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A Genetic Linkage Map for Cattle

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ABSTRACT

We report the most extensive physically anchored linkage map for cattle produced to date. Three-hundred thirteen genetic markers ordered in 30 linkage groups, anchored to 24 autosomal chromosomes (n = 29), the *X* and *Y* chromosomes, four unanchored syntenic groups and two unassigned linkage groups spanning 2464 cM of the bovine genome are summarized. The map also assigns 19 type I loci to specific chromosomes and/or syntenic groups and four cosmid clones containing informative microsatellites to chromosomes *13*, *25* and *29* anchoring syntenic groups U11, U7 and U8, respectively. This map provides the skeletal framework prerequisite to development of a comprehensive genetic map for cattle and analysis of economic trait loci (ETL).

GENOME maps exist in one form or another for nearly 30 species (O'BRIEN and GRAVES 1991; O'BRIEN *et al.* 1993). The most comprehensive maps for mammals cover the human (genetic linkage, WEISSENBACH *et al.* 1992; cytogenetic, GDB™, CUTICCHIA *et al.* 1993) and mouse (genetic linkage, DIETRICH *et al.* 1992; cytogenetic, GBase, Bar Harbor, ME and COPELAND *et al.* 1993) genomes. Two classes of loci (type I and type II; O'BRIEN 1991) form the basis for construction of gene maps within most species. Type I loci represent evolutionarily conserved coding sequences useful in comparative mapping strategies (O'BRIEN 1991) where polymorphic loci are not essential. Type II loci, hypervariable DNA segments or variable number of tandem repeat microsatellites (di-, tri- or tetra-nucleotide repeats), are extremely polymorphic and generally specific to closely related species.

Currently, cattle (FRIES *et al.* 1993), swine (ANDERSSON *et al.* 1993) and sheep (ANSARI *et al.* 1993) maps are primarily cytogenetic maps with few microsatellite assignments. The most current bovine genome map (FRIES *et al.* 1993) reported a total of 295 polymorphisms at 150 of the 350 physically assigned type I (257) and type II (93) loci. Thirty-two linkage groups were reported containing 122 loci (42 are microsatellites) spanning 13 autosomal chromosomes (haploid n = 29) and 26 syntenic groups. In sharp contrast to the murine map (COPELAND *et al.* 1993), only 27% (69 of 257) of the assigned type I loci (FRIES *et al.* 1993) were polymorphic in cattle and only a limited number of species related primer sequences flanking microsatellites have been published. However, estimates of recombination frequency between loci, locus order within linkage group and genome/chromosomal coverage of polymorphic markers essential to systematically search for loci that affect phenotypes of interest are not available.

The relative ease of developing and genotyping microsatellites in large kindred families using the polymerase chain reaction (PCR; SAIKI *et al.* 1985, 1988), with a minute amount of DNA and two flanking site-specific oligonucleotide primers allows rapid development of saturated genetic linkage maps (DIETRICH *et al.* 1992; WEISSENBACH *et al.* 1992). This approach has lead to screening of microsatellites for monogenic traits and the concomitant identification of economic trait loci (ETL) in horses (RUDOLPH *et al.* 1992), pigs (MACLENNEN and PHILLIPS 1992), cattle (HOESCHELE and MEINERT 1990; GEORGES *et al.* 1993a,b) and sheep (MONTGOMERY *et al.* 1993). However, the lack of a high density linkage map and availability of markers for identifying polygenic loci affecting quantitative traits (GEORGES *et al.* 1993a,b) has limited progress toward marker-assisted-selection (MAS). A saturated microsatellite based linkage map for cattle would provide the foundation for identification of loci contributing to the genetic variance for economic traits (ETL) and the exploitation of MAS for phenotypes of interest (FRIES 1993).

We report the addition of 172 microsatellites, three RFLPS and four single-strand-conformational-polymorphisms (SSCP), nine erythrocyte antigens and seven serum proteins to the developing bovine ge-

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TABLE 1

Population structure and breed composition of reference families

Population	N^a	Sire breed	N^b	Dam breed	N^c
Hereford backcross	1	Brahman × Hereford	6	Hereford	36
Angus backcross	1	Brahman × Angus	7	Angus	40
Four-breed cross	2	Gelbvieh × Simmental	2	Longhorn × Hereford	23
			2	Longhorn × Angus	12
			2	Piedmontese × Hereford	35
			2	Piedmontese × Angus	22
			1	Nelore × Hereford	12
Total	4		22		180

[a] Number of bulls used in each reference population.
[b] Number of cows in the MOET scheme for each reference population.
[c] Number of progeny from each MOET mating scheme.

nome map. In addition, we assign 19 coding genes to individual chromosomes or syntenic groups and assign linkage groups to three chromosomes and syntenic groups. The map presented contains a total of 313 polymorphic markers, with average levels of heterozygosity of ~53%, ordered in 30 linkage groups anchored to 24 autosomal chromosomes, both sex chromosomes and four unassigned syntenic groups (two linkage groups remain unanchored) spanning 2464 cM of the bovine genome.

MATERIALS AND METHODS

Reference family structure: Linkage data were developed in three unique populations of kindred families, including grandparents, related through common F_1 sires in a multiple ovulation embryo transfer (MOET) scheme (Table 1). Two paternal half-sib F_1 (Gelbvieh × Simmental) bulls were used to construct a four-breed cross consisting of 17 fullsib families. The F_1 dams were produced by mating Piedmontese, Longhorn or Nellore bulls to Hereford or Angus dams. Two backcross populations were produced by mating a Brahman × Hereford bull to six Hereford cows and a Brahman × Angus bull to seven Angus cows. Crosses were designed to maximize heterozygosity of one or both parents and obtain samples of diverse gene pools.

Acquisition of microsatellites: The map was constructed primarily with microsatellites ($(CA)_n/(GT)_n$) from M13, plasmid, lambda or cosmid libraries of bovine genomic DNA or from published *Bovidae* polymorphisms and sequences (GenBank, EMBL). Bovine genomic DNA was digested to completion with *Mbo*I and fragments separated by electrophoresis on 1.2% agarose gels. Fragments from 350–500 bp were recovered by electroelution, ligated into M13mp18, transformed into XL-1 Blue cells and sequentially hybridized with ^{32}P-end-labeled $(CA)_{11}$ and $(GT)_{11}$ oligonucleotide probes (WEBER and MAY 1989). Care was taken to avoid prominent *Mbo*I fragments from 1.715 and 1.709 satellite DNAs migrating at less than 350 bp. DNA from positive clones was initially sequenced with only ddC or ddG. This identified clones containing short repeats or repeats too close to the 5′ or 3′ ends to provide adequate sequence for primer design (Primer; Version 0.5; S. E. LINCOLN, M. J. DALY and E. S. LANDER, unpublished data). Primer sequences from microsatellite positive clones identified by screening genomic Embl3 lambda phage, plasmid and cosmid (G. A. HAWKINS *et al.* in press) libraries with $(CA)_n(GT)_n$ oligos were obtained by sequencing with degenerate primer cocktails containing only $(GT)_n/(TG)_n$ or $(CA)_n/(AC)_n$ (YUILLE *et al.* 1991).

TABLE 2

Microsatellite informativeness by source

Source	No. of markers[a]	No. of informatives[b]	Mean no. of alleles
Random			
M13	236	126 (53)	7.2
Cosmid	14	11 (78)	7.8
Lambda	14	9 (64)	4.9
Plasmid	21	13 (61)	5.7
Published[c]			
Coding genes	28	16 (57)	
Random	93	88 (95)	
Sheep	30	17 (35)	5.3
Total	468	280 (58)	6.8

[a] Total number primers pairs tested.
[b] Includes primer pairs tested that were sufficiently informative to be linked (% informative).
[c] Primer pairs obtained from GenBank, literature or collaborators.

The significant chromosomal and DNA sequence conservation among *Bovidae* prompted a search for cattle and sheep di-, tri- and tetra-nucleotide repeat sequences in GenBank (BENSON *et al.* 1993) and EMBL databases using Fasta (Genetics Computer Group, Madison, Wisconsin; GCG). Size restrictions were imposed for each of the three classes of microsatellites (>6 for any dinucleotide repeat, >3 for any trinucleotide repeat and >2 for any tetranucleotide repeat).

Cosmid mapping: Fluorescent *in situ* hybridization (FISH) was used to localize cosmids to bovine metaphase chromosomes as described by SOLINAS TOLDO *et al.* (1993). The presence of doublets of fluorescein isothiocyanate spots on the same pair of chromosomes in 5–10 metaphase spreads was sufficient evidence for the assignment. Assignment to a specific chromosome band was by measuring the distance of the signal from the centromere (FLcen) and by applying this value to the corresponding idiogrammatic chromosome of the standard (ISCNDA 1989, 1990).

Data collection and analysis: Eighty (80) ng of genomic DNA from each animal was aliquoted (Biomek 1000 Workstation; Beckman Instruments) into 96-well microtiter plates (Falcon; Becton Dickinson Labware, Oxnard, California)

and amplified in the presence of 50 mM KCl, 1.5 mM $MgCl_2$ (unless otherwise indicated; Table 3), 10 mM Tris-HCl pH 9.0, 30 μm each of unlabeled dCTP, dTTP, and dGTP, 0.4 μM each of two primer pairs, and 0.35 units of either *Taq* or *Tth* DNA polymerase in a final volume of 12 μl. PCR products were radioisotopically labeled by including 0.1 μCi [α-^{32}P]dATP (3000 ci/mmol, New England Nuclear) and 3.0 μM dATP. The standard thermocycling protocol was as follows: initial step of 3 min at 94° followed by 25–30 cycles of 1 min at 94°, 30 sec at the annealing temperature and 1 min at 72° then ending with a 4 min extension phase at 72° on either a MJ Research PTC96 Thermocycler (MJ Research) or a Hybaid Omni-Gene (Hybaid Ltd., Middlesex, England). Primer pairs were multiplexed whenever sizes of alleles and PCR conditions allowed. End-labeled primers were used when direct incorporation of ^{32}P into amplified products increased subbanding and hindered scoring. The amplified product was diluted with an equal volume of loading buffer (95% formamide, 10 mM EDTA, 0.1% Bromophenol Blue, 0.1% Xylene Cyanol) denatured 4 min at 75° and electrophoresed on 7% denaturing polyacrylamide gels (Amresco, Solon, Ohio) between 3 and 6 hr (based on product size) at 40 V/cm. Allele size was approximated by comparison to M13mp18 ssDNA sequencing ladders. Single-strand-conformational-polymorphisms (ORITA *et al.* 1989) were determined essentially as described for microsatellites except for nondenaturing conditions. Gels were vacuum dried for 15 min onto 3 MM chromatography paper (Whatman Int. Ltd., Maidstone, England) and exposed overnight on X-ray film.

Genotypes based on RFLPs were determined either by Southern transfer and hybridization (SAMBROOK *et al.* 1989) or by digestion of PCR product resulting from amplification of a site that was known to be polymorphic due to a point mutation reported in the literature.

Grandparental, parental and progeny genotypes were independently scored for each marker and entered into an interactive database (KEELE *et al.* 1994). Software was developed (D. BEHRENS, unpublished data) that compared independently scored genotypes and reported discrepancies. When genotype differences could not be resolved between independent scorers after reexamination of the autoradiograms or following reamplification and rescoring of the product, data were excluded from analysis. Because of the half-sib relationships among fullsib families, CRI-MAP 2.4 (GREEN *et al.* 1989) was selected for linkage analysis. Markers were placed into linkage groups based on two-point LOD (>3.0) scores and ordered within group using multipoint linkage analysis following a procedure similar to LANDER *et al.* (1987). Spurious linkages were identified and eliminated by comparing the maximum log-likelihood of a marker to its associated linkage group to the log-likelihood at a recombination frequency of 0.5. After preliminary alignment, the CHROMPIC option of CRI-MAP 2.4 was used to identify unlikely double-crossovers. Data contributing to double crossovers were reexamined and, if suspect, regenerated for second analysis.

RESULTS

Marker informativeness: A total of 468 microsatellite markers (GT:CA repeats) were tested. Two-hundred eighty (60.0%) were sufficiently informative to be included in linkage groups. The source and sequences of informative microsatellites are summarized in Tables 2 and 3. Approximately 0.12% of the total recombinant M13 random genomic clones produced informative microsatellites. Approximately 35% of the primer pairs failed to amplify useful products. The number of alleles per locus ranged from 1–18 and 50 of the microsatellites defined loci with 10 or more alleles. Less than 10% of microsatellites from random libraries were monomorphic. As expected, there was a positive relationship between the number of dinucleotide repeats and number of alleles at a given locus (WEBER 1990; BECKMAN and WEBER 1992; SUNDEN *et al.* 1993). Approximately 15% of the random clones contained bovine SINE elements (LENSTRA *et al.* 1993; KAUKINEN and VARVIO 1992). When one primer was derived from repetitive sequence, only 50% of the primer pairs provided useful data. Database searches did not yield any useful tri- or tetranucleotide repeats suitable for primer design.

Three bovine coding sequences (*MYF5, myogenic factor 5; CAST, Calpastatin,* and *LGB, beta lactoglobulin*) screened by RFLP in our reference families either by traditional procedures (SAMBROOK *et al.* 1989) or by restriction endonuclease digestion of PCR products are included in this linkage map. Data for *CAST* (BISHOP *et al.* 1993) and *MYF5* were generated using radiolabeled bovine specific probes. Primer pairs flanking polymorphic restriction sites in the coding sequence *LGB* were synthesized from published sequence (FRIES *et al.* 1993). The polymorphisms for *HSP70-1* (*70 kD heat shock protein*), *PTH* (*parathyroid hormone*), *GH* (*growth hormone*) and *GFAP* (*glial fibrillary acidic protein*) were detected using SSCP (ORITA *et al.* 1989). Eleven erythrocyte antigens and seven serum proteins commonly used for parentage testing were typed in a subset of our reference populations (KAPPES *et al.* 1994). Nine erythrocyte antigens and five serum proteins were informative in at least one reference family and linked to markers previously assigned (Table 3) to chromosomes and/or syntenic groups (Figure 1).

Thirty-nine of 369 (10.6%) genetic markers genotyped in our reference populations were monomorphic for all reference parents. Average heterozygosity for all markers was calculated for reference parents grouped according to species and cross. As expected, *Bos taurus* × *Bos indicus* F_1 crosses were most heterozygous (74.7% ± 1.5%, $P < 0.001$) followed by *Bos taurus* × *Bos taurus* (59.5% ± 2.8%, $P < 0.001$) and *Bos taurus* (47.2% ± 0.95%, $P < 0.001$) purebreds. The average weighted mean heterozygosity for all parents was 52.8% ± 1.6%. Similar heterozygosity levels have been observed in humans (63%, HUDSON *et al.* 1992), intraspecific crosses between inbred strains of mice (50%, DIETRICH *et al.* 1992), interspecific hybrid mice (90%, DIETRICH *et al.* 1992) and pigs (54.4% for White Composite (WC, Landrace, Large White, Chester White, Yorkshire) boars, 65.9% for WC-Duroc sows and 81.4% for WC-Chinese sows

TABLE 3

Locus, primer sequences, PCR conditions, informative meioses, number and size of alleles by chromosome and syntenic group

Chromosome	Syntenic group	Locus	Type	Forward primer sequence (5′ → 3′)	Reverse primer sequence (5′ → 3′)	Annealing temperature	Informative meioses	Allele (bp)		
								Max.	Min	N^a
1	10	*BM6438*	MS	TTGAGCACAGACACAGACTGG	ACTGAATGCCTCCTTTGTGC	56	145	272	256	4
		*AGLA17**	MS	Table 4			73	219	213	3
		RM095	MS	R. A. McGraw, Univ. Georgia, Athens			201	131	111	5
		ILSTS004	MS	Brezinsky *et al.* (1992b)			215	106	90	5
		BM4307	MS	ATAACACAAAAAGTGGAAAACACTC	ATTTTATCTCAGGTCCCTTTTTATC	58	229	203	187	6
		*INRA011**	MS	Table 4			119	215	203	3
		BM1312	MS	CCATGTGCTGCAACTCTGAC	GGAATGTTACTGAACCTCTCCG	58	278	119	105	7
		BM6506	MS	GCACGTGGTAAAGAGATGGC	AGCAACTTGAGCATGGCAC	58	209	209	191	6
		BR2724	MS	GTAGACAGTGTTCCTGCACAGC	CCATGGGGTCTCAATCATTC	58	276	159	139	9
		BM864	MS	TGGTAGAGCAATATGAAGGCC	GGAAATCCAAGAAAGAGGGG	58	338	274	214	14
		*TGLA130**	MS	Table 4			261	226	218	5
		BL28	MS	TATCATTGTGA-TATTGGAAATGTTC	GATTTCCCCAGCTTTACTTGC	54	70	114	112	2
		BM1824	MS	GAGCAAGGTGTTTTTCCAATC	CATTCTCCAACTGCTTCCTTG	58	317	192	180	6
		TF[b]*	PROT	Table 4			96			4
		*MAF46†**	MS	Table 4			36	106	98	4
		BM148	MS	AGGCACAGTACCACCCCTC	CTCAGCCTCAGCACCATG	56	131	105	97	3
		BM3205	MS	TCTTGCTTCCTTCCAAATCTC	TGCCCTTATTTTAACAGTCTGC	54	239	212	204	5
3	6	*BM2924*	MS	GATGGAGGCTGGAGAAATTG	TCTAATGGGTGGGACTCCG	56	302	145	137	5
		BR4502	MS	AGCCCACTCCAATATTCTTGC	AGAATCTCGGCAGGCTTTTC	58	143	176	160	7
		RM038	MS	R. A. McGraw, Univ. Georgia, Athens			33	102	94	3
		BM862	MS	GAAAGAACCCCTGGAGAAGG	TCATGGACAGAGGAGCCTG	54	201	148	124	6
		*INRA003**	MS	Table 4			287	184	160	9
		BM723	MS	ACCCTTGGTTTTCTGCTGG	CATCCTGTGTGAGTGTTGTGG	54	279	171	105	9
		BL41	MS	CCTCGCCATCTTTATTCCT	AAGATCAACTTATTCCTCACAGTGG	58	121	258	240	8
		FCGR2[c]	MS	GGTCTTCATTGGTGTTTTCTCC	GAGCTGCCCTAGATGAGGTG	58	157	197	183	5
		RM065	MS	R. A. McGraw, Univ. Georgia, Athens			176	150	140	5
		EAL[d]	EA				55			3
		*UWCA7**	MS	Table 4			187	100	84	5
		*INRA006**	MS	Table 4			292	120	106	8
4	13	*AGLA227**	MS	Table 4			237	177	171	3
		BR6303	MS	TGAGCCATAGAATTAAGATTCAAGC	TTTGTTCCTCTTTATTTTCTTCTGC	56	295	223	215	5
		RM088	MS	R. A. McGraw, Univ. Georgia, Athens			264	150	124	8
		BM6458	MS	AAATTTAACCCTTTGGAAAAGC	AGTGTGGGGTAGAGCACTGG	54	328	145	129	7
		BL21	MS	TGTGTGGATTGGACTTGAGG	TTTCCCCCACTTGTGACATC	58	144	218	206	5
		BM6437	MS	GAGGAAATACAGAACTCAGCCG	TCAAACAGCATCTAGGCGG	56	188	297	243	10
		BM1224	MS	AGGAACCACATTGGGTAGTCC	TCCCTCTCTCCCTGAGGC	54	161	179	165	6
		RM067	MS	R. A. McGraw, Univ. Georgia, Athens			198	102	90	4
		*MAF50†**	MS	Table 4			180	168	152	8
		BM1260	MS	AAGTACATGCATGCTGCTGC	TCCTAAGTTCCATCAACAGGTG	58	83	133	120	9
		MAF70†	MS	Buchanan and Crawford (1992)			267	149	121	11
5	3	*BM6026*	MS	GCAACTAAGACCCAACCAAC	ACTGATGTGCTCAGGTATGACG	56	178	168	148	10
		BP1	MS	AAAATCCCTTCATAACAGTGCC	CATCGTGAATTCCAGGGTTC	56	258	328	302	10

		MYF-5[e]	RFLP	CLARK *et al.* (1990)			32			2
		*AGLA293**	MS	Table 4			212	257	237	10
		BL23	MS	TCAATCCCTGGGTCAGGAAG	CTTATTTCAAAATTCGGTTGGG	54	161	256	242	5
		*BMC1009***	MS	GCACCAGCAGAGAGGACATT	ACCGGCTATTGTCCATCTTG	58	180	289	179	9
		BM321	MS	AAGGGTCAGACAAAACTTAGCA	ATCCTTGCCCTAATTCTCATTC	60	140	126	110	6
		BL37	MS	GCAATCCCACTCTCCAGGTG	CATTCATGTTGCTGTAAATGGC	58	134	260	238	5
		RM084	MS	R. A. MCGRAW, Univ. Georgia, Athens			238	140	130	6
		RM500	MS	R. A. MCGRAW, Univ. Georgia, Athens			272	132	124	4
		BR2936	MS	GAGCCTTGTGGGCTACAGTC	GAAGATTGCAAATGGAAAGACC	58	241	152	130	7
		MAF23†*	MS	Table 4			210	105	103	2
		*AGLA254**	MS	Table 4			318	214	158	17
		BM1819	MS	AGCACTGTGGGAATTATGGG	TGGAATGAGCCAGCTCAAG	58	241	128	114	10
		IGF-1[f]*	MS	GCTTGGATGGACCATGTTG	CACTTGAGGGGCAAATGATT	58	249	231	225	4
		BM315	MS	TGGTTTAGCAGAGAGCACATG	GCTCCTAGCCCTGCACAC	60	183	163	107	12
		BM733	MS	ATGCTCCTTGTGCTCTCACC	GCCATAGGAGAAAAACTTGGG	56	114	174	166	5
		BM43	MS	AGGGAGGGTCACCTCTGC	CTTGTACTCGTAGGGCAGGC	56	113	175	157	7
		*ETH152**	MS	Table 4			234	204	192	6
		BM2830	MS	AATGGGCGTATAAACACAGATG	TGAGTCCTGTCACCATCAGC	58	230	203	149	15
		BM49	MS	TCACTAAACCAGGGGCGG	GAGGCAGGCAAAATCAGAAC	58	66	105	97	4
6	15	*BM2320*	MS	GGTTCCCAGCAGCAGTAGAG	CCCATGTCTCCCGTTACTTC	58	240	152	128	9
		BP7	MS	GACCTTTTCACTGCCCTCTG	TTTATTTCTGAGTGTTTGGGGC	54	137	307	295	6
		CSN3[g]*	MS	ATGCACCCTTAACCTAATCCC	GCACTTTATAAGCACCACAGC	58	337	226	216	5
		BM4311	MS	TCCACTTCTTCCCTCATCTCC	GAAGTATATGTGTGCCTGGCC	58	213	105	93	7
		ALB[h]	PROT				33			2
		GC[i]	PROT				110			2
		BM1236	MS	CTGAACCACCACGGAAGC	AGTCCATGGGGTTGCAAG	54	88	128	116	7
		BM415	MS	GCTACAGCCCTTCTGGTTTG	GAGCTAATCACCAACAGCAAG	54	124	177	163	6
		RM028	MS	R. A. MCGRAW, Univ. Georgia, Athens			225	110	96	3
		BM4621	MS	CAAATTGACTTATCCTTGGCTG	TGTAACATATGGGCTGCATC	58	203	145	137	4
		BM4528	MS	CAGAATCCATACACATGTCAACA	AGGAACAGGTATAGGAATATTGGA	58	194	276	238	7
		BM143	MS	ACCTGGGAAGCCTCCATATC	CTGCAGGCAGATTCTTTATCG	58	109	122	90	13
		BM1329	MS	TTGTTTAGGCAAGTCCAAAGTC	AACACCGCAGCTTCATCC	58	276	161	145	8
7	22	***CAST***[j]	RFLP	BISHOP *et al.* (1993)			65			2
		ILSTS006	MS	BREZINSKY *et al.* (1993b)			305	295	283	7
		RASA[k]*	MS	Table 4			137	183	177	3
		OarAE129†	MS	Penty *et al.* (1993)			82	144	136	3
		BM1853	MS	AGCCTTTTGTAGGTGTTCATTG	ATGGGGTTGCAAAGAGTCAG	56	259	106	94	5
		BM6117	MS	GTTCTGAGGTTTGTAAAGCCC	GGTGAGCTACAATCCATAGGG	58	237	114	110	3
		BM741	MS	GCCCCTGAAGGAATGGTG	CCAAAAGGTCCTATCTCCAAA	56	105	184	172	4
		ILSTS001	MS	BREZINSKY *et al.* (1992a)			127	94	77	5
		*TGLA176**	MS	Table 4			123	92	74	6
		BP41	MS	TCCCATCTTCACCAAAGAGC	AAGAACCCGCTTCCAAGG	50	169	326	312	6
		RM006	MS	R. A. MCGRAW, Univ. Georgia, Athens			82	122	116	4
		BM2607	MS	GGCCTGTGACTCCTTGTAGG	TTCCTGTGGGCTGGCTAG	58	113	135	131	3
8	18	*BM711*	MS	CAGCATCAGCAACTAACATAGG	TGGACCATGAGGGAAGTCTC	56	124	183	157	9
		HEL9	MS	KAUKINEN and VARVIO (1993)			280	165	143	12
		*TGLA13**	MS	Table 4			184	209	183	9
		BM4006	MS	CAATGTGCATTATTTCCAAAGTG	AGAAATAACTCTTTCTCCTTGGAGG	56	138	119	97	8
		RM032	MS	R. A. MCGRAW, Univ. Georgia, Athens			43	106	98	2
		BP2	MS	GAGAAGGGAAGACATTACGGG	CTCTGAGCAGGCAGTGTTTG	56	147	368	352	8
		BM310	MS	AAAGCAAGATTTAAAGCAGAAACA	ACCACCAACCATCTTGAGGA	52	289	136	126	6
		BM3419	MS	CTACTTCTGCACTCCAGCCC	GCCAAAGAAAGCTGAAGCC	58	179	150	134	4

TABLE 3

Continued

Chromosome	Syntenic group	Locus	Type	Forward primer sequence (5′ → 3′)	Reverse primer sequence (5′ → 3′)	Annealing temperature	Informative meioses	Allele (bp)		N^a
								Max.	Min	
10	5	*BM1237*	MS	TCATCTTGGGCATAAGACAGG	ATTGTTCCCAGCATCTTAGAGG	58	260	223	187	9
		BM6418	MS	AAGGTACCAGAAAGATGGCTG	AACAGATTGGATTTCCCAAGG	54	32	158	142	6
		BRRIBO[l]	MS	CACCCGTACCCTCACTGC	TCACAACCCTCTTCTCACCC	58	284	252	157	12
		BM6305	MS	GAGATTGGCTTATTTCACTCGC	GAGCAACTAAGCACACATGAGG	60	177	149	123	8
		BM875	MS	ACCTATCTCATTTGGCTTCTGG	AAAAAACCCCAAACAACAACC	58	166	111	95	5
		RM090	MS	R. A. McGraw, Univ. Georgia, Athens			302	144	118	9
		BM888	MS	AGGCCATATAGGAGGCAAGCTT	CTCGGTGAGCTCAAAACGAG	58	274	183	173	6
		BR1603	MS	AACAGCTTTCTGATTTATTCTCTCC	CTGTACGTAGTGTTGCAGAGTCG	56	192	135	113	8
		BR6027	MS	CATGACTAAGCCACTAAGACGC	ACTGAGAACAAAAGGAGAAGCG	60	193	136	124	7
		*TGLA433**	MS	Table 4			223	198	178	7
		EAZ[d]	EA				72			3
		BP31	MS	ACGCACCTTTATGTTCATTGC	TTCTTTCACTTTAGGTCCATCC	54	229	205	199	4
		ILSTS005	MS	Brezinsky *et al.* (1993a)			105	185	181	3
		Oar*AE64*†	MS	Ede *et al.* (in press)			209	104	102	2
11	16	*LGB*[m]*	RFLP	Table 4			30			2
		HEL13	MS	Kaukinen and Varvio (1993)			256	197	177	7
		BM6491	MS	TCTGCCCCTCACCATGTC	GGCCACACCTCAGCTCAC	56	231	173	165	3
		*TGLA436**	MS	Table 4			274	108	102	4
		BM746	MS	CTATCTGTTTCCCCAGCTTCC	GCCCAGGTTAATGACAGAGC	56	170	152	146	4
		BM6445	MS	GTGTCTGTCAAAAGATGAATGG	GACAACTGCTTCTCGTTGGG	58	275	175	159	6
		*TGLA327**	MS	Table 4			187	123	111	6
		RM096	MS	R. A. McGraw, Univ. Georgia, Athens			314	116	90	8
		BM304	MS	CTGGTGTTCCTTTCATATCAACC	GGCACGTACTAACCTGTAAAACC	56	298	127	107	8
		BM2818	MS	TTCTGTGGTTGAAGAGTGTTCC	CAATGGCTAAGAGGTCCAGTG	56	138	120	104	6
		BP38	MS	CCAAATGATGGTTCAAGTTTG	GCTCATCATAAAGGGAATTCAG	50	79	320	298	4
		BM716	MS	AGTACTTGGCTTGCTTTGCTC	TTAAATTTCCATCTCACCCTGG	56	172	155	114	8
		BM827	MS	GGGCTGGTCGTATGCTGAG	GTTGGACTTGCTGAAGTGACC	58	131	214	208	3
13	11	*AGLA232**	MS	Table 4			322	183	157	12
		BL42	MS	CAAGGTCAAGTCCAAATGCC	GCATTTTTGTGTTAATTTCATGC	58	247	238	232	4
		BM720	MS	ACATCTCATTCTTGTGTCATGG	GAAATTCAGTTTAGGGTTCCCC	56	318	240	210	14
		*BMC1222***	MS	CCAATTTTGCAGATAAGAAAACA	CCTGAGTGTTCCTCCTGAGT	58	183	302	272	12
		*TGLA23**	MS	Table 4			197	116	92	9
14	24	*BM6425*	MS	AGTTGAACCTGGGTCTCCTG	TGCAATGGCAGTGAAAAAAG	54	310	192	172	7
		CA2[n]*	PROT	Table 4			21			12
		BM2934	MS	CCAATTGTCTTCCTAGCTCTTC	CTGTTAGTTCTGCCAAAATCCC	56	299	103	81	8
		BM4305	MS	CCAAGACATGAAAGCAATCTG	CTCTAGGTACATCCATGTTGCA	58	250	168	148	8
		RM066	MS	R. A. McGraw, Univ. Georgia, Athens			75	103	97	3
		BM4513	MS	GCGCAAGTTTCCTCATGC	TCAGCAATTCAGTACATCACCC	58	256	161	141	10
		BM302	MS	GAATTCCCATCACTCTCTCAGC	GTTCTCCATTGAACCAACTTCA	56	176	154	140	7
		ILSTS008	MS	Kemp *et al.* (1993)			244	181	179	2
		RM011	MS	R. A. McGraw, Univ. Georgia, Athens			66	119	95	6
		BM4630	MS	TGGTTTGCTGGTGAGATTAGG	TTCATAATGGGGTGAGTGAGTG	56	195	165	151	7
		ILSTS011	MS	Brezinsky *et al.* (1993c)			59	271	261	5

15	19	*BM848*	MS	TGGTTGGAAGGAAAACTTGG	CCTCTGCTCCTCAAGACAC	58	244	227	215	5
		BM4439	MS	TGTCAAATTATGAAACAAGGAAGC	GAATTCCACGTCACAGAGTCG	58	15	140	136	2
		*TGLA75**	MS	Table 4			258	157	143	6
		EAA^{d}*	EA				132			8
		HBB^{o}*	MS	GCAGCAATCAGTACAAAAGAGG	GCAACTGGCAAAATTTCATTC	60	241	190	172	8
		PTH^{p}*	SSCP	FRIES *et al.* (1993)			34			2
		HEL1	MS	KAUKINEN *and* VARVIO (1993)			205	114	100	5
		MAF65†	MS	BUCHANAN *et al.* (1992)			56	109	105	2
		ADCY2^{q}	MS	AAAGTGACACAACAGCTTCTCC	ACAAGTGAGTGCGTAACAAAGG	58	223	205	185	6
		BR3510	MS	GCTGGTGGGTTGTTTACCAC	ACCCCGTGGACTGTAGTCTG	58	217	114	90	9
		*MGTG13B**	MS	FRIES *et al.* (1993)			206	141	133	5
16	1	***EAR***$'^{d}$	EA				104			2
		*INRA013**	MS	D. VAIMAN *et al.* (unpublished data)			264	197	177	7
		BM1706	MS	ACAGGACGGTTTCTCCTTATG	CTTGCAGTTTCCCATACAAGG	58	301	259	233	10
		BM719	MS	TTCTGCAAATGGGCTAGAGG	CACACCCTAGTTTGTAAGCAGC	54	113	155	147	5
		BR6504	MS	AATACCATGGACAGAGGAGCC	AGGTTCAGGTCACCACAATACC	56	297	145	125	8
		BM1311	MS	AAGTGCTGGGCACGACTG	GGTGGGAGCTGAAATCACC	58	213	133	125	5
		BM4025	MS	TCGAATGAACTTTTTTGGCC	CACTGACTATGTGACTTTGGGC	56	241	146	128	8
		BM121	MS	TGGCATTGTGAAAAGAAGTAAA	ACTAGCACTATCTGGCAAGCA	58	319	160	118	14
		BM6121	MS	CTGTTTGCTATAATTTTGTGGAGG	TGGCATTCTACGAGACCACA	60	230	164	138	11
		*TGLA245**	MS	Table 4			255	161	129	11
		BM6430	MS	CCAGGCTCTTCCTCCTGTTC	GGGAAGGAGACTTAGGGCC	52	136	164	105	9
17	23	*BM1233*	MS	TGGCAGGTGGATTCTTTACC	ATGTACAACTGAATCACTCCGC	58	184	180	168	6
		BM1862	MS	AAGCAAAAAGGCTGATGGC	TTGCAGATACTGGCAAGTGG	58	306	224	191	16
		*TGLA170**	MS	Table 4			207	101	81	5
		BL50	MS	GAGCATAGTGCCCTGCATAC	TAGCATTGTCTACGGCATGG	58	113	216	210	4
		BM8125	MS	CTCTATCTGTGGAAAAGGTGGG	GGGGGTTAGACTTCAACATACG	58	315	123	109	6
		ETH185^{g}	MS	Table 4			226	243	222	8
		BM305	MS	ACACAATAAGAGTGTGGCATCC	GTGTCCTTTTGACTCACTGTGC	60	246	135	101	13
		OarFCB48†	MS	BUCHANAN and CRAWFORD (1993a)			267	154	146	5
		OarVH98†	MS	HANRAHAN *et al.* (1993)			202	161	133	10
18	9	*BM7109*	MS	CAGGTAAAAGAGCGGCTTTG	CAGCTTCATGCCCTAGAAGG		321	168	156	6
		ILSTS002^{g}	MS	KEMP *et al.* (1992)			260	137	123	6
		*UWCA5**	MS	Table 4			43	125	123	2
		EAC^{d}	EA				173			25
		BM2078	MS	CCCAAAAGAAGCCAGGAAG	TCAGAGTTTGGGGTCCTCAG	58	347	141	92	12
19	21	*BMC1013*	MS	AAAAATGATGCCAACCAAATT	TAGGTAGTGTTCCT-TATTTCTCTGG	54	237	244	218	5
		*ETH3**	MS	Table 4			296	125	105	8
		GFAP^{r}	SSCP	B. W. KIRKPATRICK *et al.* (unpublished data)			34			2
		GH^{s}*	SSCP	B. W. KIRKPATRICK (1992); Table 4			41			3
		PTF2^{t}	PROT				158			2
		MAP2C^{u}	MS	MOORE *et al.* (1992)			209	98	90	5
		EAT$'^{d}$	EA				74			3
		RM099	MS	R. A. MCGRAW, Univ. Georgia, Athens			240	125	119	3
		KRT10^{v}*	MS	FRIES *et al.* (1993)			162	183	173	6
		OarFCB193†	MS	BUCHANAN and CRAWFORD (1993b)			207	104	102	2
		ILSTS014	MS	BREZINSKY *et al.* (1993c)			107	130	126	3
		BP20	MS	TCTGTGGGTGAACAAGCAAG	GGCTCCCTAAAGACCCACTC	56	284	233	219	8
		HEL10	MS	KAUKINEN and VARVIO (1993)			236	114	98	7
		BM6000	MS	ACAGCAATGCCATGGACC	TGCCATTTGGATGTGTGC	58	187	118	106	4
20	20b	*BM5004*	MS	TCTGGAGTGAATGTTTCTGAGG	TTGTGATGAGCACCTGAAGG	58	252	154	120	10

TABLE 3

Continued

Chromosome	Syntenic group	Locus	Type	Forward primer sequence (5′ → 3′)	Reverse primer sequence (5′ → 3′)	Annealing temperature	Informative meioses	Allele (bp)		N^a
								Max.	Min	
		*AGLA29**	MS	Table 4			325	164	144	9
		***ANPRC**^{w}*	MS	GCCATCCCTTTCCCTTAATC	CCCCACAAAGCTACACCG	58	60	209	196	5
		BM4107	MS	AGCCCCTGCTATTGTGTGAG	ATAGGCTTTGCATTGTTCAGG	58	214	191	157	8
		BM713	MS	TGCCTACCTCTTAGGAGTCCA	TCAGACAGAACTGAGGACATGC	58	266	112	100	6
		*TGLA304**	MS	Table 4			308	100	86	7
		BM1225	MS	TTTCTCAACAGAGGTGTCCAC	ACCCCTATCACCATGCTCTG	56	117	253	227	10
		RM106	MS	R. A. McGraw, Univ. Georgia, Athens			214	136	122	6
		HEL12	MS	Kaukinen and Varvio (1993)			326	167	147	7
		BM3517	MS	GTGTGTTGGCATCTGGACTG	TGTCAAATTCTATGCAGGATGG	58	300	124	104	8
21	4	*HEL5*	MS	Kaukinen and Varvio (1993)			281	165	149	7
		BM3413	MS	TCCCTGGTAACCAATGAATTC	CAATGGATTTGACCCTCCC	58	184	192	170	9
		*AGLA233**	MS	Table 4			67	250	246	3
		BM103	MS	CTAGCTGCTGGCTACTTGGG	GGCTGCTCTGGGCTATTG	56	156	160	148	7
		BP33	MS	AGGCCTCTGAATTCCTCTCC	AACCAGCAGTCTTGCTCTCTC	50	191	271	253	7
		***EAS**^{d}*	EA				66			9
		*ETH131**	MS	Table 4			344	173	141	18
		*UWCA4**	MS	Table 4			195	93	75	6
		*BMC5221***	MS	AGCAAGGAGAACAGGCATTC	CTTCTTTGGCAGCACAGTTTC	58	153	171	169	2
		BM846	MS	GACCACTGGACCACCAGG	CTGGTAAAAAGCAATGATGCC	58	260	268	240	8
		*TGLA122**	MS	Table 4			315	173	137	8
23	20a	*BM1905*	MS	GTCCATGGGTTCACAAAGAG	ACGCCTGCTGATGCTGTAG	58	193	199	170	11
		BM1443	MS	AATAAAGAGACATGGTCACCGG	TCGAGGTGTGGGAGGAAG	58	237	163	137	7
		BP34	MS	ATTTGAAAAGGCCTGTGAGG	TAGCTTGACTCCAACCTCTTCC	50	54	320	310	4
		BM1818	MS	AGCTGGGAATATAACCAAAGG	AGTGCTTTCAAGGTCCATGC	58	321	272	258	8
		PRL^{x}**	MS	Fries *et al.* (1993)			60	162	156	3
		CYP21^{y}**	MS	Fries *et al.* (1993)			165	224	188	13
		EAM^{d}**	EA	Table 4			21			3
		BOLA-DRBP1^{z}**	MS	Fries *et al.* (1993)			194	137	121	9
		HSP70-1^{aa}**	SSCP	GGATTGCTCATGTTTGTTATGG	CTTGGAAGTAACAGAAACGGG	58	212	225	202	11
		BM1258	MS	GTATGTATTTTTCCCACCCTGC	GAGTCAGACATGACTGAGCCTG	58	243	112	100	7
		*UWCA1**	MS	Table 4			236	130	102	9
		RM033	MS	R. A. McGraw, Univ. Georgia, Athens			62	165	149	4
		BM47	MS	ACAGGAAGGAGAAGGGGAAG	CCGGGGTCACATGACTCTG	56	189	126	94	12
24	28	*MAF35*†	MS	Swarbrick *et al.* (1991)			29	114	98	4
		*AGLA269**	MS	Table 4			226	258	208	16
		*TGLA351**	MS	Table 4			145	133	121	4
		BM226	MS	ATTGCCTTGTCCGTGTATCC	CCGGCTGAATTGCTATAAGC	58	199	164	128	10
25	7	*ILSTS015*	MS	Brezinsky *et al.* (1992b)			125	275	261	3
		*TGLA414**	MS	Table 4			221	180	162	3
		*BMC8012***	MS	AATTCCATGCACAGAGGACC	GATTCCAGAAAGTTCCCCCA	58	147	215	197	10
		OarHH22†	MS	Ede *et al.* (in press)			170	126	103	8
		***OCAM**^{bb}**	MS	Fries *et al.* (1993)			97	185	181	3
		*BMC3224***	MS	CCATCACTGCTATTCTACCTCC	CACAGCCAATTTCTGATTTCA	58	210	188	182	4

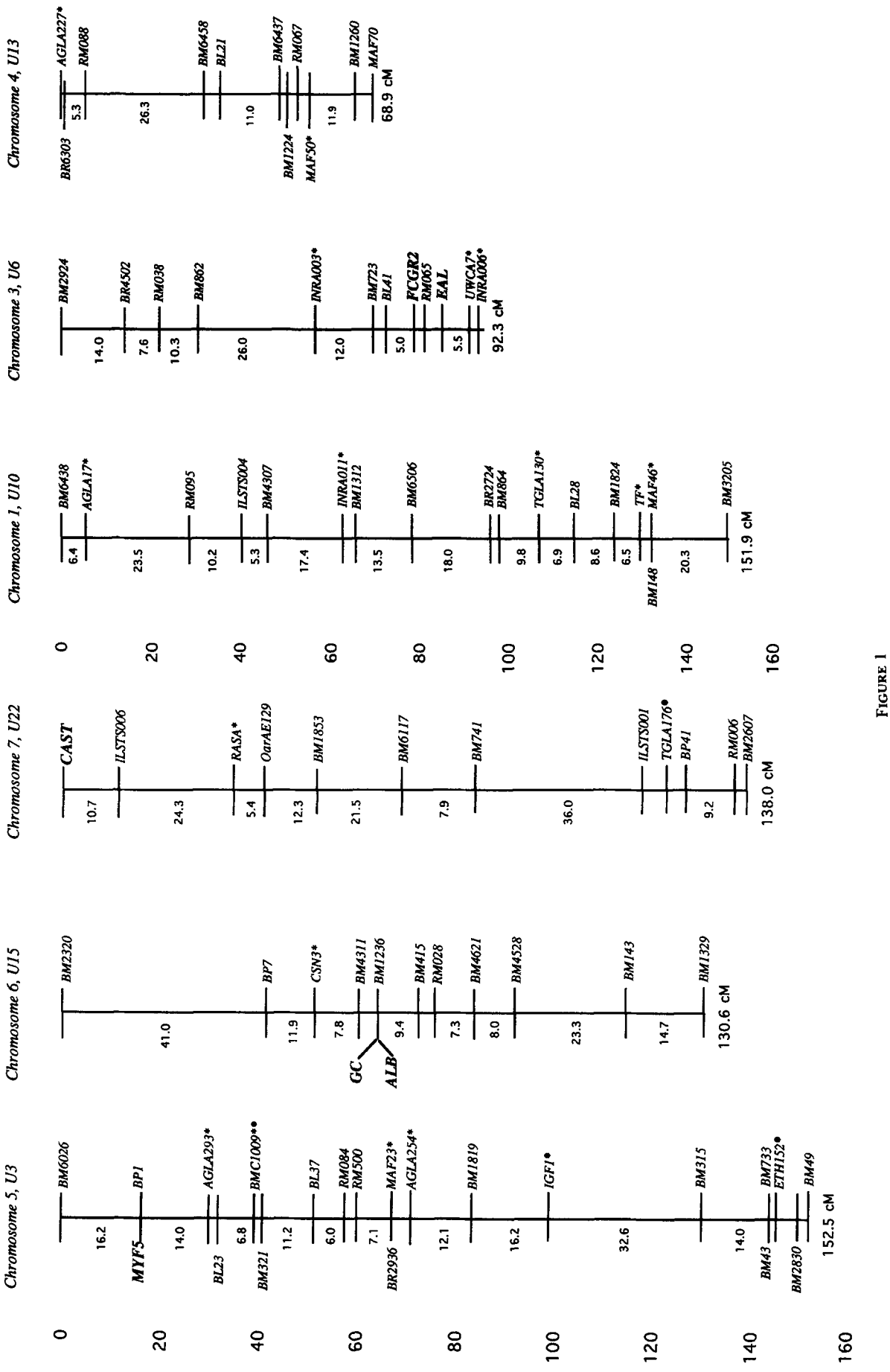
		BMC1206	MS	GGGTGGCTATGACTCCAGTG	GGTCCAGCCTTCCACCAC	58	179	140	130	5
26	26	*HEL11*	MS	KAUKINEN and VARVIO (1993)			310	193	181	7
		BM1314	MS	TTCCTCCTCTTCTCTCCAAAC	ATCTCAAACGCCAGTGTGG	54	267	167	143	7
		BM4505	MS	TTATCTTGGCTTCTGGGTGC	ATCTTCACTTGGGATGCAGG	62	305	242	204	11
		RM026	MS	R. A. MCGRAW, Univ. Georgia, Athens			80	95	85	4
		BM188	MS	AGTCGCCAAGTCGTGTCTG	GAGGAACATTGCGAGGCTAC	54	198	117	97	7
		BM6041	MS	GGCTGCTGCATGTCAGTG	GACTTGAGCTCCTCCAGGG	56	311	128	120	5
		*TGLA429**	MS	Table 4			257	177	163	6
		MAF92†	MS	CRAWFORD *et al.* (1991)			74	116	110	4
		BM804	MS	CCAGCATCAACTGTCAGAGC	GGCAGATTCTTTGCCTTCTG	58	223	158	144	6
28	29	*BM2515*	MS	GATTCCCTGACTCTCTGTCCC	AGTATTGGCAAGTCAATGGAGG	58	248	148	132	5
		*RBP3^{cc}**	MS	FRIES *et al.* (1993)			56	144	132	5
		BL25	MS	AACAGTGGCAATGGAAGTGG	AGTCAGGATCTAGTGGGTGAGTG	58	356	183	161	6
		*BMC1002***	MS	AGAGAAGGAGCGTGGCCT	CTAGAGTCCATGTGGTCGCA	60	97	204	186	5
		BP23	MS	CCCAACCCAGGAATCAAAC	TTGGCCATTACCTTGACTCC	50	78	288	272	6
29	8	*BP28*	MS	AGGTGCAGGTGAGAGGGC	CCTCCACAACACCATCCTTC	50	49	208	202	4
		BM4005	MS	AGTCCATGGGACCACAAAAG	ACTGTACAGCAAAGTGATTCAGAT	58	308	122	108	8
		*BMC4216***	MS	TGAGGGAAAAGGGAGATGG	GAGTGGTTCACAAAAATGTGC	54	134	171	161	5
		RM074	MS	R. A. MCGRAW, Univ. Georgia, Athens			204	162	139	3
	2	*BM4208*	MS	TCAGTACACTGGCCACCATG	CACTGCATGCTTTTCCAAAC	58	302	174	154	6
		BM6436	MS	AAAGACTGCTTGCCTGAAGC	CAACCAGTGATGCTGTACTCTG	58	247	208	198	6
		BMC701	MS	TGATTTCCTTTTCCAGACTTCC	ATGGGTTCCAGCACAATTTT	56	212	308	266	12
		BM4204	MS	GGGTAGGAGCTTTTGTAGGTG	GCCATCACCCTTCTCTTATATG	58	123	158	148	6
		UWCA9	MS	B. W. KIRKPATRICK *et al.* (unpublished data)			136	107	89	6
		*TGLA261**	MS	Table 4			252	289	219	16
		ILSTS013	MS	BREZINSKY *et al.* (1993c)			242	126	120	4
		BM2504	MS	CAGCTTTCCATCCCCTTTC	CTCCCATCCCAAACACAGAC	58	180	146	130	7
		BM1227	MS	CACCAGTGATATTGGCTTATGG	GGAAGAAACACTTCCAAACCC	58	141	119	111	5
		*ETH225**	MS	Table 4			315	159	141	7
		BM757	MS	TGGAAACAATGTAAACCTGGG	TTGAGCCACCAAGGAACC	58	206	220	182	10
	12	*BM1558*	MS	TGAGGAAAGCCTTGGCAG	ACTGGGCCTAGCTCCTTCTC	60	269	134	130	3
		BM1303	MS	CTTGGGAAAAATTGCCAGC	CTCTGCCGCTTGCCTCTC	54	297	147	131	5
		*AGLA13**	MS	Table 4			313	178	162	8
		BP36	MS	AAGCCTAACTCCTGGGAACC	TACAATGGGATGTTATTCAGCC	50	80	268	258	4
		BM3628	MS	CTGAGATGGACTCAGGGAGG	GTTGGATTGGAAAGGTTAGGC	58	314	263	343	8
		BM2613	MS	AAGGAGAACCTCCATCCCTG	ATGGACAGAGGAACCCAGTG	58	307	174	160	8
		BM4102	MS	CCAAATTCCACTGTGCTGC	GAGCGGCCTATCAACCCTAC	58	120	169	157	5
		HRHI^{dd}	MS	GAAAGCTGGAGCAAACATCC	AACTGCCACCACTGTCAGG	58	146	141	133	5
		OarFCB304†	MS	BUCHANAN and CRAWFORD (1993b)			58	163	137	7
	17	*BM3627*	MS	CAGTCCATGGCACCATAAAG	TCCGTTAGTACTGGCTAATTGC	58	207	158	140	7
		*TGLA431**	MS	Table 4			177	163	134	10
		*TGLA377**	MS	Table 4			213	104	96	5
		*ETH121**	MS	Table 4			194	212	173	11
		OarFCB20†	MS	BUCHANAN and CRAWFORD (1993a)			248	128	94	9
		BM4440	MS	CCCTGGCATTCAACAAGTGT	CACCCTGTTAGGAATCACTGG	58	248	147	121	10
		BP22	MS	GAAAGTAGAGGCGTGGATGC	GGAGATGCAGGTCCAATCC	50	26	377	371	3
	27	*INRA005*	MS	D. VAIMAN *et al.* (unpublished)			257	246	240	4
		BM4028	MS	ACGGAAGCAGCATCTCTTAC	ATGGAAACATGGTCTCCTGC	58	242	126	102	12
		EAB^{d}	EA				156			26
		BM6404	MS	TCCCTAATGTTGAATGGACTTC	CGAAAAGAGTCAGACACCAGC	58	187	147	127	7
		*TGLA345**	MS	Table 4			259	142	124	9

TABLE 3

Continued

Chromosome	Syntenic group	Locus	Type	Forward primer sequence (5′ → 3′)	Reverse primer sequence (5′ → 3′)	Annealing temperature	Informative meioses	Allele (bp)		N^a
								Max.	Min	
		BM860	MS	ACCAGATTGGTGGTAGTGGTG	CATGCCGTGGCTAAGACC	58	251	182	164	8
		BM1827	MS	AAGCAAGGAAATTCCGGG	AAAGATTTGGACACAACTGAGC	60	213	143	135	6
		ILSTS010	MS	BREZINSKY *et al.* (1993c)			222	292	282	5
		*TGLA28**	MS	Table 4			222	157	137	7
		BM6122	MS	TTCTCTAGGCTTATCAGTGGCC	GGAGTTGCAAAGAGCTGGAC	60	42	103	77	7
		BM6116	MS	TCTGGCATCTCAGAATCGC	GGCTGGCTCTTCCTTACTC	60	179	154	130	7
		BM6108	MS	TTCTAATGTAGAGCAAAGT-GATTGA	TGTAGGAGGGACAGATTGGG	56	249	144	116	9
		*TGLA36**	MS	Table 4			250	107	77	8
X	X	*AGLA257*	MS	Table 4			227	136	102	15
		BM2713	MS	TGAATACCTGTTTCCAGCCC	CTCCTAAGTCCAGGAAGCCC	56	124	155	142	3
		BM4321	MS	CACAACTGAGTGACTGAGGACG	AGCAGCCTAAATGTCCGTTG	58	272	114	110	2
		BM4604	MS	TCTATACTGACACAAGCCCAGG	AAAGTCCTTCAGGCAGAAAAG	56	231	175	163	5
		INRA30	MS	CIAMPOLINI *et al.* (1993)			139	166	156	4
		BM6017	MS	TCTTCTGTTTTCCTCCATCCC	GGAAACTAGCTTATGCTGTGGG	58	185	139	112	10
		BR215	MS	GGGTTGCAGAGAGTTAGACATG	TTTGCAGCCACTTTAAGCTC	58	78	150	136	6
		ETH123	MS	FRIES *et al.* (1993)			38	112	110	2
		TGLA325	MS	GEORGES and MASSEY (1993)			275	144	96	10
Y	Y	*BM861*	MS	TTGAGCCACCTGGAAAGC	CAAGCGGTTGGTTCAGATG	56	174	158	156	2
Unassigned	*A*	*OarFCB11*†	MS	BUCHANAN and CRAWFORD (1993b)			332	168	139	10
		BM2113	MS	GCTGCCTTCTACCAAATACCC	CTTCCTGAGAGAAGCAACACC	58	201	143	123	11
		BM4117	MS	CCCTGAAGTGTCAGTGGACC	ACTCAGGTGTGCCTGGAGC	58	138	117	105	5
		BM1223	MS	AGGCAAATTGTGTTTCCAGC	TCATAAGGGTTTGGAGGCTG	58	300	171	141	12
		BM6444	MS	CTCTGGGTACAACACTGAGTCC	TAGAGAGTTTCCCTGTCCATCC	58	251	157	147	5
Unassigned	*B*	*BM203*	MS	GGGTGTGACATTTTGTTCCC	CTGCTCGCCACTAGTCCTTC	58	332	233	203	11
		BM17052	MS	CGACTGAGCTACCAGGGAAG	ACAAGCAAAGGCCAATGAAC	56	148	197	175	2
		BM1857	MS	GCTGTGGCTGTGCTTGTG	AGTAACTGCCCCCGGAAG	54	269	137	103	5
		BM1856	MS	GGCCTCAAGTTTCATCCATG	CATCAGCATGAAGCAACCC	58	16	151	148	3
		RM209	MS	R. A. MCGRAW, Univ. Georgia, Athens			265	145	115	9
		BM6526	MS	CATGCCAAACAATATCCAGC	TGAAGGTAGAGAGCAAGCAGC	56	301	172	142	8
		BM871	MS	TTCCTCAAACTGTGAACACACC	CCATGAGGTCACAAAGGGTC	58	290	147	125	9
		BM3507	MS	GCCCAAAGAAAGAAGTATGTGC	TAGTGCGGAGTCAGTCATGTG	58	346	187	159	14

* Anchored loci.
** Anchored loci from cosmid clones.
[a] Number of alleles.
[b] *Transferrin.*
[c] *Fc fragment of IgG, low affinity II*; SYMONS and CLARKSON (1992).
[d] Erythrocyte antigens L, Z, A, C, R′, M, T′, S and B.
[e] *Myogenic factor 5.*
[f] *Insulin-like growth factor I*; genBank Accession #X64400.
[g] *Kappa-casein.*
[h] *Albumin.*
[i] Vitamin D binding protein.
[j] *Calpastatin.*
[k] *RAS p21 protein activator (GTPase activating protein).*
[l] *Brain ribonuclease*; SASSO *et al.* (1991).
[m] Lactoglobulin, beta.
[n] Carbonic anhydrase II.
[o] *Hemoglobin, beta*; GenBank Accession #M63453.
[p] *Parathyroid hormone.*
[q] *Calmodulin-independent adenylate cyclase 2*; LIPKIN *et al.* (1989).
[r] *Glial fibrillary acidic protein.*
[s] *Growth hormone.*
[t] *Post-transferrin factor 2.*
[u] *Microtubule-associated protein 2.*
[v] *Cytokeratin class I gene cluster.*
[w] *Atrial-natriuretic peptide C receptor*; SAHEKI *et al.* (1991).
[x] *Prolactin.*
[y] *Cytochrome P450, subfamily XXI (steroid 21-hydroxylase).*
[z] *Major histocompatibility complex, class II, DR beta, pseudogene.*
[aa] *Seventy kilodalton heat-shock protein*; GROSZ (1992).
[bb] *Opiod binding and cell adhesion molecule.*
[cc] *Retinol-binding protein 3, interstitial.*
[dd] *Histamine receptor, H1 subclass*; YAMASHITA *et al.* (1991).
† Microsatellite primer pairs derived from ovine genomic libraries.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BL23
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6.8
BM321
BMC1009**
11.2
BL37
6.0
RM084
RM500
7.1
BR2936
MAF23*
AGLA254*
12.1
BM1819
16.2
IGF1•
32.6
BM315
14.0
BM43
BM733
ETH152•
BM2830
BM49
152.5 cM
Chromosome 6, U15
BM2320
41.0
BP7
11.9
CSN3*
7.8
BM4311
BM1236
GC
ALB
9.4
BM415
RM026
7.3
BM4621
8.0
BM4528
23.3
BM143
14.7
BM1329
130.6 cM
Chromosome 7, U22
CAST
10.7
ILSTS006
24.3
RASA*
5.4
OarAE129
12.3
BM1853
21.5
BM6117
7.9
BM741
36.0
ILSTS001
TGLA176•
BP41
9.2
RM006
BM2607
138.0 cM
Chromosome 1, U10
BM6438
6.4
AGLA17*
23.5
RM095
10.2
ILSTS004
5.3
BM4307
17.4
INRA011*
BM1312
13.5
BM6506
18.0
BR2724
BM864
9.8
TGLA130*
6.9
BL28
8.6
BM1824
6.5
TF*
MAF46*
BM148
20.3
BM3205
151.9 cM
Chromosome 3, U6
BM2924
14.0
BR4502
7.6
RM038
10.3
BM862
26.0
INRA003*
12.0
BM723
BL41
5.0
FCGR2
RM065
EAL
5.5
UWCA7*
INRA006*
92.3 cM
Chromosome 4, U13
BR6303
AGLA227*
5.3
RM088
26.3
BM6458
BL21
11.0
BM1224
BM6437
MAF50*
RM067
11.9
BM1260
MAF70
68.9 cM
0
20
40
60
80
100
120
140
160

FIGURE 1

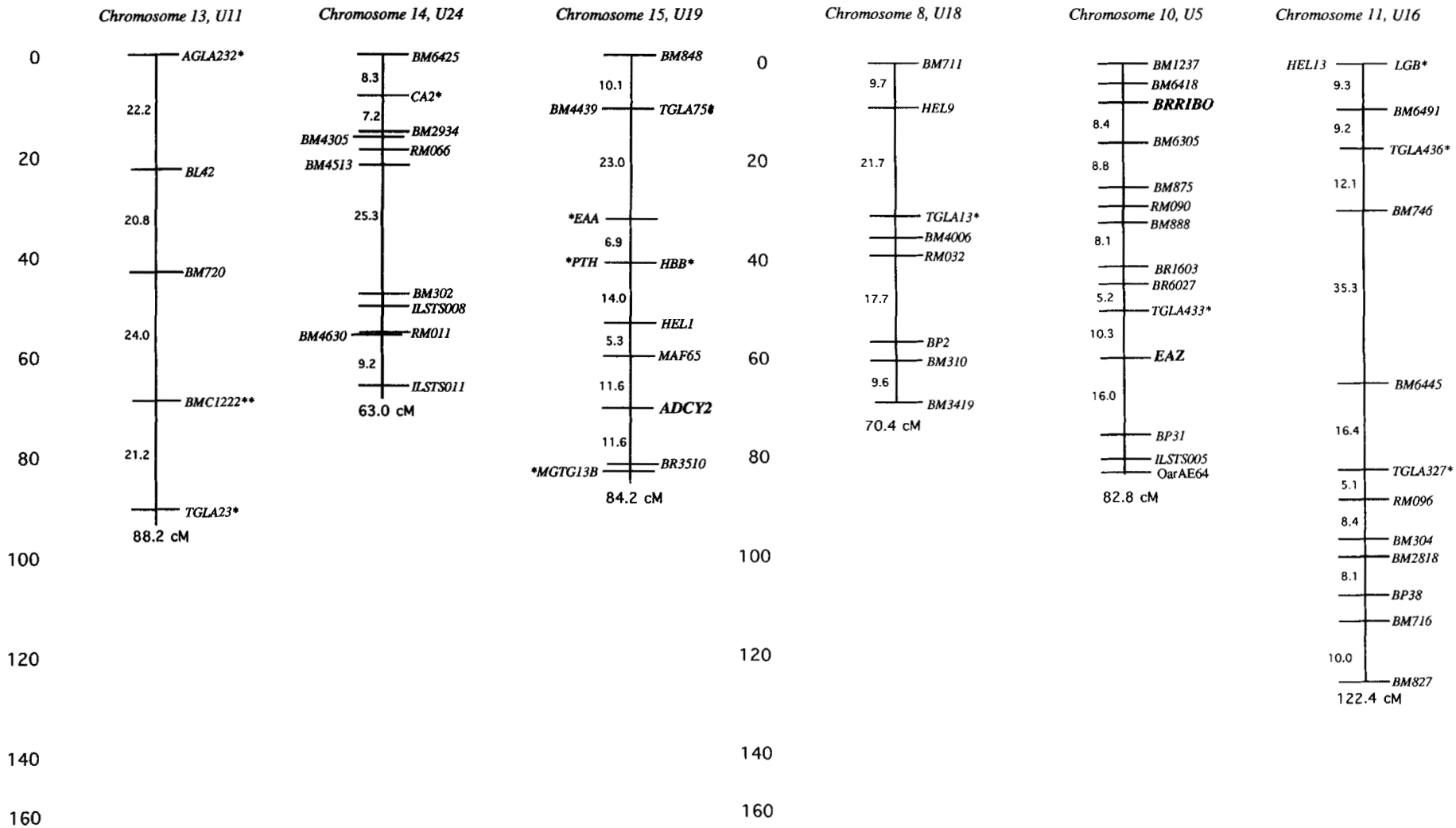

FIGURE 1.—Continued

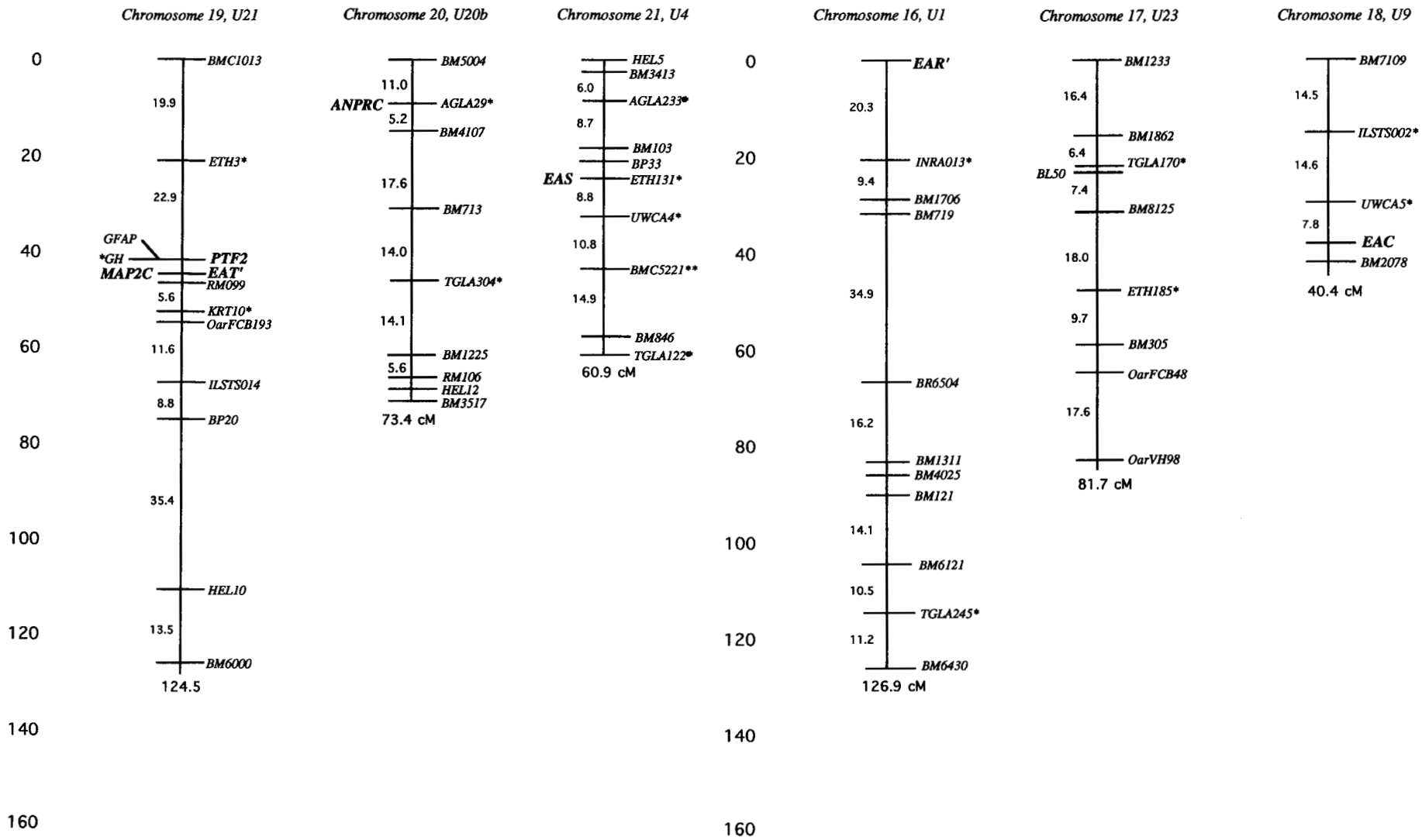

FIGURE 1.—Continued

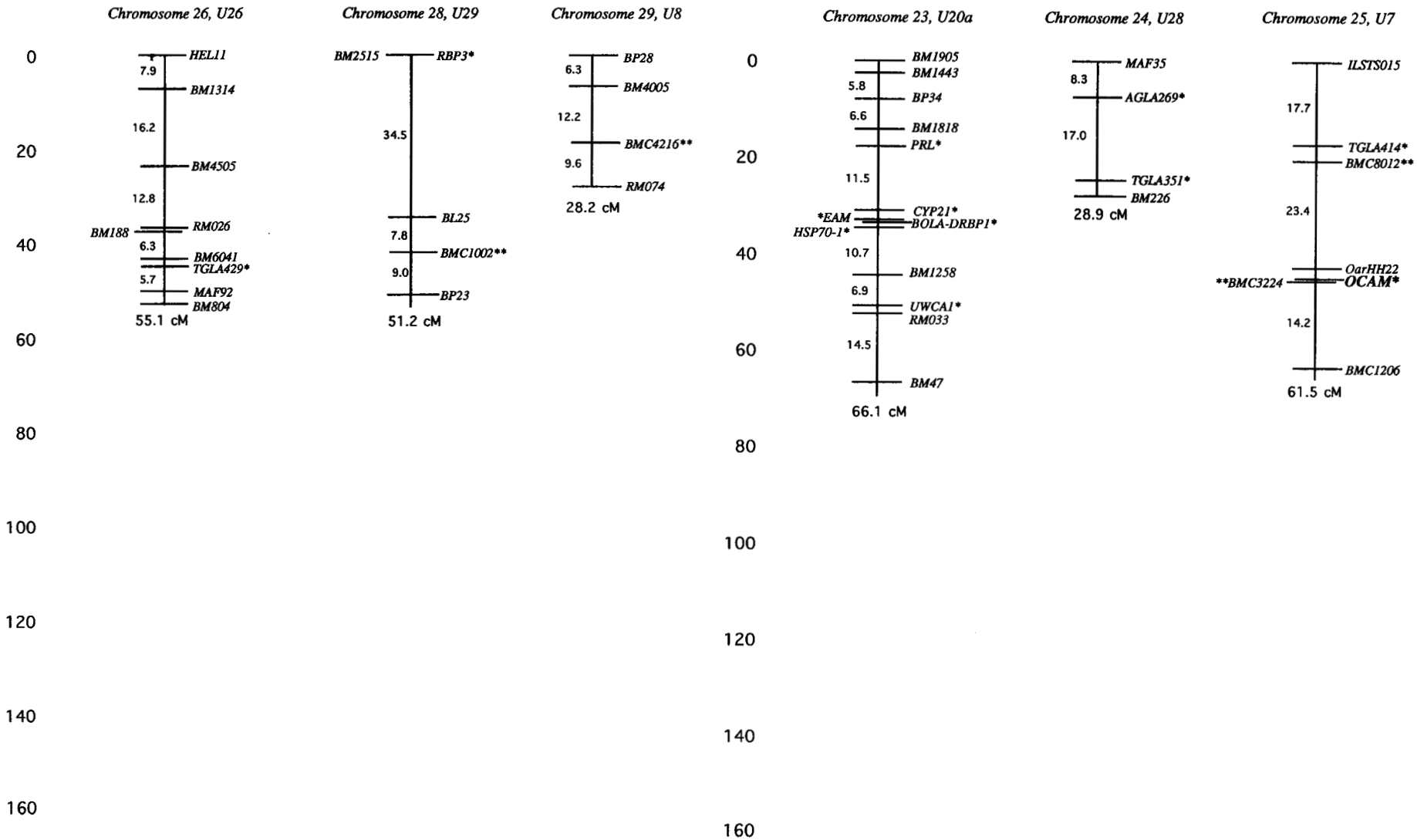

FIGURE 1.—Continued

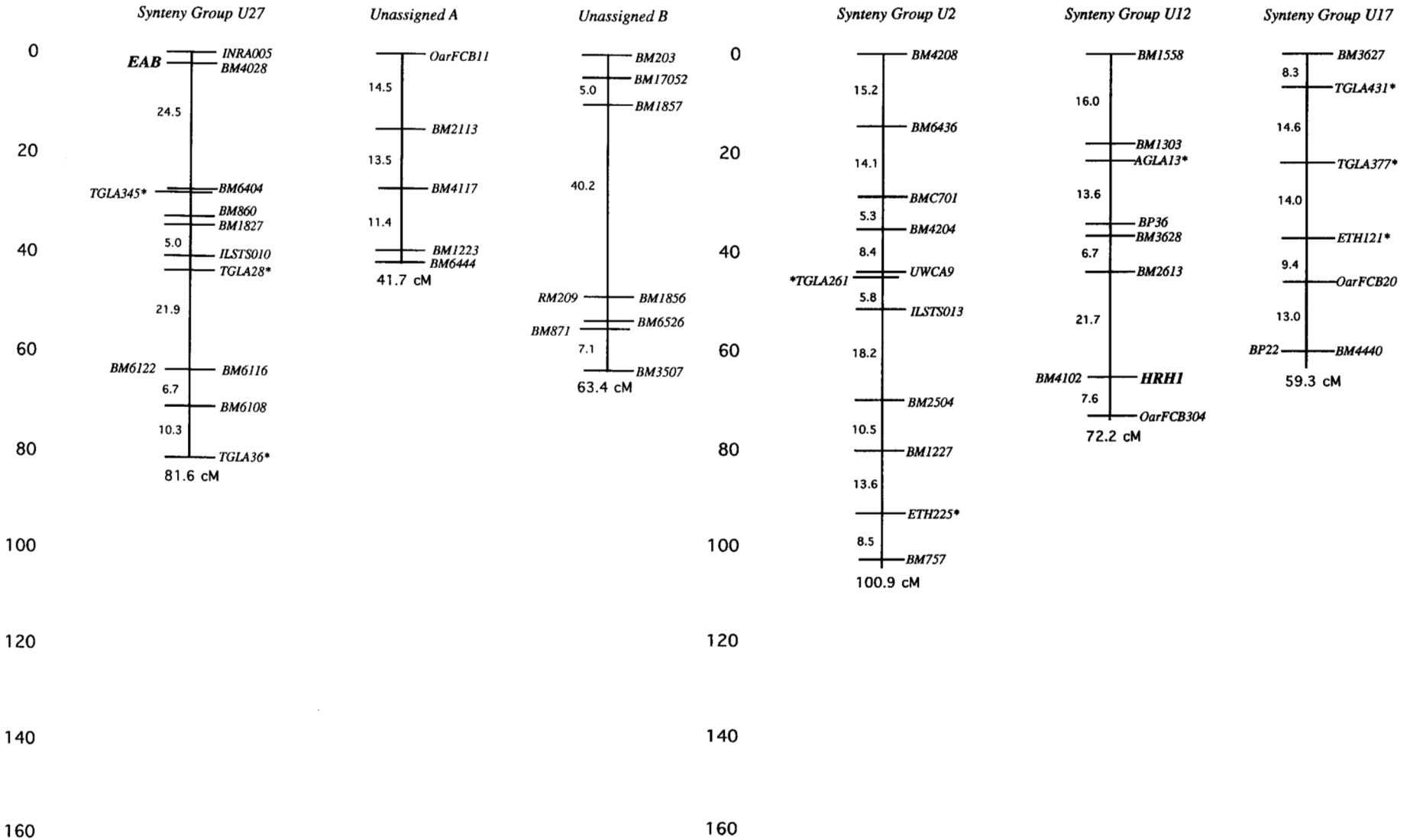

FIGURE 1.—Genetic linkage map of the bovine. Chromosomes and synteny asignments are indicated at the top of the idiogram. Centromeres and telomeres are arbitrary since no attempt was made to orient linkage groups for this publication. Markers listed with single (*) asterisks were used as previously mapped loci for anchoring linkage groups. Those markers with double (**) asterisks were anchors derived from cosmids mapped in this study. Centimorgans (cM) are based on Kosambi's map function. Estimated total coverage of each linkage group is given at the bottom of each ideogram and all intervals greater than 5 cM are indicated on the left of each diagram.

TABLE 4

References and chromosomal/synteny group assignments for anchor loci

Marker	Type	Chromosome	Synteny	Type of assignment[a]	Reference
AGLA17	MS	*1*	10	S	GEORGES and MASSEY (1992)
INRA011	MS			S	VAIMAN *et al.* (1992)
TGLA130	MS			S	GEORGES and MASSEY (1992)
TF	Protein			*L,R,S*	THREADGILL *et al.* (1991)
MAF46[b]	MS			S	SWARBRICK *et al.* (1992a)
INRA003	MS	*3*	6	S	VAIMAN *et al.* (1992)
INRA006	MS			S	VAIMAN *et al.* (1992)
UWCA7	MS			L	SUN *et al.* (1993)
AGLA227	MS	*4*	13	S	GEORGES and MASSEY (1992)
MAF50[b]	MS			S	DIETZ (1992); SWARBRICK *et al.* (1992b)
AGLA293	MS	*5*	3	S	GEORGES and MASSEY (1992)
MAF23[b]	MS			S	DIETZ (1992); SWARBRICK *et al.* (1990)
AGLA254	MS			S	GEORGES and MASSEY (1992)
IGF-I	MS			S	BISHOP *et al.* (1991)
ETH152	MS			P,S	STEFFEN *et al.* (1993)
CSN3	MS	*6*	15	L,N,R,S	THREADGILL and WOMACK (1990)
RASA	MS	*7*	22	A,P,S	EGGEN *et al.* (1992)
TGLA176	MS			S	GEORGES and MASSEY (1992)
TGLA13	MS	*8*	18	S	GEORGES and MASSEY (1992)
TGLA433	MS	*10*	5	S	GEORGES and MASSEY (1992)
LGB	RFLP	*11*	16	A,R,S,L	HAYES and PETIT (1993)
TGLA436	MS			S	GEORGES and MASSEY (1992)
TGLA327	MS			S	GEORGES and MASSEY (1992)
AGLA232	MS	*13*	11	S	GEORGES and MASSEY (1992)
TGLA23	MS			L,P,S	DIETZ (1992)
CA2	Protein	*14*	24	L,R,S	THREADGILL *et al.* (1990)
TGLA75	MS	*15*	19	L,P,S	GEORGES and MASSEY (1992)
A	EA			L	LARSEN (1971)
HBB	MS			A,L,R,S	BARENDSE *et al.* (1991)
PTH	SSCP			A,L,R,S	FRIES *et al.* (1988)
MGTG13B	MS			L,P,S	DIETZ (1992)
INRA013	MS	*16*	1	S	D. VAIMAN *et al.* (unpublished data)
TGLA245	MS			S	GEORGES and MASSEY (1992)
TGLA170	MS	*17*	23	S	GEORGES and MASSEY (1992)
ETH185	MS			P,S	STEFFEN *et al.* (1993)
ILSTS002	MS	*18*	9	S	M. GEORGES (personal communication)
UWCA5	MS			L	SUN *et al.* (1993)
ETH3	MS	*19*	21	A,S	R. FRIES (personal communication)
GH	SSCP		21	R,S	FRIES *et al.* (1993)
KRT10	MS		21	A,R,S	FRIES *et al.* (1991)
AGLA29	MS	*20*	20b	S	GEORGES and MASSEY (1992)
TGLA304	MS			S	GEORGES and MASSEY (1992)
AGLA233	MS	*21*	4	S	GEORGES and MASSEY (1992)
ETH131	MS			P,S	STEFFEN *et al.* (1993)
UWCA4	MS			A	SUN *et al.* (1993)
TGLA122	MS			L,P,S	GEORGES and MASSEY (1992)
PRL	MS	*23*	20a	L,R,S,T	HALLERMAN *et al.* (1988)
CYP21	MS			L,R,S	SKOW *et al.* (1988)
M	EA			L	LEVEZIEL and HINES (1984)
BOLA-DRBP1	MS			L,R	CREIGHTON *et al.* (1992)
HSP70-1	SSCP			A	GALLAGHER *et al.* (1993); GROSZ (1992)
UWCA1	MS			A	SUN *et al.* (1993)
AGLA269	MS	*24*	28	S	GEORGES and MASSEY (1992)
TGLA351	MS			S	GEORGES and MASSEY (1992)
TGLA414	MS	*25*	7	S	GEORGES and MASSEY (1992)
OCAM	MS			S	DIETZ (1992)
TGLA429	MS	*26*	26	S	GEORGES and MASSEY (1992)

TABLE 4

Continued

Marker	Type	Chromosome	Synteny	Type of assignment[a]	Reference
RBP3	MS	*28*	29	R,S	THREADGILL and WOMACK (1991); GALLAGHER *et al.* (1993)
TGLA261	MS		2	S	GEORGES and MASSEY (1992)
ETH225	MS			P,S	STEFFEN *et al.* (1993)
AGLA13	MS		12	S	GEORGES and MASSEY (1992)
TGLA431	MS		17	S	GEORGES and MASSEY (1992)
TGLA377	MS			L,P,S	GEORGES and MASSEY (1992)
ETH121	MS			P,S	STEFFEN *et al.* (1993)
TGLA345	MS		27	S	GEORGES and MASSEY (1992)
TGLA28	MS			S	GEORGES and MASSEY (1992)
TGLA36	MS			L,P,S	GEORGES and MASSEY (1992)

[a] Type of assignment was adopted from FRIES *et al.* (1993) as follows: A—*In situ* hybridization to metaphase chromosomes; L—linkage/family studies; N—neighbor analysis; P—PCR analysis; R—restriction digests; S—somatic cell hybrids; T—single sperm typing.
[b] Denotes marker derived from ovine genomic libraries.

with WC-Meishan the most heterozygous breed type at 83.9%; ROHRER *et al.* 1994). Calculation of heterozygosity for inter- and intraspecific crosses allows prediction of the probability that an individual animal will be heterozygous at any randomly chosen locus. This type of information is crucial for determining the number of markers needed to expand the linkage map to a desired level of coverage and to determine the number of animals or markers needed to search for economic trait loci (ETL) particularly when heterozygosities are as low as in *Bos taurus* × *Bos taurus* crosses.

Linkage analyses and map construction: Three-hundred three markers were genotyped in up to 180 progeny (Table 1) with an average of 0.99 informative meioses/genotype/animal and were assigned to 30 autosomal linkage groups (Figure 1). Linkage groups were anchored to 24 autosomal chromosomes, and four unassigned synteny groups, U2, U12, U17 and U27. Two linkage groups containing 13 microsatellites spanning a total of 105.1 cM were unassigned. Linkage groups were anchored by three serum proteins, 11 microsatellites associated with type I loci, two erythrocyte antigens, two RFLPs and 43 microsatellites assigned by somatic cell panel or *in situ* hybridization to metaphase chromosomes (Table 4). Five anchor loci were placed on chromosomes *1*, *5*, *15* and *23*; three on chromosomes *11* and *21*; and three on synteny group U27. The remaining 18 chromosomes and three synteny groups have either one or two anchors each. We were unable to assign linkage groups to chromosomes *2*, *9*, *12*, *22* or *27* and synteny group U14. A limited number of informative meioses precluded the formation of linkage groups on the sex chromosomes although nine markers cosegregated with the *X* and one marker with the *Y* chromosomes.

Linkage groups were initially formed based upon two-point linkage of coinformative markers with LOD scores > 3.0. Markers with the highest two-point LOD were used to sequentially build a multiloci linkage group based on that linear order which maximized the log-likelihood. Marker interval and estimated size of each linkage group are a function of the sex-averaged rate of recombination using Kosambi mapping units (KOSAMBI 1944). For intervals greater than 25 cM, marker inclusion was determined by fixing the recombination rate of the large interval to 0.5 and comparing the resulting log-likelihood to the maximum log-likelihood. The linkage group was kept intact if the difference in log-likelihood was 3.0 or greater. In cases where a marker was linked to two previously separate linkage groups, multipoint analysis was used to determine whether one or both linkages were spurious. Orientation of marker order relative to physical chromosomal landmarks (*i.e.*, centromeres and telomeres) was arbitrary since relatively few markers (55) have been positionally assigned on chromosomes in the cattle genome (FRIES *et al.* 1993).

Two-thousand four-hundred sixty-four cM of the bovine genome were covered. Linkage groups (30) range in size from 28.2–152.5 cM (mean 74.2 cM) and contain between 4 and 21 markers (mean 10.1). Forty-four percent of the 273 total intervals were less than or equal to 5 cM, 48% were from 5 cM to 20 cM and 8% were greater than 20 cM. The average interval between linked markers was 8.9 cM. Marker interval estimates for the bovine genome are unavailable in the extant map (FRIES *et al.* 1993) for direct comparison. However, the average interval reported in pig was 5.5 cM (ROHRER *et al.* 1994) while both human (WEISSENBACH *et al.* 1992) and mouse (COPELAND *et al.* 1993) maps have estimated intervals of less than 3 cM. Only 12 (4.4%) of 273 intervals were ≥25 cM (max = 41 cM). Of these, only two were supported by

log-likelihood differences <6.0 (3.0 for chromosome *6* and 4.5 for chromosome *7*). No linkage group contained more than one interval ≥25 cM.

New chromosomal, syntenic and gene assignments: Syntenic groups, U11, U7 and U8, are assigned to chromosomes *13*, *25* and *29*, respectively, using cosmids containing informative microsatellites (*BMC1222*, *BMC8012* and *BMC3224*, and *BMC4216*, respectively; Figure 1 and Table 3) further merging the bovine physical (FRIES *et al.* 1993) and linkage maps and increasing chromosome specific coverage to 2045 cM (83% of 2464). Integration of the two maps is important for comparative analyses to other species maps for identification of possible coding genes influencing a particular phenotype of interest. The assignment of synteny group U11 to chromosome *13* is supported by two-point linkage of the microsatellite *BMC1222* (chromosome *13q12*) to *TGLA23* (LOD 5.8), assigned to U11 by DIETZ (1992) in a hybrid somatic cell panel. *BMC1222* is also linked to *BM720* (LOD 6.8) and *TGLA23* is linked to *BM720* (LOD 4.9). DIETZ (1992) also assigned *OCAM* (*opiod binding and cell adhesion molecule*) to synteny group U7. We anchor U7 to chromosome *25* by *in situ* hybridization of two cosmids, *BMC3224* (chromosome *25q24*) and *BMC8012* (chromosome *25q15*). The type II associated microsatellite for *OCAM* links to microsatellites derived from each of the two cosmids, *BMC3224* (LOD 16.3) and *BMC8012* (LOD 4.3). The two-point LOD between *BMC3224* and *BMC8012* was also 4.3. Cosmid *BMC4216* was anchored by *in situ* hybridization to chromosome *29q13*. We indirectly assign syntenic group U8 to chromosome *29* based upon the previous assignment of *protein Kinase C, beta 1* (*PRKCB1*) to cattle syntenic group U8 (WOMACK *et al.* 1991) and the *in situ* mapping of *PRKCB1* to sheep chromosome *24*, the homologue of cattle *29* (ISCNDA 1989, 1990), by *in situ* hybridization (ANSARI *et al.* 1993).

DISCUSSION

We have integrated 172 new microsatellite markers with 118 previously reported, three RFLPs and four SSCPs associated with type I markers, nine erythrocyte antigens and seven serum proteins into a skeletal map of the bovine genome. Twelve of the 24 linkage groups assigned to specific chromosomes contain markers for coding genes physically anchored in the map of FRIES *et al.* (1993). We have anchored nine cosmids containing microsatellites to seven chromosomes, placed linkage groups on three chromosomes, *13*, *25* and *29* anchoring syntenic groups U11, U7 and U8, respectively. The map represents an initial attempt to estimate genetic distances between coinformative markers and order loci within linkage groups. It is based on 63,607 genotypes for 303 polymorphic genetic markers typed in 22 fullsib bovine families totaling 180 progeny. These 303 markers provide the basis for assignment of 28 linkage groups to 24 autosomal chromosomes (haploid $n = 29$) and four synteny groups covering 2,359 cM of the 2,464 cM in total detectable coverage. Only two linkage groups remain unanchored. We have also assigned linkage groups to all but one (U14) of the known syntenic groups (FRIES *et al.* 1993) with the exception of synteny group U25 whose existence is speculative (J. E. WOMACK, unpublished data). Syntenic or linkage groups also remain to be assigned to chromosomes *2*, *9*, *12*, *22* and *27*. However, chromosomal homology and comparison of physical assignments between cattle and sheep (ANSARI *et al.* 1993) suggest synteny groups U17 and U12 reside on chromosomes *2* and *22*, respectively.

The accuracy of interval order is of particular importance to the dissection of complex quantitative traits. An overall average of 81 coinformative meioses per marker is present in the current map. As only 70 phase known coinformative meioses are required to correctly order markers spaced 10–25 cM apart with a probability of 0.95, marker orders are well supported. However, at intervals less than 5 cM, marker order remains tentative since 100 coinformative meioses are needed for an ordering error rate of only 5% (J. W. KEELE, unpublished data). Additional markers should be rapidly placed on the bovine linkage map since the probability that a new marker will be within 20 cM of existing linked markers is approximately 0.97. However, two factors potentially limit rapid development of a saturated bovine linkage map. The overall yield of informative primer pairs is low: 35% of the total primer pairs developed from bovine M13 libraries yielded informative data for linkage analysis compared with 78% for human (WEISSENBACH *et al.* 1992) and approximately 80% for porcine (G. A. ROHRER, unpublished data). A similar yield of informative markers has been noted in sheep (A. CRAWFORD, unpublished data). Interspecific crosses such as *Bos taurus* × *Bos indicus* are more heterozygous than intraspecific crosses or purebreds hence use of diverse crosses speeds development of the linkage map (COPELAND *et al.* 1993).

In addition to saturating the bovine genome with type II markers, we are merging the bovine cytogenetic and linkage maps by physically assigning (anchoring) cosmid and lambda genomic clones containing informative microsatellites to chromosomes. Continuous database searches will provide additional type II markers flanking, or within, type I loci. Our initial observations suggest that this parallel approach will rapidly provide sufficient anchors for each chromosome to orient each linkage group relative to the centromere and telomere and rapidly expand genomic coverage. As the bovine physical and linkage

maps are merged, new assignments of type I markers to chromosomes using a variety of approaches will improve the comparative map between the human, mouse and livestock genomes. Map resolution will also improve as templates of type II markers selected from several sources are genotyped across diverse bovine pedigrees. In summary, the number of informative markers linked in the present bovine genetic map provides an initial framework from which informative templates of markers can be selected in a concerted effort to identify ETL in any breed or breed cross.

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LITERATURE CITED

ANDERSSON, L., A. L. ARCHIBALD, J. GELLIN and L. B. SCHOOK, 1993 1st Pig Gene Mapping Workshop (PGM1), 7 August 1992, Interlaken, Switzerland. Anim. Genet. **24:** 205–216.

ANSARI, H. A., P. D. PEARCE and D. W. MAHER, 1993 Regional assignment of anchored reference loci to sheep chromosomes. Proc. 8th North American Colloquium on Domestic Animal Cytogenetics and Gene Mapping, Univ. Guelph, Guelph, Ontario, Canada, pp. 59–61.

BARENDSE, W., S. M. ARMITAGE, J. E. WOMACK and D. J. HETZEL, 1991 Comparison of gene order of three bovine chromosomal segments to the human (Abstract). Cytogenet. Cell Genet. **58:** 2123.

BECKMAN, J. S., and J. L. WEBER, 1992 Survey of human and rat microsatellites. Genomics **12:** 627–631.

BENSON, D., D. J. LIPMAN and J. OSTELL, 1993 GenBank. Nucleic Acids Res. **21:** 2963–2965.

BISHOP, M. D., A. TAVAKKOL, D. W. THREADGILL, F. A. SIMMEN, R. C. M. SIMMEN, *et al.*, 1991 Somatic cell mapping and restriction fragment length polymorphism analysis of bovine *insulin-like growth factor I*. J. Anim. Sci. **69:** 4306–4311.

BISHOP, M. D., M. KOOHMARAIE, J. KILLEFER and S. KAPPES, 1993 Rapid communication: restriction fragment length polymorphisms in the bovine *Calpastatin* gene. J. Anim. Sci. **71:** 2277.

BREZINSKY, L., S. J. KEMP and A. J. TEALE, 1992a ILSTS001: a polymorphic bovine microsatellite. Anim. Genet. **23:** 81.

BREZINSKY, L., S. J. KEMP, J. WOMACK and A. J. TEALE, 1992b A panel of bovine microsatellite genetic markers. XXII International Conference on Animal Genetics, International Society for Animal Genetics, Interlaken, Switzerland, p. 62.

BREZINSKY, L., S. J. KEMP and A. J. TEALE, 1993a *ILSTS005*: a polymorphic bovine microsatellite. Anim. Genet. **24:** 73.

BREZINSKY, L., S. J. KEMP and A. J. TEALE, 1993b *ILSTS006*: a polymorphic bovine microsatellite. Anim. Genet. **24:** 73

BREZINSKY, L., S. J. KEMP and A. J. TEALE, 1993c Five polymorphic bovine microsatellites (*ILSTS010-014*). Anim. Genet. **24:** 75.

BUCHANAN, F. C., and A. M. CRAWFORD, 1992 Ovine dinucleotide repeat polymorphism at the *MAF70* locus. Anim. Genet. **23:** 185.

BUCHANAN, F. C., and A. M. CRAWFORD, 1993a Ovine microsatellites at the *OarFCB5*, *OarFCB19*, *OarFCB20*, *OarFCB48*, *OarFCB129* and *OarFCB226* loci. Anim. Genet. (in press).

BUCHANAN, F. C., and A. M. CRAWFORD, 1993b Ovine microsatellite at the *OarFCB11*, *OarFCB128*, *OarFCB193*, *OarFCB266* and OarFCB304 loci. Anim. Genet. **23:** 145.

BUCHANAN, F. C., P. A. SWARBRICK and A. M. CRAWFORD, 1992 Ovine dinucleotide repeat polymorphism at the *MAF65* locus. Anim. Genet. **23:** 85.

CIAMPOLINI, R., K. GOUDARZI, D. VAIMAN and H. LEVEZIEL, 1993 A new bovine dinucleotide repeat microsatellite: microsatellite *Inra30*. Anim. Genet. **24:** 221.

CLARK, T. G., J. MORRIS, M. AKAMATSU, R. A. MCGRAW and R. IVARIE, 1990 A bovine homolog to the myogenic determination factor *myf-5*: sequence conservation and 3′ processing of transcripts. Nucleic Acids Res. **18:** 3147–3153.

COPELAND, N. G., N. A. JENKINS, D. J. GILBERT, J. T. EPPIG, L. J. MALTAIS, *et al.*, 1993 A genetic linkage map of the mouse: current applications and future prospects. Science **262:** 57–66.

CRAWFORD, A. M., F. C. BUCHANAN and P. A. SWARBRICK, 1991 Ovine dinucleotide repeat polymorphism at the *MAF92* locus. Anim. Genet. **22:** 371–372.

CREIGHTON, P., A. EGGEN, R. FRIES, S. A. JORDAN, J. HETZEL, *et al.*, 1992 Mapping of bovine markers *CYP21*, *PRL*, and *BoLA DRBP1* by genetic linkage analysis in reference pedigrees. Genomics **14:** 526–528.

CUTICCHIA, A. J., K. H. FASMAN, D. T. ROBBINS, J. ROBERT and P. L. PEARSON, 1993 The GDB™ human genome database annotation. Nucleic Acids Res. **2:** 3003–3006.

DIETRICH, W., H. KATZ, S. E. LINCOLN, H. SHIN, J. FRIEDMAN, *et al.*, 1992 A genetic map of the mouse suitable for typing intraspecific crosses. Genetics **131:** 423–447.

DIETZ, A. B., 1992 Analysis of the prolactin related proteins and placental lactogen gene family and the development of sequence-tagged-site based bovine gene map. Ph.D. Thesis, College Station, Texas: Texas A&M Univ.

EDE, A. J., C. A. PIERSON, H. M. HENRY and A. M. CRAWFORD, 1993 Ovine microsatellites at the OarAE64, OarHH22, OarHH56, OarHH62 and OarVH4 loci. Anim. Genet. (in press).

EGGEN, A., S. SOLINAS TOLDO, A. B. DIETZ, J. E. WOMACK, G. STRANZINGER, *et al.*, 1992 *RASA* contains a polymorphic microsatellite and maps to bovine syntenic group U22 on chromosome *7q24-qter*. Mamm. Genome **3:** 559–563.

FRIES, R., 1993 Mapping the bovine genome: methodological aspects and strategy. Anim. Genet. **24:** 111–116.

FRIES, R., R. HEDIGER and G. STRANZINGER, 1988 The loci for *parathyroid hormone* and *beta-globin* are closely linked and map to chromosome 15 in cattle. Genomics **3:** 302–307.

FRIES, R., D. W. THREADGILL, R. HEDIGER, A. GUNAWARDANA, M. BLESSING, *et al.*, 1991 Mapping of bovine *cytokeratin* sequences to four different sites on three chromosomes. Cytogenet. Cell Genet. **57:** 135–141.

FRIES, R., A. EGGEN and J. E. WOMACK, 1993 The bovine genome map. Mamm. Genome **4:** 405–428.

GALLAGHER, D. S., M. D. GROSZ, J. E. WOMACK and L. C. SKOW, 1993 Chromosomal localization of *HSP70* genes in cattle. Mamm. Genome **4:** 388–390.

GALLAGHER, D. S., A. M. RYAN, L. S. LIOU, K. N. SASTRY and J. E. WOMACK, 1993 Somatic cell mapping of *conglutinin* (CGN1) to cattle syntenic groups U29 and flourescence *in situ* localization to chromosome 28. Mamm. Genome **4:** (in press).

GEORGES, M., and J. MASSEY, 1992 Polymorphic DNA markers in Bovidae (World Intellectual Property Org., Geneva) WO Publ. No. 92/13102.

GEORGES, M., A. B. DIETZ, A. MISHRA, D. NIELSEN, L. S. SARGEANT,

et al., 1993a Microsatellite mapping of the gene causing weaver disease in cattle will allow the study of an associated quantitative trait locus. Proc. Natl. Acad. Sci. USA **90:** 1058–1062.

GEORGES, M., R. DRINKWATER, T. KING, D. NIELSEN, L. S. SARGEANT, *et al.*, 1993b Microsatellite mapping of a gene affecting horn development in *Bos taurus*. Nature Genet. **4:** 206–210.

GREEN, P., K. FALLS and S. CROOKS, 1989 Documentation for CRI-MAP, version 2.4. Washington University School of Medicine, St. Louis.

GROSZ, M. D., 1992 Molecular genetics of bovine *70 kilodalton heat shock protein* (*HSP70*) genes. Ph.D. Thesis, College Station, Texas: Department of Veterinary Anatomy, College of Veterinary Medicine, Texas A&M University.

GROSZ, M. D., J. E. WOMACK and L. C. SKOW, 1992 Syntenic conservation of *HSP70* genes in cattle and humans. Genomics **14:** 863–868.

HALLERMAN, E. M., J. L. THIELMAN, J. S. BECKMAN, M. SOLLER and J. E. WOMACK, 1988 Mapping of bovine *prolactin* and *rhodopsin* genes in hybrid somatic cells. Anim. Genet. **19:** 123.

HANRAHAN, V., A. J. EDE, C. A. PIERSON and D. F. HILL, 1993 Ovine microsatellites at the *OarVH98*, *OarVH110*, *OarVH116*, *OarVH117* and *OarVH130* loci. Anim. Genet. **24:** 223

HAWKINS, G. A., M. D. BISHOP, S. M. KAPPES and C. W. BEATTIE, 1994 Cycle sequencing of (CA)n microsatellites from cosmid inserts using degenerate primers. BioTechniques (in press).

HAYES, C. H., and E. J. PETIT, 1993 Mapping of the *β-lactoglobulin* gene and of an *immunoglobulin M heavy chain*-like sequence to homologous cattle, sheep and goat chromosomes. Mamm. Genome **4:** 207–210.

HOESCHELE, I., and T. R. MEINERT, 1990 Association of genetic defects with yield and type traits: the weaver locus effect on yield. J. Dairy Sci. **73:** 2503–2515.

HUDSON, T. J., M. ENGELSTEIN, M. K. LEE, E. C. HO, M. J. RUBENFIELD, *et al.*, 1992 Isolation and chromosomal assignment of 100 highly informative human simple sequence repeat polymorphisms. Genomics **13:** 622–629.

ISCNDA, 1989, 1990 International system for cytogenetic nomenclature of domestic animals, edited by D. DIBERADINO, H. HAYES, R. FRIES, S. LONG. Cytogenet. Cell. Genet. **53:** 65–79.

KAPPES, S. M., M. D. BISHOP, J. W. KEELE, M. C. T. PENEDO, H. C. HINES *et al.*, 1994 Linkage of bovine erythrocyte antigen loci B, C. L, S, Z, R′, and T and the serum protein loci post-transferrin 2 (PTF2), vitamin D binding protein (GC) and albumin (ALB) to DNA microsatellite markers. Anim. Genet. (in press).

KAUKINEN, J., and S. L. VARVIO, 1992 Artiodactyla retroposons: association with microsatellites and use in Sine morph detection by PCR. Nucleic Acids Res. **20:** 2955–2958.

KAUKINEN, J., and S. L. VARVIO, 1993 Eight polymorphic bovine microsatellites. Anim. Genet. **24:** 148.

KEELE, J. W., J. E. WRAY, D. W. BEHRENS, G. A. ROHRER, S. L. F. SUNDEN *et al.*, 1994 A conceptual database model for genomic research. Comput. Biol. (in press).

KEMP, S. J., L. BREZINSKY and A. J. TEALE, 1992 *ILSTS002*: a polymorphic bovine microsatellite. Anim. Genet. **23:** 184.

KEMP, S. J., L. BREZINSKY and A. J. TEALE, 1993 *ILSTS008*: a polymorphic bovine microsatellite. Anim. Genet. **24:** 74.

KIRKPATRICK, B. W., 1992 Detection of a three allele single-strand-conformational-polymorphism (SSCP) in the fourth intron of the bovine *growth hormone* gene. Anim. Genet. **23:** 179–181.

KOSAMBI, D. B., 1944 The estimation of map distances from recombination values. Eugenics **12:** 172–175.

LANDER, E. S., P. GREEN, J. ABRAHAMSON, A. BARLOW, M. J. DALY, *et al.*, 1987 Mapmaker: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics **1:** 174–181.

LARSEN, B., 1971 Blood groups and polymorphic proteins in cattle and swine. Ann. Gene Sel. Anim. **3:** 59–70.

LENSTRA, J. A., J. A. F. VAN BOXTEL, K. A. ZWAAGSTRA and M. SCHWERIN, 1993 Short interspersed nuclear element (SINE) sequences of the *Bovidae*. Anim. Genet. **24:** 33–39.

LEVEZIEL, H., and H. C. HINES, 1984 Linkage in cattle between the major histocompatibility complex (*BoLA*) and the *M* blood group system. Genet. Sel. Evol. **16:** 405–416.

LIPKIN, V. M., N. V. KHRAMTSOV, S. G. ANDREEVA, M. V. MOSHNYAKOV, G. V. PETUKHOVA, *et al.*, 1989 *Calmodulin-independent bovine brain adenylate cyclase.* Amino acid sequence and nucleotide sequence of the corresponding cDNA. FEBS Lett. **254:** 69–73.

MACLENNEN, D. H., and M. S. PHILLIPS, 1992 Malignant hyperthermia. Science **256:** 789–794.

MONTGOMERY, G. W., A. M. CRAWFORD, J. M. PENTY, K. G. DODDS, A. J. EDE, *et al.*, 1993 The ovine Booroola fecundity gene (*FecB*) is linked to markers from a region of human chromosome *4q*. Nature Genet. **4:** 410–414.

MOORE, S. S., W. BARENDSE, K. T. BERGER, S. M. ARMITAGE and D. J. S. HETZEL, 1992 Bovine and ovine DNA microsatellites from the EMBL and Genbank databases. Anim. Genet. **23:** 463–467.

O'BRIEN, S. J., 1991 Mammalian genome mapping. Current Opinion in Genetics and Development **1:** 105–111.

O'BRIEN, S. J., and J. A. M. GRAVES, 1991 Report of the committee on comparative gene mapping. Cytogenet. Cell. Genet. **58:** 1124–1151.

O'BRIEN, S. J., J. E. WOMACK, L. A. LYONS, K. J. MOORE, N. A. JENKINS, *et al.*, 1993 Anchored reference loci for comparative genome mapping in mammals. Nature Genet. **3:** 103–112.

ORITA, M., Y. SUZUKI, T. SEKIYA and K. HAYASHI, 1989 Rapid and sensitive detection of point mutations and DNA polymorphisms using the polymerase chain reaction. Genomics **5:** 874–879.

PENTY, J. M., H. M. HENRY, A. J. EDE, and A. M. CRAWFORD, 1993 Ovine microsatellites at the *OarAE16*, *OarAE54*, *OarAE57*, *OarAE119* and *OarAE129* loci. Anim. Genet. **24:** 219.

ROHRER, G. A., L. J. ALEXANDER, J. W. KEELE, T. P. SMITH and C. W. BEATTIE, 1994 A microsatellite linkage map of the porcine genome. Genetics **136:** 231–245.

RUDOLPH, J. A., S. J. SPIER, G. BYRNES, C. V. ROJAS, D. BERNOCO *et al.*, 1992 Periodic paralysis in quarter horses—a sodium channel mutation disseminated by selective breeding. Nature Genet. **2:** 144–147.

SAHEKI, T., T. MIZUNO, T. IWATA, Y. SAITO, T. NAGASAWA, *et al.*, 1991 Structure of the bovine *atrial natriuretic peptide receptor (type C)* gene. J. Biol. Chem. **266:** 11122–11125.

SAIKI, R. K., S. SCHARF, F. FALONA, K. B. MULLIS, G. T. HORN, *et al.*, 1985 Enzymatic amplification of *beta-globin* genomic sequences and restriction site analysis for diagnosis of sickle-cell anemia. Science **230:** 1350–1354.

SAIKI, R. K., D. H. GELFAND, S. STOFFEL, S. J. SCHARF, R. HIGUCHI, *et al.*, 1988 Primer directed enzymatic amplification of DNA with a thermostable DNA polymerase. Science **239:** 487–491.

SAMBROOK, J., E. F. FRITSCH and T. MANIATIS, 1989 *Molecular Cloning: A Laboratory Manual*, Ed. 2, Cold Spring Harbor Laboratory, Cold Spring Harbor, N.Y.

SASSO, M. P., A. CARSANA, E. CONFALONE, C. COSI, S. SORRENTINO, *et al.*, 1991 Molecular cloning of the gene encoding the bovine *brain ribonuclease* and its expression in different regions of the brain. Nucleic Acids Res. **19:** 6469–6474.

SKOW, L. C., J. E. WOMACK, J. M. PETRASH and W. L. MILLERS, 1988 Synteny mapping of the genes for *21 steroid hydroxylase alpha-a-crystallin* and *class I bovine leukocyte antigen*. DNA **7:** 153–159.

SOLINAS TOLDO, S., R. FRIES, P. STEFFEN, H. L. NEIBERGS, W. BARENDSE, *et al.*, 1993 Physically mapped cosmid-derived microsatellite markers as anchor loci on bovine chromosomes. Mamm. Genome (in press).

STEFFEN, P., A. EGGEN, A. B. DIETZ, J. E. WOMACK, G. STRANZINGER *et al.*, 1993 Isolation and mapping of polymorphic microsatellites in cattle. Anim. Genet. **24:** 121–124.

SUN, H. S., S. WHALLON, A. PONCE DE LEON and B. W. KIRKPATRICK, 1993 Development of polymorphic bovine microsatellite markers from a cosmid library. J. Anim. Sci. **71** (Suppl.): 100.

SUNDEN, S. L. F., R. T. STONE, S. M. KAPPES, M. D. BISHOP, M. D. GROSZ, *et al.*, 1993 Relationship between repeat composition and mapping utility of bovine microsatellite markers. *Proc. 8th North American Colloquium on Domestic Animal Cytogenetics and Gene Mapping*, Univ. Guelph, Guelph, Ontario, Canada. p. 175.

SWARBRICK, P. A., F. C. BUCHANAN and A. M. CRAWFORD, 1990 Ovine dinucleotide repeat polymorphism at the *MAF23* locus. Anim. Genet. **21:** 191.

SWARBRICK, P. A., F. C. BUCHANAN and A. M. CRAWFORD, 1991 Ovine dinucleotide repeat polymorphism at the *MAF35* locus. Anim. Genet. **22:** 369–370.

SWARBRICK, P. A., A. B. DIETZ, J. E. WOMACK and A. M. CRAWFORD, 1992a Ovine and bovine dinucleotide repeat polymorphism at the *MAF46* locus. Anim. Genet. **23:** 182.

SWARBRICK, P. A., J. HOWES, and A. M. CRAWFORD, 1992b Ovine dinucleotide repeat polymorphism at the *MAF50* locus. Anim. Genet. **23:** 187.

SYMONS, D. B., and C. A. CLARKSON, 1992 Genomic organization and sequence of the extracellular domain exons of the bovine *FcgammaRI* receptor, an evidence for restricted binding of ruminant *IgG* to U937 cells. Mol. Immunol. **29:** 1407–1413.

THREADGILL, D. W., and J. E. WOMACK, 1990 Genomic analysis of the major bovine milk protein genes. Nucleic Acids Res. **18:** 6935.

THREADGILL, D. W., and J. E. WOMACK, 1991 Mapping *HSA10* homologous loci in cattle. Cytogenet. Cell Genet. **57:** 123.

THREADGILL, D. W., R. FRIES, L. K. FABER, G. VASSART, A. GUNAWARDANA, *et al.*, 1990 The *thyroglobulin* gene is syntenic with the *MYC* and *MOS* protooncogenes and *carbonic anhydrase II* and maps to chromosome *14* in cattle. Cytogenet. Cell. Genet. **53:** 32–36.

THREADGILL, D. W., J. P. KRAUS, S. A. KRAWETZ and J. E. WOMACK, 1991 Evidence for the evolutionary origin of human chromosome *21* from comparative gene mapping in the cow and mouse. Proc. Natl. Acad. Sci. USA **88:** 154.

VAIMAN, D., D. OSTA, D. MERCIER, C. GROHS and H. LEVEZIEL, 1992 Characterization of five new bovine dinucleotide repeats. Anim. Genet. **23:** 537.

WEBER, J. L., 1990 Informativeness of human (dC-dA)n·(dG-dT)$_n$ polymorphisms. Genomics **7:** 524–530.

WEBER, J. L., and P. E. MAY, 1989 Abundant class of human DNA polymorphisms which can be typed using the polymerase chain reaction. Am. J. Hum. Genet. **44:** 388–396.

WEISSENBACH, J., G. GYAPAY, C. DIB, A. VIGNAL, J. MORISSETTE, *et al.*, 1992 A second-generation linkage map of the human genome. Nature **359:** 794–801.

WOMACK, J. E., A. B. DIETZ, D. S. GALLAGHER, L. LI, N. ZHANG, *et al.*, 1991 Assignment of 47 additional comparative anchor loci to the bovine synteny map. Cytogenet. Cell. Genet. **58:** 2132.

YAMASHITA, M., H. FUKI, K. SUGAMA, Y. HORIO, S. ITO, *et al.*, 1991 Expression cloning of cDNA encoding the bovine *histamine H1 receptor*. Proc. Natl. Acad. Sci. USA **88:** 11515–11519.

YUILLE, M. A. R., D. R. GOUDIE, N. A. AFFARA and M. A. FERGUSON-SMITH, 1991 Rapid determination of sequences flanking microsatellites. Nucleic Acids Res. **19:** 1950.

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