS500	Sonstegard <i>et al.</i> (1997a)	58	2	1-00	167-169
BMS501	Stone <i>et al.</i> (1995)	54	4	0-63	125-133
BMS503	Primer pair sequences in USDA-MARC database	50	1	0-00	199
BMS504	Stone <i>et al.</i> (1995)	56	1	0-00	88
BMS511	Stone <i>et al.</i> (1995)	56	1	0-00	100
BMS513	Stone <i>et al.</i> (1995)	52	3	1-00	147-153
BMS514	Primer pair sequences in USDA-MARC database	52	4	0-50	122-130
BMS517	Stone <i>et al.</i> (1995)	58	4	0-75	191-203
BMS518	Stone <i>et al.</i> (1995)	54	1	0-00	145
BMS522	Stone <i>et al.</i> (1995)	58	3	0-50	120-124
BMS527	Stone <i>et al.</i> (1995)	58	3	0-75	157-189
BMS528	Stone <i>et al.</i> (1995)	58	6	0-50	137-174
BMS529	Stone <i>et al.</i> (1995)	58	1	0-00	93
BMS538	Stone <i>et al.</i> (1995)	54	5	0-86	138-146
BMS542	Primer pair sequences in USDA-MARC database	54	1	0-00	174
BMS571	Primer pair sequences in USDA-MARC database	60	1	0-00	129

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BMS574	Stone <i>et al.</i> (1995)	58	8	1.00	139–163
BMS585	Stone <i>et al.</i> (1995)	58	3	0.50	117–133
BMS599	Stone <i>et al.</i> (1995)	56	1	0.00	189
BMS603	Primer pair sequences in USDA-MARC database	50	1	0.00	149
BMS621	Primer pair sequences in USDA-MARC database	58	1	0.00	77
BMS629	Primer pair sequences in USDA-MARC database	58	6	0.88	149–163
BMS631	Stone <i>et al.</i> (1995)	58	2	1.00	174–188
BMS639	Stone <i>et al.</i> (1995)	58	1	0.00	122
BMS647	Primer pair sequences in USDA-MARC database	58	3	0.86	134–146
BMS648	Stone <i>et al.</i> (1995)	58	4	0.88	176–182
BMS651	Stone <i>et al.</i> (1995)	58	2	0.75	91–125
BMS657	Primer pair sequences in USDA-MARC database	64	2	0.13	121–135
BMS66	Stone <i>et al.</i> (1995)	50	2	0.25	178–180
BMS678	Stone <i>et al.</i> (1995)	54	6	0.75	102–128
BMS689	Stone <i>et al.</i> (1997)	58	6	0.50	130–168
BMS693	Stone <i>et al.</i> (1995)	58	4	0.50	150–160
BMS694	Stone <i>et al.</i> (1995)	60	3	0.50	159–167
BMS695	Stone <i>et al.</i> (1995)	58	2	0.25	80–84
BMS703	Stone <i>et al.</i> (1995)	58	4	0.50	144–156
BMS710	Stone <i>et al.</i> (1995)	58	7	0.88	104–138
BMS719	Stone <i>et al.</i> (1995)	50	2	0.38	120–122
BMS740	Stone <i>et al.</i> (1995)	54	5	0.75	110–124
BMS742	Stone <i>et al.</i> (1995)	50	1	0.00	121
BMS744	Stone <i>et al.</i> (1995)	56	6	0.75	130–148
BMS745	Stone <i>et al.</i> (1995)	58	2	0.63	93–95
BMS772	Stone <i>et al.</i> (1995)	58	7	0.88	127–145
BMS778	Stone <i>et al.</i> (1995)	58	2	0.50	129–135
BMS792	Stone <i>et al.</i> (1995)	58	7	1.00	124–168
BMS796	Primer pair sequences in USDA-MARC database	50	2	0.25	480–486
BMS803	Stone <i>et al.</i> (1995)	58	1	0.00	122
BMS807	Stone <i>et al.</i> (1995)	58	3	1.00	111–125
BMS812	Stone <i>et al.</i> (1995)	56	6	0.88	110–132
BMS817	Stone <i>et al.</i> (1995)	54	1	0.00	114
BMS820	Stone <i>et al.</i> (1995)	58	3	0.57	116–120
BMS823	Stone <i>et al.</i> (1995)	56	6	0.75	100–128
BMS824	Primer pair sequences in USDA-MARC database	58	7	0.88	102–114
BMS835	Stone <i>et al.</i> (1995)	58	8	1.00	155–177
BMS861	Stone <i>et al.</i> (1995)	58	3	0.13	124–126
BMS862	Stone <i>et al.</i> (1995)	58	4	0.63	129–135
BMS868	Stone <i>et al.</i> (1995)	56	1	0.00	192
BMS875	Stone <i>et al.</i> (1995)	58	5	0.50	110–120
BMS882	Stone <i>et al.</i> (1995)	58	4	1.00	109–115
BMS887	Stone <i>et al.</i> (1995)	58	6	1.00	144–156
BMS903	Stone <i>et al.</i> (1995)	58	2	1.00	64–68
BMS904	Stone <i>et al.</i> (1995)	58	1	0.00	96
BMS907	Stone <i>et al.</i> (1995)	60	5	0.88	84–104
BMS911	Stone <i>et al.</i> (1995)	58	2	1.00	91–101
BMS918	Stone <i>et al.</i> (1995)	50	1	0.00	101
BMS921	Primer pair sequences in USDA-MARC database	60	3	1.00	118–122
BMS929	Stone <i>et al.</i> (1995)	58	1	0.00	112
BMS937	Stone <i>et al.</i> (1995)	58	1	0.00	125

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
BMS938	Stone <i>et al.</i> (1995)	58	2	1.00	166–168
BMS941	Stone <i>et al.</i> (1995)	54	5	1.00	96–106
BMS947	Stone <i>et al.</i> (1995)	58	1	0.00	106
BMS948	Stone <i>et al.</i> (1995)	54	2	0.75	105–106
BMS960	Stone <i>et al.</i> (1995)	58	2	0.00	123–125
BMS963	Stone <i>et al.</i> (1995)	58	2	0.38	121–135
BMS975	Stone <i>et al.</i> (1995)	56	6	0.50	75–109
BMS980	Stone <i>et al.</i> (1995)	58	2	0.13	116–118
BMS995	Stone <i>et al.</i> (1995)	58	5	0.63	121–145
BMSB719OV	Primer pair sequences in USDA-MARC database	50	2	0.25	106–107
BOLA-DRB1	Fries <i>et al.</i> (1993)	54	5	0.60	105–147
BOLA-DRB2	Fries <i>et al.</i> (1993)	58	3	0.75	139–143
BP1	Bishop <i>et al.</i> (1994)	54	2	0.13	283–289
BP11	Primer pair sequences in USDA-MARC database	56	1	0.00	136
BP17	Primer pair sequences in USDA-MARC database	60	10	0.88	282–416
BP28	Bishop <i>et al.</i> (1994)	58	8	0.86	218–254
BP31	Bishop <i>et al.</i> (1994)	58	6	0.63	211–223
BP33	Bishop <i>et al.</i> (1994)	58	6	0.75	251–279
BP34	Bishop <i>et al.</i> (1994)	52	5	0.50	298–308
BP38	Bishop <i>et al.</i> (1994)	50	1	0.00	278
BP7	Bishop <i>et al.</i> (1994)	54	2	0.13	290–292
BR215	Bishop <i>et al.</i> (1994)	58	3	1.00	122–134
BR2936	Bishop <i>et al.</i> (1994)	56	9	0.88	115–139
BR6027	Bishop <i>et al.</i> (1994)	50	1	0.00	135
BRN	Sasso <i>et al.</i> (1991)	60	4	1.00	243–253
CSN3	Bishop <i>et al.</i> (1994)	58	7	0.75	345–371
CSSM18	Cockett <i>et al.</i> (1994)	58	5	0.63	120–132
CSSM19	Moore <i>et al.</i> (1994)	58	3	0.50	156–160
CSSM25	Moore <i>et al.</i> (1994)	56	4	1.00	174–190
CSSM3	Moore <i>et al.</i> (1994)	58	6	0.88	252–274
CSSM32	Moore <i>et al.</i> (1994)	56	2	1.00	214–220
CSSM33	Moore <i>et al.</i> (1994)	58	1	0.00	148
CSSM39	Moore <i>et al.</i> (1994)	58	1	0.00	182
CSSM4	Moore <i>et al.</i> (1994)	58	6	1.00	196–214
CSSM41	Moore <i>et al.</i> (1994)	58	4	0.63	126–132
CSSM47	Moore <i>et al.</i> (1994)	58	2	0.63	130–132
CSSM65	Moore <i>et al.</i> (1995)	58	3	0.38	155–159
CSSM66	Moore <i>et al.</i> (1995)	60	7	0.88	180–202
ETH10	Solinas-Toldo <i>et al.</i> (1993)	54	1	0.00	213
ETH11	Solinas-Toldo <i>et al.</i> (1993)	52	1	0.00	109
ETH225	Steffen <i>et al.</i> (1993)	58	5	1.00	136–158
ETH9	Solinas-Toldo <i>et al.</i> (1993)	60	1	0.00	220
FAS	Yoo <i>et al.</i> (1996)	56	6	0.50	146–166
HAUT1	Kossarek <i>et al.</i> (1993c)	56	2	0.13	135–141
HAUT14	Thieven <i>et al.</i> (1995)	58	7	0.63	189–241
HBB	GenBank acc. no. M63453	58	4	0.83	171–209
HEL10	Kaukinen & Varvio (1993)	58	4	0.75	113–137
HEL11	Kaukinen & Varvio (1993)	58	5	0.50	167–191
HEL14	Vaiman <i>et al.</i> (1994a)	58	3	1.00	204–218
HEL6	Kaukinen & Varvio (1993)	56	2	0.25	242–246
HMH1R	Yamashita <i>et al.</i> (1991)	60	4	1.00	122–148
HU414	GenBank acc. no. M97491	58	1	0.00	142
HUJ246	Shalom <i>et al.</i> (1994)	62	3	1.00	264–280
HUJ616	Shalom <i>et al.</i> (1993)	58	4	0.75	124–158
HUJII77	Shalom <i>et al.</i> (1994)	58	3	1.00	197–217
IAP	Weissig <i>et al.</i> (1993)	64	1	0.00	174

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
IDVGA-9	Mezzelani <i>et al.</i> (1995)	58	3	0.50	91–95
IDVGA-10	Mezzelani <i>et al.</i> (1995)	58	4	0.29	155–183
IDVGA-45	Mezzelani <i>et al.</i> (1995)	56	3	0.50	183–193
IDVGA-46	Mezzelani <i>et al.</i> (1995)	58	1	0.00	204
IDVGA-59	Mezzelani <i>et al.</i> (1995)	58	1	0.00	239
IGF-1	Kirkpatrick (1993)	58	3	0.38	229–233
IL4	Buitkamp <i>et al.</i> (1995)	58	1	0.00	89
ILSTS004	Brezinsky <i>et al.</i> (1993)	54	4	1.00	96–116
ILSTS005	Kemp <i>et al.</i> (1995)	58	5	0.75	188–214
ILSTS008	Kemp <i>et al.</i> (1993)	60	2	0.60	171–173
ILSTS011	Brezinsky <i>et al.</i> (1992)	58	4	1.00	269–283
ILSTS012	Kemp <i>et al.</i> (1995)	58	1	0.00	85
ILSTS017	Kemp <i>et al.</i> (1995)	58	3	1.00	130–140
ILSTS018	Guerin <i>et al.</i> (1994)	58	4	0.50	177–187
ILSTS023	Kemp <i>et al.</i> (1995)	60	1	0.00	149
ILSTS026	Kemp <i>et al.</i> (1995)	58	4	1.00	150–158
ILSTS028	Kemp <i>et al.</i> (1995)	58	5	0.88	131–171
ILSTS030	Kemp <i>et al.</i> (1995)	58	4	1.00	152–166
ILSTS035	Kemp <i>et al.</i> (1995)	58	1	0.00	191
ILSTS036	Kemp <i>et al.</i> (1995)	58	1	0.00	141
ILSTS037	Kemp <i>et al.</i> (1995)	58	1	0.00	244
ILSTS043	Kemp <i>et al.</i> (1995)	58	3	0.50	117–137
ILSTS045	Kemp <i>et al.</i> (1995)	58	3	0.29	162–180
ILSTS047	Kemp <i>et al.</i> (1995)	60	1	0.00	149
ILSTS049	Kemp <i>et al.</i> (1995)	58	4	0.50	160–166
ILSTS050	Kemp <i>et al.</i> (1995)	58	6	0.75	144–160
ILSTS053	Kemp <i>et al.</i> (1995)	58	4	0.71	160–176
ILSTS058	Kemp <i>et al.</i> (1995)	58	5	1.00	116–191
ILSTS059	Kemp <i>et al.</i> (1995)	58	5	0.88	156–170
ILSTS060	Kemp <i>et al.</i> (1995)	58	10	0.86	213–245
ILSTS061	Kemp <i>et al.</i> (1995)	58	3	1.00	141–161
ILSTS062	Kemp <i>et al.</i> (1995)	58	5	0.75	199–225
ILSTS065	Kemp <i>et al.</i> (1995)	56	2	0.43	115–117
ILSTS068	Kemp <i>et al.</i> (1995)	58	1	0.00	127
ILSTS070	Kemp <i>et al.</i> (1995)	56	5	0.71	80–94
ILSTS072	Kemp <i>et al.</i> (1995)	56	3	1.00	160–170
ILSTS087	Kemp <i>et al.</i> (1995)	58	8	0.75	143–163
ILSTS092	Kemp <i>et al.</i> (1995)	58	1	0.00	159
ILSTS104	Kemp <i>et al.</i> (1995)	56	1	0.00	180
INRA006	Vaiman <i>et al.</i> (1992)	58	5	0.83	118–142
INRA011	Vaiman <i>et al.</i> (1992)	54	4	0.86	208–244
INRA023	Vaiman <i>et al.</i> (1994a)	52	1	0.00	145
INRA026	Vaiman <i>et al.</i> (1994a)	56	5	0.67	93–115
INRA030	Vaiman <i>et al.</i> (1994b)	50	3	0.38	173–177
INRA035	Vaiman <i>et al.</i> (1994b)	58	8	0.75	120–140
INRA049	Vaiman <i>et al.</i> (1994a)	56	5	1.00	142–164
INRA063	Vaiman <i>et al.</i> (1994b)	56	7	0.88	163–177
INRA071	Vaiman <i>et al.</i> (1994b)	58	4	0.75	204–210
INRA072	Vaiman <i>et al.</i> (1994a)	56	4	1.00	161–171
INRA081	Vaiman <i>et al.</i> (1994b)	56	10	0.88	152–200
INRA084	Vaiman <i>et al.</i> (1994b)	58	1	0.00	103
INRA090	Vaiman <i>et al.</i> (1994b)	58	1	0.00	179
INRA100	Vaiman <i>et al.</i> (1994b)	54	2	0.50	138–139
INRA107	Vaiman <i>et al.</i> (1994a)	58	5	0.67	162–208
INRA108	Vaiman <i>et al.</i> (1994a)	58	2	0.25	144–150
INRA111	Vaiman <i>et al.</i> (1994b)	58	2	0.75	145–147
INRA112	Vaiman <i>et al.</i> (1994b)	58	1	0.00	146
INRA119	Vaiman <i>et al.</i> (1994b)	58	1	0.00	118
INRA120	Vaiman <i>et al.</i> (1994b)	58	1	0.00	151

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
INRA121	Vaiman <i>et al.</i> (1994b)	58	1	0.00	106
INRA122	Vaiman <i>et al.</i> (1994a)	54	2	0.67	147–149
INRA129	Vaiman <i>et al.</i> (1994b)	58	2	0.00	155–157
INRA131	Vaiman <i>et al.</i> (1994b)	58	4	0.75	98–112
INRA132	Vaiman <i>et al.</i> (1994b)	58	5	0.63	152–178
INRA133	Vaiman <i>et al.</i> (1993)	56	3	0.14	220–226
INRA135	Vaiman <i>et al.</i> (1994a)	58	7	1.00	127–143
INRA144	Eggen <i>et al.</i> (1992)	58	8	0.80	119–213
INRA175	Vaiman <i>et al.</i> (1993)	58	6	0.75	172–200
INRA177	Vaiman <i>et al.</i> (1994b)	56	1	0.00	68
INRA183	Velkala <i>et al.</i> (1995)	56	3	0.38	95–135
INRA192	Vaiman <i>et al.</i> (1993)	56	2	0.14	131–133
INRA194	Vaiman <i>et al.</i> (1993)	56	2	0.13	134–136
JAB1	Williams <i>et al.</i> (1995)	58	7	0.88	235–251
JAB4	Williams <i>et al.</i> (1995)	56	2	0.40	181–185
JAB8	Williams <i>et al.</i> (1995)	56	4	0.75	222–262
KRT10	Fries <i>et al.</i> (1993)	50	3	0.75	169–171
MAP2C	Moore <i>et al.</i> (1992)	54	4	0.83	92–100
MILSTS077	Kemp <i>et al.</i> (1995)	58	1	0.00	218
OBESE	Stone <i>et al.</i> (1996)	52	1	0.00	96
OCAM	Fries <i>et al.</i> (1993)	54	4	1.00	221–235
POTCHA	Garcia-Guzman <i>et al.</i> (1992)	56	5	0.75	139–151
PTH	Fries <i>et al.</i> (1993)	48	1	0.00	146
RBP3	Fries <i>et al.</i> (1993)	58	5	0.71	138–152
RM004	Kossarek <i>et al.</i> (1993a)	58	7	1.00	138–152
RM012	Kossarek <i>et al.</i> (1994a)	58	1	0.00	104
RM019	Kossarek <i>et al.</i> (1994a)	58	1	0.00	81
RM024	Kossarek <i>et al.</i> (1994a)	58	5	0.88	130–142
RM033	Kossarek <i>et al.</i> (1994b)	62	1	0.00	141
RM041	Kossarek <i>et al.</i> (1995a)	58	1	0.00	80
RM065	McGraw <i>et al.</i> (1997)	54	4	1.00	143–175
RM066	Kossarek <i>et al.</i> (1995a)	52	1	0.00	179
RM067	Kossarek <i>et al.</i> (1993b)	54	2	0.60	81–83
RM074	Kossarek <i>et al.</i> (1993c)	56	1	0.00	118
RM088	Kossarek <i>et al.</i> (1995a)	54	1	0.00	114
RM090	McGraw <i>et al.</i> (1997)	56	1	0.00	106
RM106	Kossarek <i>et al.</i> (1993c)	54	3	1.00	142–150
RM137	McGraw <i>et al.</i> (1997)	58	1	0.00	148
RM138	Primer pair sequences in USDA-MARC database	62	1	0.00	143
RM150	McGraw <i>et al.</i> (1997)	58	5	0.50	141–179
RM179	Kossarek <i>et al.</i> (1995b)	58	1	0.00	115
RM209	Kossarek <i>et al.</i> (1994c)	54	2	0.25	103–104
RM232	McGraw <i>et al.</i> (1997)	58	2	0.38	111–121
RM321	McGraw <i>et al.</i> (1997)	58	3	0.43	92–98
RM331	Primer pair sequences in USDA-MARC database	58	1	0.00	100
RM356	McGraw <i>et al.</i> (1997)	58	3	0.75	128–134
RM500	Barendse <i>et al.</i> (1994)	54	1	0.00	134
SRN	Moore <i>et al.</i> (1992)	60	2	0.50	130–132
TEXAN10	Burns <i>et al.</i> (1995)	58	2	0.50	120–124
TEXAN2	Holder <i>et al.</i> (1994)	48	5	1.00	123–155
TEXAN3	Holder <i>et al.</i> (1994)	54	1	0.00	126
TEXAN4	Holder <i>et al.</i> (1994)	58	1	0.00	128
TEXAN5	Holder <i>et al.</i> (1994)	54	1	0.00	148
TEXAN6	Burns <i>et al.</i> (1995)	56	3	1.00	159–171
TEXAN9	Burns <i>et al.</i> (1995)	58	1	0.00	82
TGLA122	Georges & Massey (1992)	58	3	1.00	138–160
TGLA141	Georges & Massey (1992)	58	3	0.13	128–130

Table 1. continued

Locus	Reference	Temp. (°C)	Allele no.	Heterozygosity	Size (bp)
TGLA170	Georges & Massey (1992)	50	1	0.00	92
TGLA179	Georges & Massey (1992)	58	1	0.00	92
TGLA182	Georges & Massey (1992)	58	2	0.00	188–190
TGLA245	Georges & Massey (1992)	58	1	0.00	127
TGLA254	Georges & Massey (1992)	58	1	0.00	97
TGLA261	Georges & Massey (1992)	58	7	0.88	244–266
TGLA28	Georges & Massey (1992)	58	1	0.00	134
TGLA337	Georges & Massey (1992)	56	6	0.50	107–123
TGLA351	Georges & Massey (1992)	58	1	0.00	129
TGLA429	Georges & Massey (1992)	58	5	0.38	195–213
TGLA441	Georges & Massey (1992)	50	5	1.00	118–132
URB002	Ma <i>et al.</i> (1996)	50	4	1.00	177–227
URB010	Ma <i>et al.</i> (1996)	50	2	1.00	215–229
UWCA19	Sun <i>et al.</i> (1994)	50	1	0.00	82
UWCA20	Sun <i>et al.</i> (1994)	50	1	0.00	73
UWCA25	Kirkpatrick (1995)	58	2	0.50	134–138
UWCA28	Kirkpatrick (1995)	58	6	0.25	112–146
UWCA46	Sun <i>et al.</i> (1995)	60	6	0.88	135–149
XBM11	Ponce de Leon (1996)	58	2	1.00	183–185
XBM24	Ponce de Leon (1996)	58	3	1.00	217–229

When cattle and sheep DNA were amplified with the same primers, median fragment sizes were not significantly different (Table 2). However, associations between species for allele number and the range of allele sizes within a primer pair were significantly lower in sheep. Attempts to explain the loss in heterozygosity as a result of interspecific priming (Kondo *et al.* 1993; Pepin *et al.* 1995) do not appear to be supported by our observations. The results in Table 2 indicate that there is little difference between fragment length in cattle and sheep when amplified under similar conditions with the same primer pairs. We cannot rule out altered repeat structure as a basis for this phenomenon (interrupted *vs* non-inter-

rupted), because a significant number of loci have not been sequenced in sheep. Fragment length differences have been observed for microsatellite loci between human and chimpanzee. Attempts have been made to explain this difference by directional evolution and variation in evolutionary rate between species (Rubinsztein *et al.* 1995a,b) or by ascertainment bias in microsatellite selection based upon a minimum repeat-length criterion (Ellegren *et al.* 1995). Ascertainment bias or evolutionary divergence do not appear to be contributing to this data set because no significant difference in median fragment length was detected between cattle and sheep.

Table 2. Microsatellite allele number, median fragment size (MFS), heterozygosity (H) and range of allele sizes (Range) for common bovine markers in cattle and sheep<sup>†</sup>

	Allele no.	MFS (bp)	H (%)	Range (bp)
Bovine mean ( $\pm$ SD) <sup>‡</sup>	4.5 $\pm$ 2.1	145.7 $\pm$ 43.3	60.1 $\pm$ 28.1	12.1 $\pm$ 9.5
Ovine mean ( $\pm$ SD) <sup>§</sup>	3.2 $\pm$ 2.1	148.0 $\pm$ 48.9	45.3 $\pm$ 38.6	10.7 $\pm$ 13.6
Difference ( $\pm$ SE)	1.3 $\pm$ 0.11**	-2.3 $\pm$ 1.32	14.8 $\pm$ 1.88**	1.4 $\pm$ 0.66*

<sup>†</sup>Bovine-derived microsatellites ( $n = 551$ ) that produced genotypes with both sheep and cattle DNA.

<sup>‡</sup>Sires ( $n = 2$ ) and dams ( $n = 8$ ) of a four-way *Bos taurus* cross population (Bishop *et al.* 1994).

<sup>§</sup>Sires ( $n \leq 8$ ) from sheep reference families.

\* $P < 0.05$ , \*\* $P < 0.001$ .

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