A Microsatellite Linkage Map of the Porcine Genome

Gary A. Rohrer, Leeson J. Alexander, John W. Keele, Tim P. Smith and Craig W. Beattie

USDA, ARS, Roman L. Hruska U.S. Meat Animal Research Center (MARC), Clay Center, Nebraska 68933

Manuscript received August 23, 1993
Accepted for publication September 11, 1993

ABSTRACT

We report the most extensive genetic linkage map for a livestock species produced to date. We have linked 376 microsatellite (MS) loci with seven restriction fragment length polymorphic loci in a backcross reference population. The 383 markers were placed into 24 linkage groups which span 1997 cM. Seven additional MS did not fall into a linkage group. Linkage groups are assigned to 13 autosomes and the *X* chromosome (haploid $n = 19$). This map provides the basis for genetic analysis of quantitative inheritance of phenotypic and physiologic traits in swine.

SPECIES-SPECIFIC, high-density linkage maps comprised of highly polymorphic markers are essential to conduct comprehensive searches for loci that affect phenotype(s) of interest (FRIES 1993). The discovery of microsatellites (MS), abundant, multiallelic, codominant markers uniformly distributed throughout the genome (LITT and LUTY 1989; WEBER and MAY 1989; WINTERO, FREDHOLM and THOMSEN 1992), provided the technology required to rapidly produce linkage maps useful in identifying segregating loci of interest (LUONGO *et al.* 1993). Since MS are typed by amplifying DNA via the polymerase chain reaction (PCR) and then electrophoresed to separate fragments based on length, the procedure is easily automated (DIETRICH *et al.* 1992). Microsatellites, as sequence tagged sites (STS), are easily distributed anywhere in the world by publishing or submitting sequences of primers to public access databases further facilitating map construction.

One focus of genetic efforts to maintain dietary meat as a major protein source centers on identifying markers segregating with rapid lean growth, improved reproductive performance and disease resistance using a marker-assisted selection strategy. Unfortunately, current maps of major livestock species are cytogenetic in nature with few MS assignments (FRIES, EGGEN and WOMACK 1993). This has limited identification of loci associated with phenotypic or quantitative traits (GEORGES *et al.* 1993a, 1993b). Comparative genome mapping (WOMACK 1987; FRIES 1993) has assigned genes (type I markers) selected from human:mouse maps (O'BRIEN *et al.* 1993) using somatic cell hybrid panels (WOMACK and MOLL 1986) or *in situ* hybridization (CHOWDHARY *et al.* 1989). Linkage groups anchored by restriction fragment length polymorphisms (RFLPs) within type I markers are few (FRIES, EGGEN and WOMACK 1993) as they are often uninformative or only slightly polymorphic within or between livestock breeds (FRIES 1993). In cattle, only 27% of the mapped type I loci have reported polymorphisms compared with 87% of anonymous type II markers (FRIES, EGGEN and WOMACK 1993). FRIES, EGGEN and WOMACK (1993) tabulated ~350 loci organized into 32 linkage groups that span 13 chromosomes and 26 syntenic groups in cattle (haploid $n = 30$). Type I markers have now been assigned to 20 of 26 sheep autosomes (haploid $n = 27$) (ANSARI, PEARCE and MAHER 1993).

An accurate assessment of total cM covered in the swine genome is difficult when only ~120 markers have been placed in 25 linkage groups (12 chromosomally assigned) (ANDERSSON *et al.* 1993). Only 38 of 73 MS loci published to date are linked (ANDERSSON *et al.* 1993). The most extensive individual reports are by FREDHOLM *et al.* (1993), who linked 14 markers into six linkage groups (67 total cM) and ELLEGREN *et al.* (1993), who placed 59 (total) markers in 13 linkage groups covering ~288 cM. The problem is compounded by a lack of markers on 5 of 18 autosomes (ANDERSSON *et al.* 1993).

In spite of the paucity of markers, swine represent a livestock species of choice for mapping quantitative trait loci (QTLs). Global production of pork as a dietary alternative to beef is at an all-time high (FOWLER 1992). The amount of muscle relative to fat is a heritable trait (WARWICK and LEGATES 1979). For mapping purposes, generation interval is relatively short and progeny number high. As omnivores, with a cardiovascular and gastrointestinal physiology similar to humans, swine also make excellent models for human disease (HODSON 1985). Genetic lines for such diverse human diseases as obesity (MERSMANN, POND and YEN 1982) and cancer (TISSOT, BEATTIE and AMOSS 1987) are readily available for mapping purposes.

Our results based on 383 informative DNA markers

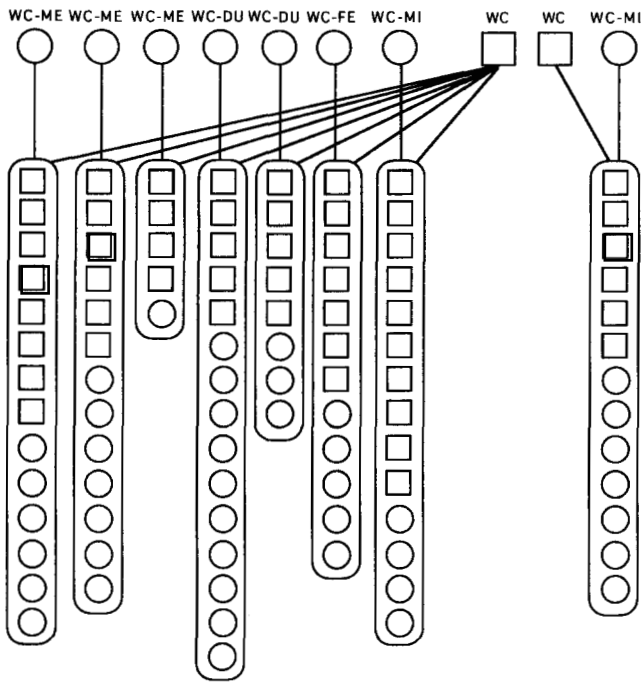

FIGURE 1.—Backcross family of two WC (1/4 Chester White, 1/4 Large White, 1/4 Landrace and 1/4 Yorkshire) boars mated to eight F_1 sows. DU, Duroc; FE, Fengjing; ME, Meishan; MI, Minzhu.

assigned to 13 autosomal and the *X* chromosome and 9 unassigned linkage groups spanning 1997 cM represents the first linkage map in swine sufficient to initiate a genetic analysis for any heritable trait. It represents our first step to create a high-density linkage map and initiate a systematic search for loci affecting phenotypes of interest (FRIES 1993).

MATERIALS AND METHODS

Generation of GT:CA dinucleotide microsatellites: Procedures were performed essentially as described in SAMBROOK, FRITSCH and MANIATIS (1989). Porcine genomic DNA (20 μg) was digested with *Mbo*I restriction enzyme, the products were fractionated on a 1% agarose gel and the gel section corresponding to 200- to 500-bp excised. Size fractionated DNA (80 ng) was ligated into 500 ng of *Bam*HI-digested, dephosphorylated M13 mp18 RF DNA in a 100 μl reaction at 4° overnight. The ligation mixture was transformed into competent *Escherichia coli* (XL1-Blue, Stratagene, La Jolla, Calif.) cells and the resulting library (100,000 plaques approx.) plated at 2,000 plaques per 150-mm agar plate. Plaques were transferred onto nylon membranes and sequences were screened with 5′-[^{32}P]-labeled $(GT)_{11}$ and $(CA)_{11}$ oligonucleotides (T4 polynucleotide kinase; [γ-^{32}P]-ATP 5,000 Ci/mmol). Filters were then washed with 2×SSC (0.3 M NaCl, 0.03 M Na_3 citrate), 0.1% SDS at 65° for 30 min, positive plaques purified and rescreened with the labeled $(GT)_{11}$ and $(CA)_{11}$ oligonucleotides. Positive phage were grown, single stranded DNA (ssDNA) extracted and sequenced (SANGER, NICKLEN and COULSON 1977) using Sequenase (USB, Cleveland, Ohio). The program PRIMER (Version 0.5; M. J. DALY, S. E. LINCOLN and E. S. LANDER, unpublished data) was used to design primer pairs for PCR based genotyping. Although where possible primers were only made from unique sequences of these clones, 14% of MS used in this study contained a short porcine repetitive element (SINGER, PARENT and EHRLICH 1987) adjacent to the dinucleotide repeat. Primer pairs with one oligonucleotide designed from nonrepetitive sequence and the other oligonucleotide possessing a high level of similarity to the repetitive element are denoted as *Swr* and loci not associated with the repetitive element are designated *Sw*. Approximately 200–300 primer pairs were obtained from each ligation reaction. Oligonucleotide pairs for 14 loci were identified by scanning porcine sequences in GENBANK and EMBL databases (GCG Corp., Madison, WI). Only those MS containing at least eight simple sequence repeats were selected.

Data collection and analysis: The genetic linkage map was constructed by genotyping 104 animals from two generations of a divergent, intraspecific backcross between the commercial meat producing White Composite swine (1/4 Chester White, 1/4 Large White, 1/4 Landrace and 1/4 Yorkshire:WC) and Duroc (DU; a North American breed) or the phenotypically different Chinese breeds: Fengjing (FE), Meishan (ME) and Minzhu (MI) (Figure 1). Microsatellites were genotyped by adapting previously reported procedures (JOHANSSON, ELLEGREN and ANDERSSON 1992) to 10-μl reactions. A total of 12.5 ng of genomic DNA, 5 pmol of each primer and 0.45 units of Taq DNA polymerase were used in each reaction. Concentration of dNTP was reduced to 30 μM each and a few markers required $MgCl_2$ concentrations greater than 1.5 mM. Samples were heated to 92° for 2 min, 30 cycles of: 30 sec at 94°, 30 sec at annealing temperature and 30 sec at 72° followed with a 5 min extension at 72°. PCR products were radioisotopically labeled, by either end-labeling a primer or by incorporating ^{32}P, and electrophoresed between 2 and 5 hr (based on product size) at 40 V/cm on 7% acrylamide gels. When radioisotope was incorporated directly the concentration of dATP was reduced to 15 μM and 0.1 μCi of [α-^{32}P]dATP was included into the reaction. Allele size was approximated by comparison to M13 mp18 ssDNA sequencing reactions.

Direct incorporation of ^{32}P into amplified products increased sub-banding but was more economical to produce than end-labeled PCR products. End-labeled primers were used when sub-banding hindered accurate scoring, *e.g.*, *Swr* markers. This strategy permitted genotyping MS which otherwise could not be scored. Multiplexing two, three and occasionally four sets of primers enhanced data acquisition, improved scoring accuracy and reduced costs.

For those markers in which one parent and some of its offspring had an allele that would not amplify (null allele), the situation was rectified by reducing the specificity of primer annealing or markers that retained a null allele were coded as such (fragment size of 0 in Table 1). Animals whose genotypes were ambiguous (*e.g.*, homozygous *129/129* vs heterozygous *129/0*) were not scored.

Traditional RFLP were produced by standard Southern blotting of 10 μg of digested genomic DNA and hybridization (SAMBROOK, FRITSCH and MANIATIS 1989) with a radiolabeled probe. Genetic variability at the major histocompatibility complex was mapped with RFLPs for the class I locus *PD6* (EHRLICH *et al.* 1987) and class II loci *DQα* (*DQA*) (HIRSCH *et al.* 1990) and *DRβ* (*DRB*) (PRATT *et al.* 1990) developed in our laboratory (T. P. SMITH and C. W. BEATTIE, unpublished data). Two other loci were investigated with polymorphisms found with *Bgl*II for *kappa-casein* (*CASK*) (LEVINE *et al.* 1992) (R. STONE, unpublished results) and reported for *glucose phosphate isomerase* (*GPI*) (DAVIES *et al.* 1992a). Two RFLP were assayed by digesting PCR-amplified products. *Growth hormone* (*GH*) was amplified as described (KIRKPATRICK 1992a) and analyzed by three re-

TABLE 1

Microsatellite marker names, primer oligonucleotide sequences and PCR conditions

Marker name[a]	Forward primer	Reverse primer	PCR temp.[b]	Frag. Size[c] Max	Min	Alleles[d]
PGHAS	GTCACAGTGGATGGCATTTG	ACATCCCTAAGGTCGTGGC	65	366	322	12
ATP2	GCTGCATAGGGAGCTGTAGG	TAATGATGGTGGTGGTTAGTGC	62	252	246	4
DAGK	CTATTCCCCATGAACCCATG	TCCCAGTGGGAAAAAAAAGT	58[3.0]	132	110	5
IFNG	ATTAGACCCCTAGCCTGGGA	GTTGGTCCTGTTCTCCAATAGG	62	243	0	6
CRC	GGGCAGCTAAGGTGAGGAG	TGAAGGCCACCACGGTGTACAG	55[3.0]	331	270	4
IGF1	GCTTGGATGGACCATGTTG	CACTTGAGGGGCAAATGATT	58	237	223	7
OPN	CCAATCCTATTCACGAAAAAGC	CAACCCACTTGCTCCCAC	58	164	142	7
TNFB	CTGGTCAGCCACCAAGATTT	GGAAATGAGAAGTGTGGAGACC	60[3.0]	213	174	7
CH13	TTGGCATCCTTGTTGAAAACC	TTCATATGCTGCAGGTGTGGC	62	137	125	7
S0001	TGGATGGGTCTCATTCTCAG	TGATTCCTAGCCTGAGAAGC	50	189	175	6
S0002	GAAGCCCAAAGAGACAACTGC	GTTCTTTACCCACTGAGCCA	62	209	189	5
S0003	GAAGTGTTAAGGAAAGCCTT	AGCCTCAGTTTCTCTACCTA	60	162	131	6
S0004	GATTATGGACACGGAAGGAT	GTCCTATTTCTTGCACAGTC	55	172	164	4
S0005	TCCTTCCCTCCTGGTAACTA	GCACTTCCTGATTCTGGGTA	60	241	203	8
S0007	TTACTTCTTGGATCATGTC	GTCCCTCCTCATAATTTCTG	55	197	155	11
S0008	GAGGCAGTGTGTTCTATTCA	GCCATGTGTAAAGTGTTGCT	58	191	177	6
S0009	AAACATACCAAGAAGCCCAG	TAATCTTTGCCATCCCTTGT	62	132	122	5
S0010	TTAACATGGCTGTCTGGACC	GTCCCTGTCCAACCATAAGA	60	124	102	9
S0061	AAGCAGAAGGGATCTCTCTA	GCTGTTTCTGGGTTCTCTTA	55	187	167	6
S0062	AAGATCATTTAGTCAAGGTCACAG	TCTGATAGGGAACATAGGATAAAT	55	196	146	7
S0063	ACCCCTAGCCTGGAAACTTC	GGCAGTGGCAGGAGTTTATC	66	221	186	9
S0064	TGAGCTGGAGGTTAGCTACC	TGTCAGAAAGACTGCTTGCG	58	160	93	10
S0066	ACATTTAAGGTGAAGCAGCAAGTG	TGTCATCAACATTGAGAATTGGTG	62	158	136	4
S0067	GGGAGCCACAACAAAGAAGG	GGCCTGGAGTGTGGGACTAG	65	113	0	7
S0068	AGTGGTCTCTCTCCCTCTTGCT	CCTTCAACCTTTGAGCAAGAAC	62	260	211	10
S0069	TGCAAAACTAATGTTTGTGTTGCC	CATATGCCACAGGTGTGACCTAAA	62	171	0	9
S0070	GGCGAGCATTTCATTCACAG	GAGCAAACAGCATCGTGAGC	62	293	0	8
S0073	ACTGAAACAGGAATTCAGATCC	TGAAGTATTATGGCATCATGGA	55	123	105	9
S0071	GACATGGAATCAGGTTGCTCAA	CCAGAAGCAGGTTTTGAGATGA	65	200	168	7
S0081	AACAGAATACAAAGCATAGTATAC	CCTCTTACTCTTAATTTCCTTGCAC	60	184	172	5
S0082	CAGAAAATAAACTTGTCTAACTTG	AACCCTGTTTCATATCATTAAGCC	58	180	154	6
S0083	AGCTGCGGTATATGAAAACCTCCA	CTGCACCAAGAGATGAGGAAA	58	194	0	8
S0084	AACTCAGCCACTTGCTGGGCTGTA	TTCCATTTCAAGATGTATTCAAAG	56	120	102	9
S0086	GCACAGTCTATTGATACTGGCGTC	CTGAGAACTTCCATATGCTCCTGG	62	184	154	5
S0087	GACAAGCTCCAGGAAGCTTTCCTG	ATTGCCTTGTGATCCCAAGGGGCA	58	201	161	8
S0088	AGCTGACTTTTGAAAGCAGTGCTC	AGTCACCTCTAGGCGTGATCAGCT	58	164	148	5
S0089	CATGTACTTGTTAATAGGTAAGTA	CTGTAGTCTGCTGGGTCTCTGAGA	55	164	142	9
S0090	CCAAGACTGCCTTGTAGGTGAATA	GCTATCAAGTATTGTACCATTAGG	58	253	243	6
S0091	TCTACTCCAGGAGATAAGCCAGAT	CAGTGACTCCATGCACAGTTATGA	55	168	148	8
S0092	GGGAAACACTAAATCACTTGCCAT	GGGATCAAGACTTCACACTCCCAT	60	150	130	7
S0094	AGTTCTCAGGGAGTTCCCTCATGC	CGAGCTCGCCTATCTATCAATTCC	62	211	169	7
S0097	GACCTATCTAATGTCATTATAGT	TTCCTCCTAGAGTTGACAAACTT	58	244	208	8
S0099	CTGCCAGAGAGGCTCTTCTCAA	CATCCGCCTGGTTCCCTCCCTAT	68	177	159	6
S0100	CCTCTAGGAAGCTGTGTA	AGCCATGACAGGAACGCCAGTAG	55	179	165	5
Sw2	TGCCAATGGTGTGGCTATAA	CCCTGAAGGCTCAGATGGT	55[2.25]	126	88	9
Sw5	TTCAAGTTCCATCCTTGTTGC	AGTGTCCACAGATGGATGAATG	58	142	0	7
Sw7	TAACCATGCTTTTCCTAGGTGG	CCAGAGCTGAGTAAAAAGGTCA	65	112	89	7
Sw11	CTTTTTTGCTAACCAGCAAACC	AACACATGAGCATGCAGGTG	62	102	98	2
Sw13	TCTTAGCCAGTGCAGGCAC	GATCAATCTCTAAACTGAAGGTG	58	161	145	8
Sw14	TTCTGCACCAAAGGTTATTTTG	AAAAGCAAAACAAAAACAACCC	58	179	153	7
Sw15	GGTGCGGCCCTAAAAGAC	CTCAAATCTTGCCAACTATCCC	62	162	150	4
Sw16	CATACACCCCAGATGTGGC	CTGTGGGAGTGTAGCATCTTTG	60	172	119	7
Swr17	GTTTAAGCCACCTGGTCTATGG	ATCCTGACTTGCTTATGGCTG	58	155	143	4
Sw24	CTTTGGGTGGAGTGTGTGC	ATCCAAATGCTGCAAGCG	58	112	92	6
Sw29	AGGGTGGCTAAAAAAGAAAAGG	ATCAAATCCTTACCTCTGCAGC	61	173	131	9
Sw35	TCAAGTTGGAGAGTCTGAGGC	AAGACTGCCCACCAATGAG	58	137	129	5
Sw37	CTTTGTACACGCTGGTCCCT	GAAGCCCACCCTACAAATCA	60	226	212	4
Sw38	ACGTCTGTGTCGGTGCCT	GAGGCTCCTGATAGCAGCC	60	139	128	8
Sw45	TATGACCTGGTTGCTATGTTGG	TGTTTTCTCCCTCAGATTACC	58	194	174	7
Sw54	TCCACCCTTTCCTGCTCC	TCACAGACCAAGAGCTGTGG	63	124	112	3
Sw57	GGTTCCTTAACCTGCTGTGC	ATATGCCTTGGGTGCAGC	62	103	97	3
Sw58	TCCTACCAGAAATCCTACCACA	ATGGGAAGAGAATCTGACAAGG	58	222	204	7
Sw60	TCCGTATGCTGTGGATGTATC	CATGTTGCTGCAAATGGC	58	152	116	8
Sw61	GAGAGGGATGAGCACTCTGG	AGAGCATTCCAGGCTTCTA	62	262	238	8
Sw63	GAGAAAGGCAAACGCCTG	GTGGCTGTGGTGTAGGCC	62[3.0]	160	148	5
Sw64	AGACCAAGGGCCATGAGAG	TTCCACGTGATGTGGGATAG	58	152	136	6
Sw65	AAGAATGTGACACCATCCAGC	GCTGTAGTTCTGATTTGACCCC	65	285	251	4
Sw66	AAACGGAGAAAGGTGGGTG	GATCTTGAGCTGCCTCCG	62	127	91	8
Swr67	GTCCTCATGGAGACTAGTTGGG	TCCATGCCATGGACACAG	60	147	125	6
Swr68	TTGACCCCTAGCTGGGAAC	TTTCGTGGGCTTAGTGGC	63	253	249	3
Sw69	TCAGCTTCGTGAACAAGGG	ACCTCCCTCATCAGCTATTCC	55	166	146	5
Sw70	CCCGTACAGTCACCCACC	CTTTTCCTGGGTTGAGCAAC	62	148	120	7
Sw71	GATCACCCTTATCCCCATTC	TAGAAACACCATCATCCATTCA	62	111	93	5
Sw72	ATCAGAACAGTGCGCCGT	TTTGAAAATGGGGTGTTTCC	58	113	101	5
Sw77	ATCAGACCGAGGGTTGCC	GAAATCTGCATGGTCTCAGATG	62	146	119	6
Sw80	TGACAGCAACGTGACCAG	TGGATTGGATAAGCAATGAGG	62	176	160	8
Sw81	GATCTGGTCCTGCACAGGG	GGGGCTCTCAGGAAGGAG	60	142	0	9
Swr84	TTCAGTATTCAGAGCCACTCTG	ATCTGACATTGCTGTGGCTG	58	178	162	7

TABLE 1

Continued

Marker name[a]	Forward primer	Reverse primer	PCR temp.[b]	Frag. Size[c] Max	Min	Alleles[d]
Sw102	GATCAAGATGTACACAGGCATG	AACCTTCTATCTTCTCATGCCG	58	106	96	4
Sw104	TTTGCCCGACTTATTTCACC	ATCTGCACCCCATATTCACTG	60	237	219	4
Sw120	TTTTAAGATGTGGCTGTGTTGG	GATCACCTGCTAAGTGAAAGTCA	60	150	134	6
Sw122	TTGTCTTTTTATTTTGCTTTTGG	CAAAAAAGGCAAAAGATTGACA	58	132	110	10
Sw129	TTGTTTAGAAGTTTTGGGTTGC	TTGCATGAACTTTTCAACACTG	58	129	107	7
Sw133	GGCCTGAATTACATATGTTCCC	AATGTGGCAACAAAACAAAAG	60	150	142	5
Swr136	TTCTCTGCCGTCACTCACTG	CTGGGACCCTCCATATGATG	58	227	191	8
Sw137	CAGCAAAGTGACCCAGCC	TCCTGCTGTGAAGCACAGAG	60	135	0	6
Sw139	CGACACCCTTGGGTTTTG	ATCTAAAATGGGCCTTTGGG	60	128	120	5
Sw142	AGTTTGCAGCATTCGATTCC	ATTTGTTGCCATTCATGATCC	58	131	115	5
Sw147	TTGCCTTTCTCCATGTGACT	ACAACCTAACCATTTGTCACAGG	58	220	208	6
Sw149	TCATGTTCACAGAACACCTTCC	AGTTACGGTGGGTCGTAATCC	58	138	108	4
Sw151	TTCCCCTATGATGAGATGGC	GGTGTGGCCCTCAAAAGG	60	207	195	4
Sw152	GGATTTTAGGGCTGAATCTGC	GATGACCTTGCAATGCCC	62	182	166	5
Sw154	CAGAGGGGCAGCAGAAATAC	GATCCATGAACTTGACATGTG	60	148	0	6
Sw157	GCAATGTCCGATTCTTTTATTT	ATTGCTGTGGCTGTTGTTGT	58	168	159	4
Swr158	TCCAATTCAACTCCTGGCTC	GAATGTGCACATACCACATGC	58	200	158	8
Sw159	GATTGGGAATTTGGGGTTG	GCATTGTTGTTTTCATTTCTGC	58	159	131	5
Sw160	TCTTCCTTGTCATACATGCCC	ACTAGACAGCCAGGGTGGG	58	132	128	3
Sw163	GCTATCCCTGAGAAACAGTGTT	GATCCTAATGGGCTCAGCC	60	184	166	7
Sw168	GCACTTTCTTCCCTTACCCC	CAGTGTAAAGCATGGAAGATGC	62	116	102	4
Sw171	CAGATTGTTTAGCCTCTGTGTG	CATCTTTTCCAATGACAACATG	60	125	101	4
Sw173	CTGGGAACCTCCATGTGC	GTCCTGGGCCTTTAGGTAGG	58	216	194	6
Sw174	GCCAAAATAGCTATTGGACAGC	TCATGCTATTTTGTTCCAGATG	58	131	123	5
Sw175	TCACACCTGTATAAGAGATGCA	TGTTGGGCAAAATCTGAATT	60	126	102	6
Sw184	CTCCCTGCATATATTTTCATCC	ATCCCTAGCCTGGAAATGTC	50[3.0]	236	222	5
Sw188	ACAAACATACATCCAGTCCATG	GCTTCCCTACTGAATGCTTATG	58	150	128	5
Sw191	ATGATGGGAACTCCTGGCTC	AATTCTCAATGTCCACCATGG	58	199	153	5
Sw193	TGCCATCCTTTCTTTCATTACG	TCACTCTGAGGGGTCCTGAC	62	109	101	4
Sw194	TGCCTGCTTACATTAAGTGGG	CCTCACTTAAGAAGGTTCCTGC	58	102	98	2
Swr198	TTTCATCAGCAACTTCAGAAGG	GGTGCGGCCCTAAAAAAAAG	60	110	72	6
Swr201	TGGAAACACTCTGGCATAACC	CTCCAACTCAGCCCCTAGC	62	143	123	6
Sw205	CACAGGTCCATCACCTCATG	GGGTATCTAATGTACATCACGG	58	156	146	4
Sw206	TCAGTGTGTGAACTGTGTGTGG	TGGTATTTGGAATGAATCTTCA	55[3.0]	153	137	6
Sw207	CGCTTCACAAAATAAGTTGGG	GTTGTTACTCCCAAAAAGGTGC	58	188	170	6
Sw208	AACAAAATATTTAAAAATACTCTGTGTGTG	GCAAGAAATAAATCAAACAATCT	60	156	132	6
Sw210	TCATCACCATCATACCAAGATG	AATTCTGCCAAGAAGAGAGCC	60	242	218	8
Sw211	TCATCAAGAAAATTGGCTTGG	TGACCACAAGGAAGAAACTGG	60	152	140	5
Sw216	ATCTGGGATAATTTGGACATCC	CCCTAATCCCAGGCTCTTTC	62	140	120	5
Sw225	AGGACCCACCAAGAGTTACC	TGCTGGTAATGGGTGATTAGG	55	116	94	7
Sw236	AATGAACACTTTATTGGGGCC	GACATCTCACTGGCTGAAAGC	65	147	123	7
Sw240	AGAAATTAGTGCCTCAAATTGG	AAACCATTAAGTCCCTAGCAAA	58	114	94	8
Sw245	TGGTGCTAGCAGAACCTGTG	AAACCTGGCAACACAGCAG	60	130	106	9
Sw248	CCATCCACGTTTTTATAAATGG	CAACCTAAGTGTCCATCAATGG	58	142	114	5
Sw249	GAAAGCAGGACTTGCTCCTG	ATCATCACTCTCCCAACATGG	58	156	0	8
Swr250	CACTCAATGTCTCGAATCAAGC	CTGGGGCTGTGGTGTAGG	65	176	166	6
Sw251	CCCAATATTCATAGCAGCATTG	TGAGTAATAGCCCATTTTGCG	58	136	130	2
Sw252	CTCTGGGTCCATCCATTTTG	TTATGATGCAAAACATGGAAGC	62	179	149	7
Sw255	TGTACAGCTCTAGTTTGACCCC	TCTGCTTAGCTGCCAAACTT	58	126	122	2
Sw256	ACAAAAGCTTTTGGAGAACTCG	TAGCATAGGAACAGGTGCAGC	62	118	92	7
Sw259	CCTTTCATGCTGTATTTAACCC	CAGAGAACAGAAGTTGGGGG	55	180	0	6
Sw262	TACTTGGCTTTTTGTGACCAG	TCAGCCAAAGGGCTCTTG	62	204	200	3
Sw263	TCAGAAAATCCTCTTGCCCA	GATCCTAGGCTCAAAACAGCA	58	149	133	6
Sw268	CTGATTCACTTTCATTCGAGAA	AGCCCTTCCCTTAATATAACCC	60	149	121	7
Sw270	TTCCCTTACTGCTCCCCC	GAAAGGAGGGAGAGCTGGTC	60[3.0]	163	139	8
Sw271	TTCCAGTGGCTTTCTGTGC	CATTCATTCCCAGTGAAACTTG	58	134	108	7
Sw274	CGCACAGCGACATCTTTTTA	AAGTGCAGCCCTAAAAAGACA	60	145	107	5
Sw280	CTAGTTGTATCCATGCTGCTGC	TCCATATGCTGCACACACAG	58	231	0	10
Swr283	TGGGACTTAATTGTGATTCTGTG	GATTTGACCCCTAGCCTCG	60	158	154	3
Sw286	GGTGACAGAATACAGTTTTCCC	GATCTTCTTATTGGCCGTGTG	62	94	74	6
Sw287	TTGAAGTCTACCCATGTTGTTG	CATCCCAATGTCACTGC	60	175	160	6
Sw288	AAAATAAAAAGCATGGCCTGC	GGGAAAAAACATGTAATTGCC	60	133	103	5
Sw295	ACCTGCCAGAGTTGTGGC	AAGAGTTTCATTTCTCCCATCC	62	139	109	8
Sw301	AACCAAGCCACTTTCCCAC	GCTGAAATGCCCATCTGG	62	156	124	7
Sw304	GATCCCTGACCTGAGAACTCC	CACTGCACAGAATTGTTGGC	58	146	130	5
Sw305	AGCTTTCATTTTTTTAACCCATC	TCACCTTTCAACCCATCACC	58	108	106	2
Sw307	CTTCCACATGTCATGGATGTG	ACCTGTCTTCATGTTCACATGG	58	135	119	4
Swr308	TCCAGTCCCTTGGTCTCTTG	TTAGCCTGGGAACTTCCATG	65	160	119	8
Sw310	CAGAAGGATGAATATGCAAAATG	GTCTTTCAGGCTTGGAGGG	62	135	109	6
Swr312	ATCCGTGCGTGTGTGCAT	CTGGTGGCTACAGTTCCGAT	60	141	127	7
Sw314	CCTCCTTGAGCCTACCCTTC	CCCTAGCCCTGGAACTTCTG	62	118	102	6
Sw316	TTCTCCAGCCATCATGAGTG	AATGACCATTCCTGAGGCTG	58	159	133	8
Sw317	GGGATGCTAAAGTTGGAGGG	TTAGTGTCCTGGGCAAGGAG	62	168	154	5
Sw322	CATTCAACCTGGAATCTGGG	TCCCTGGAAAGGCTACACC	62	118	102	6
Sw328	GATCCAAACTGCCATTCTATTG	CAGGGGTGGCGCTAGAAG	62	182	0	5
Sw330	GTAAGGTCCAGACTGTATTTGGG	TCTACCCATGTGATAAAATTGCA	60	116	100	4
Sw332	TTTTCAATATCACATTCACTCATGC	TTTACAAGTGGGTAGATTAATTA	58	115	109	3
Swr334	CAAGTCAAAGACAGATACTCTGTGTG	TGTGGCATAGTTTCAGATGAGG	58	222	0	9

TABLE 1

Continued

Marker name[a]	Forward primer	Reverse primer	PCR temp.[b]	Frag. Size[c] Max	Min	Alleles[d]
Sw335	GAGTATGGGGAAAGCCACG	CCATCAACAAACTGTATGCACC	58	112	100	4
Swr340	CATTGGTGATTTGCATCCC	ATGGGCTGGCAGCTACAG	58	149	0	5
Sw342	GGGTTCTGTGGTAGTGACTGC	TCATCCACAACAGCAGAACC	55	127	91	10
Sw344	AGCTTCGTGTGTGCAGGAG	GTAGTGGTCCAAAGAGAGTGCC	55	174	150	6
Swr345	AACAGCTCCGATTCAACCC	TACTCAGCCTTAAAAGGAAGGG	55	166	140	5
Sw349	CCTGTTGTAGGCTCCATGAG	CTAGGAGTCGGCCCTGAAC	62	177	149	9
Sw352	GCCCCCATTCTCAATTCAC	GATCAAGCTCCCCTCTTCG	55	111	107	3
Sw353	CACCCCATGCCTGAATACTG	ATGTGAAGACTCATGCTTGGG	58	164	144	8
Sw354	TGGCTTCTCAGCCTCCAC	GGTTCTCCAAACAAACATAGCC	60	222	206	5
Sw373	TTTGCTGCAAAGCAATGTTC	GGTAGGATTCAATAACACCTGG	55	170	152	6
Sw374	AGTAATCCCATCCTCCCCAG	TGCTCTCCAGCCCTCAAG	62	169	141	7
Sw378	ATTATGCACCCCTACTCCCC	GATTTCTTCTTTGTTTGTGCCC	60	127	123	3
Sw382	CTGAGCCACAGAGAGCAGC	GAGTGTGTGCAAAGGGGG	65	144	132	3
Swr389	TTTTTTAGTGTTGCTGTTTTCG	GTAGGCCAGCAGCCACAG	62	122	120	2
Sw395	TTCCAAGGTTATGGAGATATCC	GATCCCTACCTCACACCACA	55	163	139	9
Sw398	AAGTGCCAATGCTTTGTTCC	CGGAGGAGAAATAAGGGTAGC	55	188	166	6
Sw403	GTGTATGTTCATGCATGGGTG	GTCTCTGCTTTGCTTGCATG	55[4.5]	114	102	5
Sw413	CAGACACACACCCCAGTGTC	AGGTCCAACCCTCCTGATG	62	174	162	5
Sw419	AATGGGAAATAGGCTCTAAGCC	TCCCCTCCCTATACATGTGC	55	174	154	6
Sw423	ACTCAGGTAATGGTAAACTATATATGTGTG	TTCTTCCACATTATTCCTTGTGG	60	149	139	5
Swr426	CCTACATATGCCGCAGGTG	GAGAAGTGGGGAAGGGACTC	62	202	184	9
Swr428	TTCCACGTAGATTTTTGACACG	ACCTGCGTCCTCATGGATAC	52	123	0	7
Sw435	ATCATGTGAGAAAAAGAACATATGTG	TGCAAGAGAACTTCCGGC	60	178	148	6
Sw436	GGACTTCTAGCCTCCAGAACTG	AATTTTCAATCACTACCACCGG	58	162	144	5
Sw439	TTCTAGCCTCCAGAACTGAGAA	CCTCCTCCATCCTCACCATA	58	179	161	5
Sw443	ACAAAGGCCAAGCCACATAC	TCACCAGGTTTCTGGGTTTC	60	134	108	7
Sw444	ATAGTTTCGGTTGGCCCAG	CTTAAGCCTCAAGCTAACAGGC	60	120	92	10
Sw445	CCTCCCTGGCACTCATTG	CACACACACAAGCAGGTGC	58	203	181	11
Sw446	GGTTTCCTGTCTGTAAAATGGG	ATCCCTGGCTGGGAACTC	60	164	118	10
Sw452	ACAGGAAAGTGACCCTGCC	TGGAACATGATGGAGGATAATG	60	97	87	5
Swr453	TTGAATTTTTTTCATGGAAACC	TCTGGACTTGCTGTGACTGTG	51	189	173	4
Sw458	TTATGGTTTCCTTTGCTGTGC	CCGTTTACTGCAGGGTAACC	62	123	117	3
Sw460	ATTGCACACCTATCTCTATGCG	AATCTCCATGTGCCGCAG	60	199	159	8
Sw467	TATACCTTTAGCGCCTAGGAGC	CTCAGCCGCTTGGATAACTC	55	130	114	7
Swr468	GCTTTAAAAACCCTCCTGCC	TGATTTGACCCTTAGCCTGG	60	166	120	7
Sw472	AAAATGAACCCTCTCCAGTTTC	TCTGAACACTACAGCCCGC	58	111	95	3
Sw480	TGCCTGGAAAAGGTCTGC	CTTCTCTCCTTGTTGCCCTG	60	144	72	6
Sw482	GGAGAAAAGAATGATTATGCAAA	CCCAGATGTCGGTTCTTTGT	58	267	257	4
Swr485	CCATTTTCAATTCATGGAAGG	CTAAGCCGCAACAGGAACTC	60	119	97	5
Sw486	GCAAATACTTGGTGGCCG	TCCATTTGCTAATAAAGAGCTGA	50	160	138	6
Sw487	TGAGCACCTCTGCTTGAGTC	ACACCTCTAAAATGGCAGTGTG	58	188	148	9
Sw489	CAAGTGTGAAATTTGTGCGG	CGAAGTGCTAACTATAAGCAGCA	55	174	156	6
Sw491	TTTAAGCCACTGCACCAGG	CAGGGAACTCCTCATAGTCCC	60	174	154	3
Sw492	TCCATCAGCTCACATAGTTAGC	ACCATGACAGGAACTCCGAG	60	146	118	7
Swr493	ATATTTAACCCATTGCAGCATG	CTGCAGCTCCACTTAGACCC	58	194	156	8
Sw497	TTAGGAACGTCTGGGTTTGG	TGGGAGCTTCCATGTGTTG	58	116	94	9
Sw510	GTTCCCATAAGCTCATCACTCA	ATATTCTGCACTTGCAGCCC	60	160	150	6
Sw511	AAGCAGGAATCCCTGCATC	CCCAGCCACCAGTCTGAC	60	205	165	7
Sw512	TATAGTGCAGTTATATCTCAATACAAATGG	TCTGACATTAATACAACCACCCC	58	157	129	7
Sw520	GCCACCGGTGTGACTCTAAA	CTTTTCCCAAGTTCACTTAGCA	62	124	102	5
Sw527	AGCAAGAGCCAGAGCATACC	TAACCTGTTGAGCCACAAAAG	62	168	128	5
Sw539	CCCATCCACGCTAAGAAGAG	TCAACGGGAACAACTTGAAG	60	150	148	2
Sw540	TCAGTGGAGGGCGAATAAAC	CCAAATCCTGGCAACACAG	58	253	229	8
Sw552	AAGAGCCAGATGGGGAGG	ACTGATAAGACATGCTGTGTGC	60	146	112	7
Sw557	TGTCCACTGGTAGATGAATGG	CTTTTGAATGTTCTTTTTCCCC	55	250	240	3
Sw575	CTACAGCCGGTGGCTACAG	AGGAATCCATTCAGCCTGG	60	157	151	3
Sw581	CCCCAGATTGACTCTAGACTCG	CATGATGGAGGATAATGTGGG	57	205	199	3
Sw589	TTCAAATCTCACCACCAGTCC	CTCATCAGCAGCAACCACC	60	150	138	6
Sw590	ATTTGCTGAGAGATAAGGTGCC	GCATTGACCAGGGTCAGG	60	271	184	4
Sw605	AGCCTTCTGTGCAGAAAAGC	CCCCAGGTTCTCTGCTCTC	58[4.5]	131	109	5
Sw607	AGCACCTGGCACAGGATAAC	GCAAGAACTGGTTTTCCAGC	58	172	152	3
Sw617	CTGGGTTTACAGTGTTCTGCC	TGTGATGGAGCCTGATAGAGG	65	157	145	4
Sw619	CACTGGTAAGTATTCACGGTGG	TATGCTTGTTCTGCATCATCG	58	147	129	7
Sw632	TGGGTTGAAAGATTTCCCAA	GGAGTCAGTACTTTGGCTTGA	58	173	157	6
Sw698	ATACAAACCATAGCCATGGACC	GATCCGATTTCAGGCCTTAA	58	224	194	5
Swr702	CTGCTGTTTCTGTTTCATCTGC	TTGCAGCTCCTGTTCAACC	65	160	152	4
Sw703	AAGATGAAGCAGGAACTCAAGG	CTTGATGGCTTTACTGTTCACC	58	140	126	7
Sw705	CTGAAGTCTTGAGATGAAACGC	TGTAGAGCATTTCAGAGGAAGC	62	163	145	5
Sw707	ACGTGCTTTTCTTTGAGCTG	AAAAACGCTAAAGAACAAAGCG	58	101	0	5
Sw709	TCTCAAGGTCACACAGCAGG	AAGGGACAGTGGTAGGCATG	58	143	127	3
Sw714	ATCTCCTTGTTAGAACTTGTGTGTG	GAGATGAATATGGGGAAAATGAAC	58	169	145	4
Sw724	TCCTAAAGGACCGAATTTAAAA	TGTGCATTAATGTCCACGTATG	55	166	144	5
Swr726	CACCACAGAGGGAACTCCTC	TCATATGCCACCGGTGTG	58	155	125	7
Sw727	ATCTCTCTGGTTTTCAGATTTTAAGG	GGCCTGGTTCCATTAGGG	58	148	144	3
Sw730	ACCAAGTGCAGGCTAAATGC	GTTACAGGCTGGGAGCAAAG	60	137	131	4
Sw732	GCAAATGAATGACCAAAAAGG	CATTTTCAATTGGATTGGTTTC	55	180	168	4
Swr741	TGCATTCTGTGTTTTTTTTTGA	GTGCCTGTGGCGTAGACC	62	144	0	6
Sw742	AATTCTACTTCTGGGGAGAGGG	CTTTTGGGAACATTTCTGCC	60	224	193	9
Sw745	CTGAGTCTTCTGGGAACTTTTC	ACAGGGCTGGTAGTGTCCC	58	211	137	7
Sw747	TGGCCCAGGAAGTTTCAG	ATCCCATATGCACCAGGC	58	153	149	3

TABLE 1

Continued

Marker name[a]	Forward primer	Reverse primer	PCR temp.[b]	Frag. Size[c] Max	Min	Alleles[d]
Sw748	CATACATACACCATGCCCATG	TTTGCCCACAGAAATGTTTAC	50	193	179	6
Sw749	TTCCCAAACCAACCAAAGAG	AGGAACTTGCCAAAATCACG	58	113	107	4
Swr750	CATGGACATTAAAAAAAGTGGTC	GGAACCTCCATGTGCCTG	58	147	140	5
Sw752	TCAAGAAATAAGGACAGGAACC	CTACCTTCCCATTTGATGCTG	60	124	108	6
Sw761	CTTTGCTCCCCATTAAGCTG	TCTAGCAAATGTCTGAGATGCC	60	161	149	6
Sw763	GGGTGCATTGTTCTCATATGG	TGCTCTAGCAACACACACCC	62	187	171	4
Sw764	TAGCAGATTGTTTAGCCTCTGTG	AAGCATCTTTTCTAAGCACAACA	60	128	112	7
Sw766	AATCAATTGTCTCCACTTCAGG	AATTCTGCCTTGTTCCAAAGG	60	164	142	6
Sw767	TGCGTGACTAGAACCCTGTG	TCACGCAGAACGTTTCAGAC	60	137	0	5
Sw769	GGTATGACCAAAAGTCCTGGG	TCTGCTATGTGGGAAGAATGC	60	139	106	7
Sw775	TTGCCTTTTAATTTCCCTACTTT	TGATGGAACATGATGGAGGA	58	176	170	3
Sw776	TAATCCGTTGCACCCCAG	CCATATGCCACAGTTTCGG	58	117	88	7
Sw779	TACATGTGCAGAAAACAGAGCC	TGTTGGCTCCACTTCTTCAC	62	107	103	3
Sw780	TCTACCAGCTAAATTGCTCACTG	TAGGACCTGGAATATACTCCCTG	62	136	116	7
Sw781	CAACTACGTCCTTCTTTTTGCC	GATCCTTGGTCTGGAAACTTG	62	198	123	8
Sw782	TCTTCACATATGAGCACCAACC	CGGAACAAGAGGAAGTGAGTG	60	99	89	4
Swr783	CATACCTGCACATCTCTTCAGC	GCAGCTATAGCTCCGATTGG	62	186	0	4
Sw787	CTGGAGCAGGAGAAAGTAAGTTC	GGACAGTTACAGACAGAAGAAGG	60	161	153	5
Sw790	CTGTGGGAGTGTAGCATCTTTG	CATACACCCCAGATGTGGC	62	172	118	7
Sw792	TACTGGGGTGAGCTTGTGTG	TTCCCTCCTCTCCTCTTTCC	62	156	140	4
Sw803	GGTCACAATTGAGGGCACTC	TCCCAAGCAACAGAAGTGC	58	104	96	3
Swr811	GCGGGTATAGCTCCGATTC	TCCTAAACCTGCTTATGCAATT	58	183	167	4
Sw813	AGTTGATTTAAAATGTTGTGCCA	AATATTTCAAAAAAAGGAATGCG	58	110	0	4
Sw816	TTCCATACGCTGTGCTTCTG	AGGATTAGGAGGGTCTTCAAGG	60	177	147	7
Sw818	TCTGATACCACGAGTATGGCC	TTTAATCTGTTGAGCCATCCG	58	179	126	9
Sw824	CTAAACTTTGAATGTCTTGCGTG	ACCAAAGCCTCGTTTCAAGA	58	179	163	6
Sw830	AAGTACCATGGAGAGGGAAATG	ACATGGTTCCAAAGACCTGTG	62	189	179	4
Sw832	ACTATCCTCTTACTCTCCCTGCA	TAGCCTGGGAATGTCCATATG	62	243	227	4
Sw833	CTGACTGTTTTGCTGCAGTG	TCCACTGAGGTCTCTCACTCTC	60	183	171	5
Sw835	TGGCTCAGAGTTTTTCACTCTG	CAGAGGTTTACCAAGTTTTGGC	60	240	218	8
Sw836	TCCAGTGACAATGTCAGGTTC	TTAGTCACTCTTTTGGAGCCTC	58	153	135	6
Sw839	GGAAACCAGGATAACAGGAGG	TAACCCACTGTACCACCAAGG	62	166	144	6
Sw840	CCTGGAAACAACCTAAGTGTCC	TTCCACATTAGTTCCGGGAC	55	137	121	5
Sw853	CTTTCTTCTGTCTGGGTGTGG	GGGAAAATAGCCTCCACCTC	62	101	89	5
Sw855	TCTCTTTTTCTCAAAACCTGCC	GGGAAACTGCTTTTACTCCAC	58	146	128	3
Sw856	AGGGGGTGGGTGATTGTG	AACTTCCCCATGCTGCTG	62	200	160	10
Sw857	TGAGAGGTCAGTTACAGAAGACC	GATCCTCCTCCAAATCCCAT	58	159	145	7
Sw859	TTCAGTTTTGGTGTAGCCCC	CAGGTGTGGCCCTAAAAAGG	60	123	85	4
Sw864	TTGCACAGATGCTAATTCTTCC	TTAAGACTGTCTTGGGCATTCC	60	178	168	6
Sw866	AGTGTGGTGTGTACTGATTTGG	CATGCAGGGAAAGGAGAGAG	60	185	146	4
Sw871	ATCCCTGTTTCCTCCACCTC	AATTAAAGCCATTCACTGGGG	60	126	102	5
Sw873	TCCATCTACACTGACCCAAATG	ACAGTAGCCAAGATATGGAAGC	60	140	134	4
Sw874	AAAAGAACCCAACTACAGCAGC	TTTATGAGGGTATCCTGACACC	60	219	191	8
Sw878	CTGGGAGCACAACAGATAGTG	CAAGCAATCAATTCCTTAAGGG	60	120	101	3
Sw882	TGGGTCTCCATCATCATGTG	TTTTCCGGGGAAACAGAAC	58	135	119	4
Sw886	AATTGGTTTGTCCAGAATTTGG	GATCATTCCCATTTGTTGAATT	58	174	142	8
Sw902	ATCAGTTGGAAATGATGGCC	CTTGCCTCAAAGAGTTGTAAGG	60	203	195	6
Sw903	TTTCTTTGACAGTTGTGCAAGG	TGAACTACAGCAGCGACCTG	58	201	195	4
Sw904	CCCCTTTCAGAAGAATGAAAA	CCTAGTGGCCAACACCAAGT	60	179	163	5
Sw905	ATCCCAACCTTCTTTCAAAGG	TCCAGTGGCAGAACAACATG	60	151	125	6
Sw906	GAGGACAATGTGAGAAAAAGAATG	TTTTTTCCTGTGATTAGAACTCTTAGG	55	184	158	7
Sw911	CTCAGTTCTTTGGGACTGAACC	CATCTGTGGAAAAAAAAAGCC	60	173	151	7
Swr915	TTCATGTTTCCCTATTACAGCA	GCTATAGCTCCAATTCGACCC	60	157	139	6
Sw916	GGAGGTGGCAATAACCAGG	CTGCCCAGGCTGTTTAAGAG	60	142	136	4
Sw917	AATCTTGGAACCTATGGCCC	CCAACAAATTTCAATCAAGTTG	58	137	117	5
Sw919	TCCAAAGTCATGAAGATTTATTC	TCACAGACCTAAATGTAAGAGCT	58	132	87	11
Sw920	CATGGAGCTGAACTTGCAAA	ATCAAGCCCAACTTAAGAATACA	60	150	142	4
Swr925	AGCTCCAATTTGACCCCAG	CTCCAAATTTCTTTGCTCAAGG	62	148	123	8
Swr926	TAGCAGACCAGAGTTTTTTTGC	TTGACCCCTAACCTGGGAG	65	115	111	2
Sw933	ACATATACTTCCGACAGCCCC	AAGAGCTTGGTGAATTGAGAGC	60	133	97	5
Sw935	GTGGTGGTTTGCCTCTTATAGC	ATATAAGGGAAAATAATCTGAAAGAGTATG	58	203	195	5
Sw936	TCTGGAGCTAGCATAAGTGCC	GTGCAAGTACACATGCAGGG	58	112	94	6
Sw937	GTGGAGAACACCAAATGCG	TGGAACTTTGAACCTGACACC	58	226	214	6
Sw938	TTATTATTTCCATTGCCATTGG	CACTTATGATGGAACATGATGG	58	157	147	4
Sw940	TACCTCTGTGTATGCAGCACG	TGAGCATCTCATTCCGTGTC	58	157	0	5
Sw940	GGCTCCAGTGTACCAGTTCC	TGTTTTCCCAGCTCTATCCG	60	144	136	4
Sw943	AGGAGGACTAGAGCGCCTG	AGAGAGGCCAAGAATAGAACCC	62	132	118	2
Sw944	CTCCAGTTCATTTGCAGTTCC	TCTTCATGTATCACAACCCTGC	58	166	164	2
Sw949	TGAGCAATGAGTTCAATGCC	TCGTTGGTGAAGGCATCC	58	204	178	8
Swr950	CTCCATGTGCTGCAGGTG	CCAAACACTCCCCTGCAC	62	163	145	8
Sw951	TTTCACAACTCTGGCACCAG	GATCGTGCCCAAATGGAC	58	136	124	5
Sw952	AACGGGCACCTGCTGTATAG	GATCATTTCTGCTGCACAGC	59	149	143	4
Sw955	CTGCTCAAAGTTTATCTTCCCC	GTCACTCCACTCTGTCTTTCCC	65	113	103	5
Sw957	AGGAAGTGAGCTCAGAAAGTGC	ATGGACAAGCTTGGTTTTCC	58	157	113	9
Sw960	TCTATGAGCCATGCTATGAACG	AGTGGCGCCAACATTAATTC	58	182	152	4
Sw962	TGAATCTCAAGCAGTAGAGCAC	TCAAGATGCCCACTCACCTC	60	160	130	5
Sw964	GTGGTTCCTCTATGCAGAGTCC	ATGTGATGAAACATGATGGAGG	58	248	220	5
Sw967	AGCAGACTGTTCATCTGTTCAG	GGGGCAGCTGAAAAGTCC	58	114	95	7
Sw969	AGCCTGGAACATTTTTGAGTG	TTTCAATTGGTTCCTGTGTCC	60	140	120	6
Sw970	AGTGGGCAAACCAATAATGC	GTCTGCCACAAGCTGACTGA	58	375	227	6

TABLE 1

Continued

Marker name[a]	Forward primer	Reverse primer	PCR$_b$ temp.	Frag. Size[c] Max	Min	Alleles[d]
Sw973	CACAGTTTGCATTGTGGGTC	TAGGGGGCCCGTAAAGTC	58	183	171	3
Sw974	GGTGAAGTTTTTGCTTTGAACC	GAAAGAAATCCAAATCCAAACC	58	166	126	9
Sw977	GATCAAGGTGAGTCTGACATTAA	CGTCACAAGTGCAGCCTTTA	58	104	96	4
Swr978	CCCGGTGATGTCAAGTGAC	CATATGCCGCAAGTGCAG	62	150	122	5
Sw980	CTTCAGTGTAGTCCAAGTGGC	GATGTTTTGCTGATAGGAAGGG	55	132	0	9
Sw983	GCAGTCCCACTCTTAGGTATATATCC	ATAATGCTGCTATGAACACTGTAGTG	60	121	95	5
Sw986	AGGAAGCAAAATCTTAAGAGGC	GGTGAGCCAGGAACAAGTATG	58	164	150	5
Swr987	TTGTTATGCCTACCTGTGTTGG	CTCCATATGCCACAGGTGTG	58	115	93	6
Sw989	CTCATTAATTTAATTGAGTGAGTGTG	CCCGTGGTTCTGACTGAACT	55	135	105	7
Sw995	TTAAGCACTTCATGGAGCTTTG	CATAATGGAAATACCGGGTCC	58	164	150	6
Swr100	CAAGGAGTATCTTTCTCACAGCA	CTGGGAACTTCCATAAGCCA	58	125	0	4
Swr1004	TGGGAACACCTGCTTCATTC	TCCATATGCCCCAAGTGTG	60	167	147	5
Swr1008	ACAGCCACCAACAGTGTTTG	GAACTTCCATATGCTGCAAGTG	62	255	203	9
Swr1021	CGCCACAAGTGAACTCC	CCGCGGGTCCAGCTATAG	60	115	93	4
Sw1026	TGGAGAGGCAATGCTGTATG	GTATTTCACCTGCAGCTCCC	60	118	97	6
Sw1027	AGCAACCTGAGCCACAGTG	GGAACTTCCACACGCCAC	60	159	133	9
Sw1030	AACTGGGGAAGTAGAAGAGCG	TCATCTCATGCCTGTGTCTAAA	58	145	137	3
Sw1031	ATCACCCAGACAAAACAATCTC	TATGTCAACCCCAAACCCC	58	117	93	4
Sw1032	ATTGGGTGGACTGATATGGT	GATCTATAAAGTGTAAATTGTGTGTG	58	171	153	3
Sw1038	CAGTCTCTGAACACAGTTCTTTCA	GCTGTTGGTGAGAGTCAATCC	58	159	137	4
Sw1041	ATCAGAAAATGGTCAACAGTTCA	GGAGAATTCCCAAAGTTAATAGG	58	103	95	5
Swr1042	TCAAACTCACATCTTTGCGTG	GCCTGGGAACCTCCTATACC	60	107	93	6
Sw1045	GGTTTTATCTTTTTCCACAAAGG	GTGAGCCCAGCCTCAAAG	55	148	144	3
Sw1053	CCCACCCACTGACTCCTG	TGTCGGGGAGTAGACTCAGG	60	116	114	2
Sw1055	CTCTTCGCTGTTGCTAACCC	CACTTGTCCCAGGCTTGG	60	97	91	4
Sw1057	TCCCCTGTTGTACAGATTGATG	TCCAATTCCAAGTTCCACTAGC	58	188	150	7
Sw1059	TCTCATGGCCAATCTTTCAC	CCTCCAACCTTCAGTTCAGC	60	215	133	11
Sw1065	TGTAGTGATGTGTCAGCACAGG	TCAGGATGACCTAACCACCC	60	124	120	3
Sw1066	GCAGGATGAACCACCCTG	CTCTTGAGGCAACCTGCTG	62	199	161	8
Sw1067	TGCTGGCCAGTGACTCTG	CCGGGGGATTAAACAAAAAG	60	175	144	7
Sw1070	CTTGCAGCATCACTCTTAGGC	TCTATGTGCCTTGGAGTGAGG	60	206	168	8
Sw1071	AGTGCTGATATCAAGCACAAGC	TCACTTCCCACCCCTTACAC	62	152	126	6
Sw1073	GGGTGCAGCCCTAGAAAAG	TCAGTACAGATTTGTTTCCCCC	62	166	150	5
Sw1080	GGGAAATTTGGATTTGAAATTG	TCCCTGTCACTGTAACTTGCC	60	189	187	2
Sw1081	AAACTGTAGAACCAGCTGGAGC	GACCCTGTAGCATTAGGACTGG	65	152	126	6
Sw1082	ATTTGTGAGATAGGCTTGGTGT	CTCACCACCTCCTCCTTCAC	65	107	89	5
Sw1083	CCTTGCTGGCCTCCTAAC	CATACTCCAAAATTTCTATGTTGA	60	147	117	5
Sw1085	CAGGCTCCCTGACTTCAGAC	TAGGTCCATCCATGTTTCTGC	60	135	117	3
Sw1089	TTTTCCCCTTCACTCACCC	GATCAAAGTCCCTTACTCCGG	58	182	142	7
Sw1092	CCTGCTATGTCTTATTGGGAGG	GATCCTGCATTGCCAAGG	58	314	224	8
Sw1094	GATCATGGTGTACCATCCTTTATA	ATTCTTGATGTTGGTACATGGTG	58	150	142	4
Swr1101	AACTTCCATATGCCACAGGTG	GGTCCTCCTCAGAAAGTCCC	62	170	122	9
Sw1105	TTCAATTCAAAGAAGTGTTTGTG	GGTCGATGATGCTCACACC	60	139	105	8
Sw1108	GTCTTCTTCACACGGAAATGC	CCCCACCTCACACATACATG	60	143	131	4
Swr1110	GATCTGATGGATTCTATTTTGTGTG	AGATGCGGCTCCAATCTG	60	194	0	7
Sw1111	AGGTCCTACTGTCCATCACAGG	GAAGCAGAGTTGGCTTACAGTG	65	181	165	6
Swr1112	CTGGGTTTTGTTTCTGTTTTTG	TGGCTTGGGAACTTCCATAC	60	107	101	4
Swr1113	ATGGAACCTGGGTTGCTTC	TGCAGCTCTGATTGCGTC	60	166	150	4
Sw1117	AGGGCCATAACTTGGAATCC	AAAAACAAAAAAGACCCCTGTG	58	178	157	5
Sw1118	ATCACCCTTCACTCAGAAATCC	GTCTGTGCCTATGCATGCAC	62	188	170	5
Sw1119	CAACCTCAAAAATGGAGAAAGG	GTTCTTGCGGTGTTTGGC	60	160	144	7
Swr1120	CAAATGGAACCCATTACAGTCC	ACTCCTAGCCCAGGAGCTTC	62	173	144	6
Sw1122	TCCCATTTTACAAGAAAAAGGTG	ACTGACATCCTCCCAGCCTA	62	135	119	5
Sw1123	GAGTCTGCCTGCATTGTGAA	TCTGTCTTTGTTTCTGTCTGTCTT	57	178	152	6
Sw1125	TAGATGTATATACTTCCATGTGTG	ATGTTGAGCTCTTAATTTTATACA	60	141	117	10
Sw1129	GATCATATGAGGAAAAGAATGTGT	CACAGGGGGAACACCTTAAT	58	155	127	6
Sw1134	TAAGTTTAGGTGCCTCATTTGATTT	GAAAACTCTCTTAGTTTCTTTATGCAA	58	146	134	5
Sw1135	TAAGTTTAGGTGCCTCATTTGATTT	GAAAACTCTCTTAGTTTCTTTATGCAA	60	192	180	7
Sw1200	AATGCAAGTGATATAAGAGCTTTTGG	GGTGGTTTTGGCTCCAATTG	60	158	130	8
Sw1201	CCAACCAACCAACAGAAAAC	CGGCACTGGTAACTCCAATT	58	212	200	4
Sw1202	TAGAGATGGTTGAGGAAAAGGC	ATGTATCCGGGTCCCTTTTC	58	132	124	3
Sw1204	ATTTTGAACATGAGTAATTCCGTG	TGATGCTCTTGTTTTCTGTATGTG	58	114	0	4
Swr1210	GGATGGGAACTCCCAAGATA	AAGAAAATATCTCAAGCCAAGGA	60	142	130	3
Swr1211	TAGACCCTCCTCTGTTCTTTCC	CATATGCTGTGGGAATGGC	62	85	81	4
Swr1218	TGTGACTATGGCATAGGCTCC	GCCTATTCAGAAATGTTCCTGG	58	199	174	8
Sw1262	TTGGGGCTCACAAAGTCAC	TTGGTAATTTCCGTATGCTGC	60	147	127	3
Sw1263	AGATGAAACTGACATCTTCTGCC	GATCAAGGAAATAACACTGCTGT	55	165	151	5

[a] Markers *SOXXX* were produced at European laboratories with numbers *S0001–S0073* contributed by FREDHOLM *et al.* (1993), numbers *S0081–S0100* were contributed by L. ANDERSSON and colleagues (ELLEGREN *et al.* 1993; JOHNASSON, ELLEGREN and ANDERSSON 1992). *CH13* is from DAVIES *et al.* (1992b). Primers for markers from structural genes were developed in our laboratory from GenBank sequences. Marker names beginning with *Sw* and *Swr* were developed in our laboratory.

[b] The PCR profiles are described in the text. The values refer to the annealing temperature and the superscripts refer to the [$MgCl_2$] (millimolar) when it was not 1.5 mM.

[c] Allele sizes were determined in relation to a sequencing ladder of M13mp18 and should be considered approximate. The number 0 refers to alleles that would not amplify in some animals.

[d] The number of alleles (including null alleles) that were observed in this study.

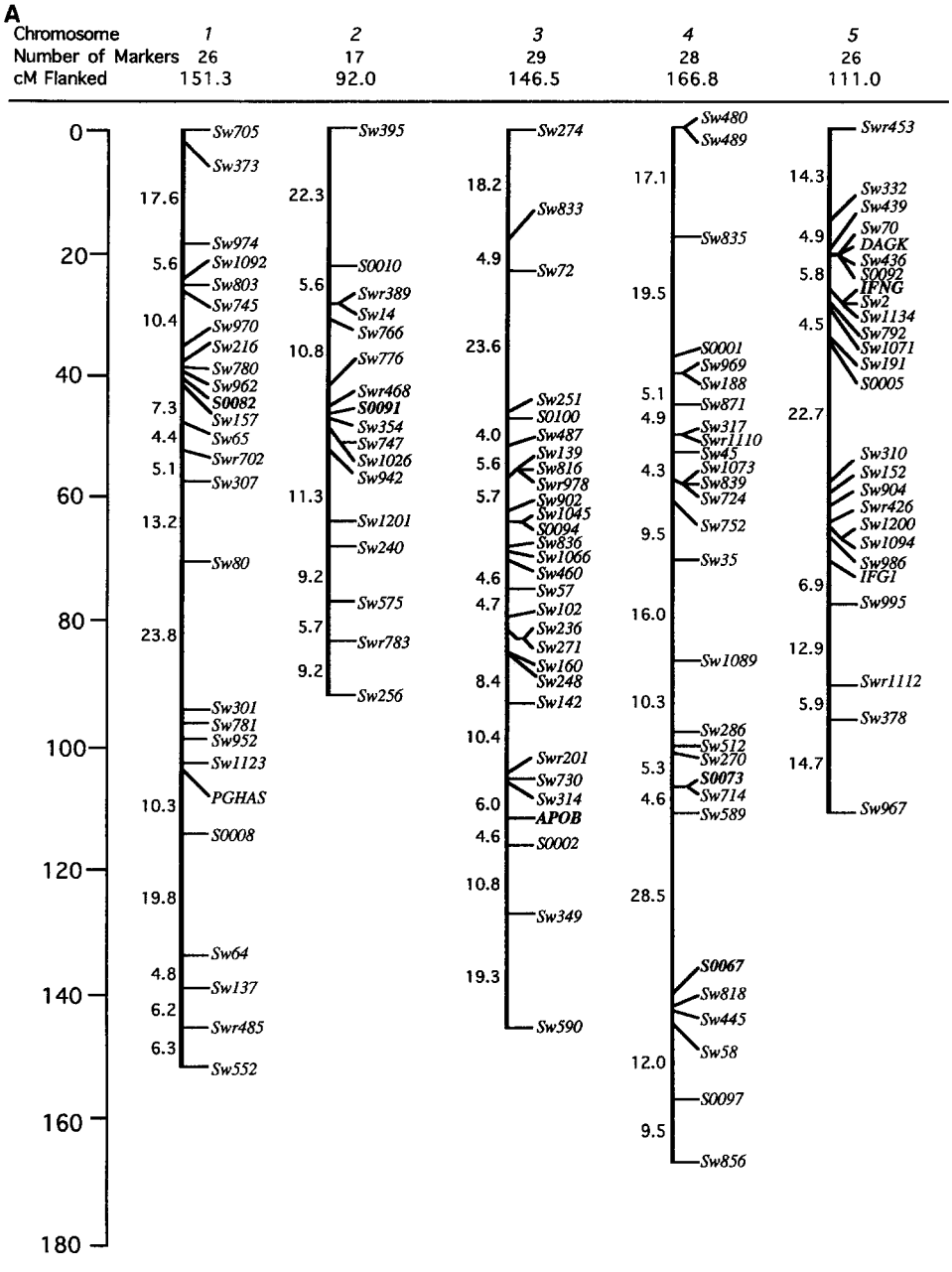

FIGURE 2.—Porcine genetic linkage map. Individual chromosomes are represented by vertical lines. The chromosome number, where known, or linkage group is indicated above together with the number of markers and length in sex-averaged Kosambi centimorgans. The interval between markers is shown on the left side when 4 cM or greater. One pair of linked markers (*Swr68/Sw983*) are not shown as no recombinants were observed. *The 56.5-cM interval on the *X* chromosome was not significant.

striction enzymes (*Apa*I, *Hae*II and *Msp*I) (KIRKPATRICK 1992a; LARSEN and NIELSEN 1993). *Apolipoprotein B* (*APOB*) was amplified using primers 3 and 7 (in KAISER *et al.* 1993) and digested with *Hinc*II. Another fragment was amplified with primers 2 and 6 (in KAISER *et al.* 1993), digested with *Hin*dIII and found to be monomorphic.

Genotypic data were independently scored and entered into the database by two individuals. Software was developed (D. BEHRENS, J. WRAY and G. A. ROHRER, unpublished data) to compare scores, verify data in concordance and report discrepancies. Discrepancies were either resolved by the scoring individuals or data eliminated from the analyses. All linkage computations were performed using CRIMAP 2.4 (GREEN, FALLS and CROOKS 1990) linkage analysis software on a DEC 5000/25 work station and based on sex-averaged recombination rates (except for markers exhibiting *X*-linked inheritance). The two sire and eight dam pedigree structure (Figure 1) prompted the selection of CRIMAP 2.4 over available software packages for linkage analyses. After preliminary alignment, the CHROMPIC option in CRIMAP along with software developed on site were used to identify unlikely double crossovers (those that occur within a 40-cM region) present in the data. Data contributing to these double crossovers were reanalyzed to determine their validity by rerunning the PCR reactions and blindly scoring the results. The number of errors remaining in these data should be negligible based on the error checking system implemented.

RESULTS

Genotyping: A two generation reference population with eight full-sib families and 94 progeny was developed with two WC boars and eight F_1 sows. Two F_1 sows were WC-DU and six F_1 females (one WC-FE, two WC-MI and three WC-ME) were produced by crossing boars from one of three Chinese breeds: FE,

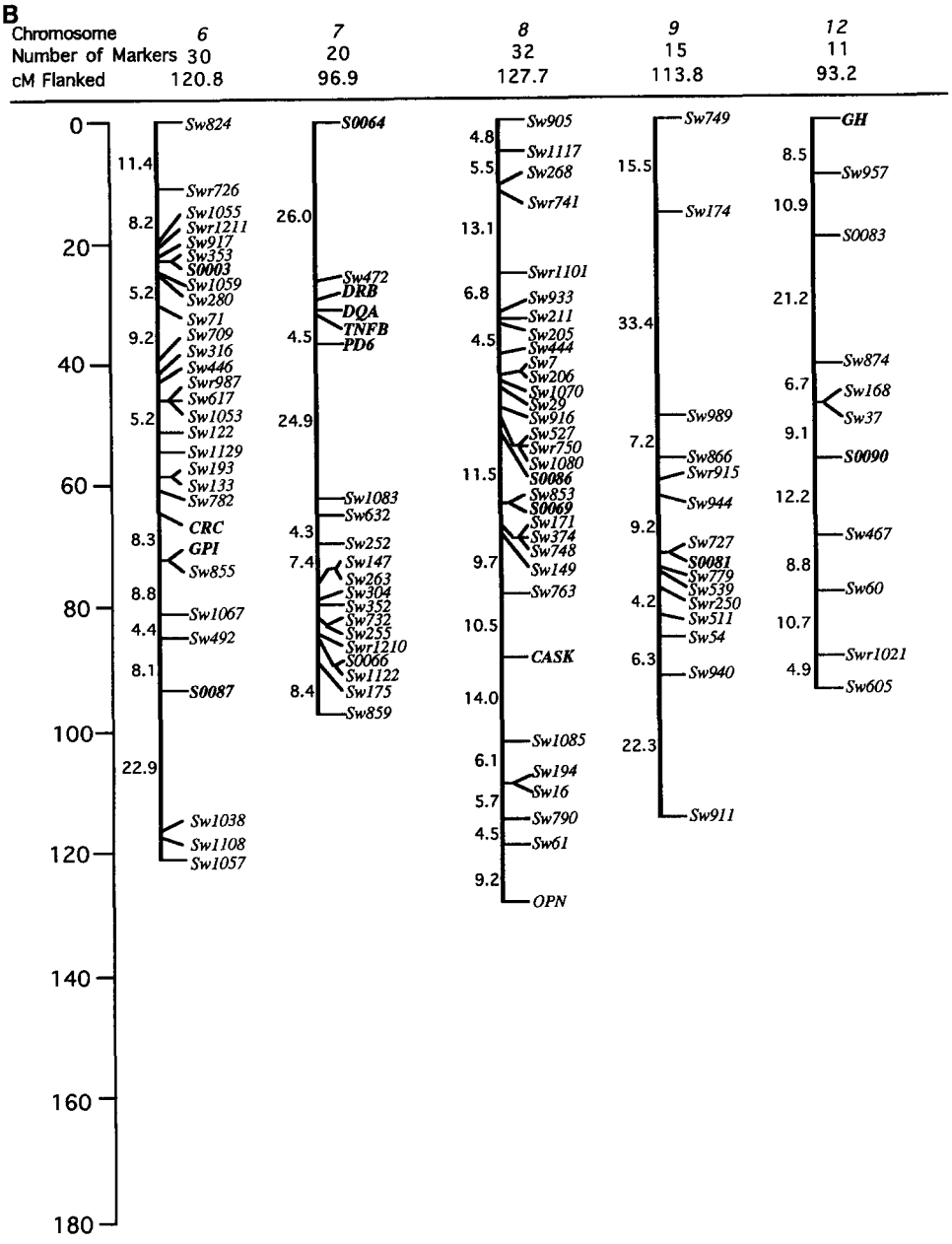

FIGURE 2.—Continued.

ME or MI with WC sows. The two DU-WC sows had litters of 15 and eight piglets; one FE-WC sow had a litter of 12; three ME-WC had litters of 14, 13 and 5; and two MI-WC sows had litters of 14 and 13. One boar sired seven of the eight litters with 81 progeny, while the other boar sired one litter (dam was MI-WC) of 13 piglets (Figure 1). The cross between North American and Chinese pigs was an attempt to design the most genetically and phenotypically diverse intraspecific cross possible in swine. The genetic diversity present in this population will increase type I marker polymorphism and facilitate development of comparative maps.

Our strategy to screen recombinant M13 swine genomic clones for GT:CA dinucleotide MS resulted in 0.24% of all recombinant M13 clones yielding primer sequences. Eighty-five percent of all primer pairs amplified locus specific products. Only 3% (11/349) of MS developed from our M13 libraries were monomorphic in our families. Forty-nine of the 338 MS markers (14%) developed in our laboratory were adjacent to a short repetitive element (SINGER, PARENT and EHRLICH 1987) (designated *Swr*; Table 1). These markers were similarly informative.

We were unable to amplify specific products from three loci (*apolipoprotein A1*, *follistatin* and *inhibin β (b)-subunit*) of 14 MS adjacent to, or within, porcine coding sequences obtained by screening the GenBank and EMBL databases. Three loci were monomorphic (*interleukin 1α*, *growth hormone* and *apolipoprotein C3*) leaving eight (73%) informative loci for analyses: *calcium activated ATPase* (*ATP2*), *diacylglycerol kinase*

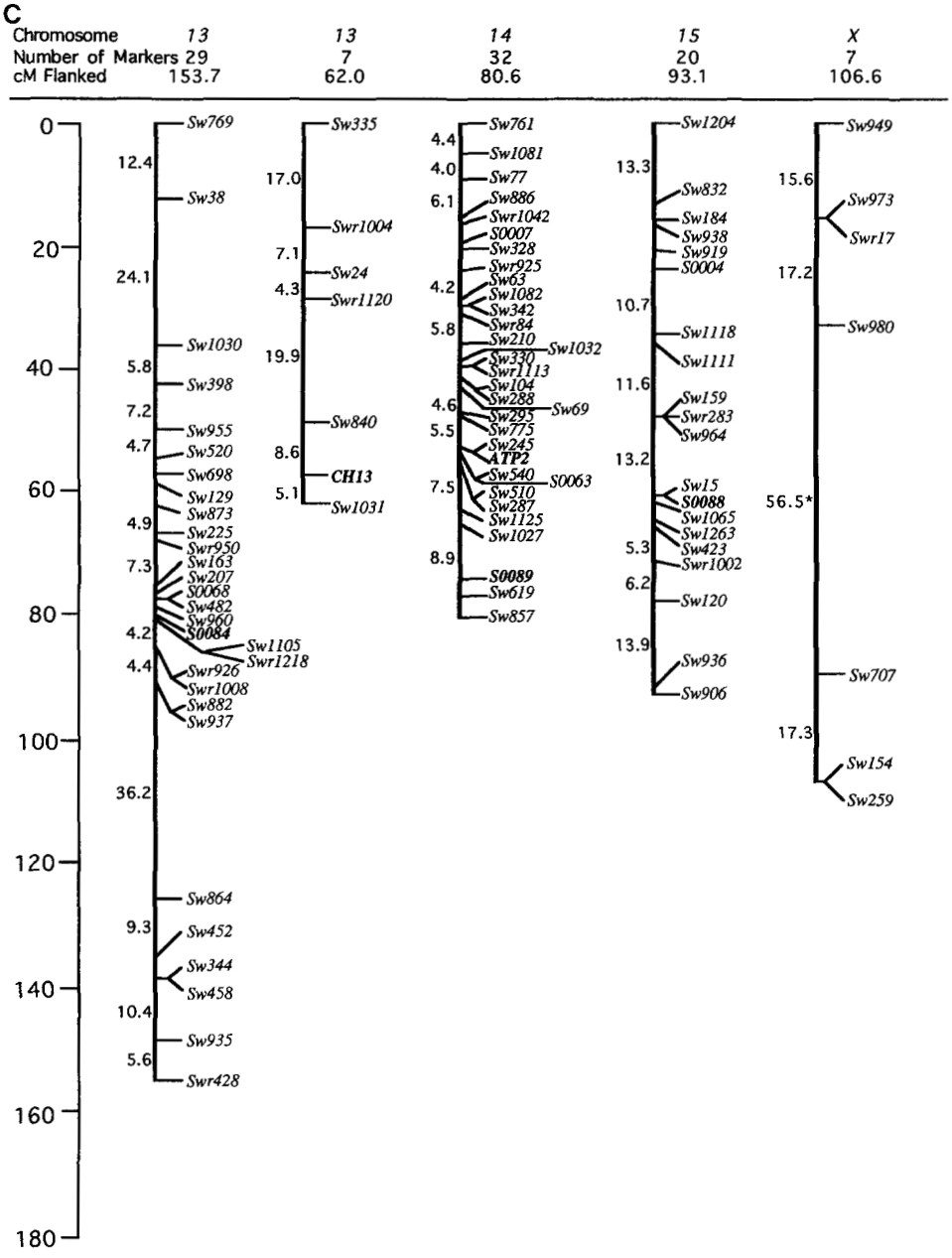

FIGURE 2.—Continued.

(*DAGK*), *insulin-like growth factor I* (*IGF1*) (KIRKPATRICK 1992b), *interferon γ* (*IFNG*), *osteopontin* (*OPN*), *pituitary glycoprotein hormone α-subunit* (*PGHAS*), *ryanodine receptor 1* (*CRC*) (BOLT, VOGELI and FRIES 1993) and *tumor necrosis factor β* (*TNFB*) (Table 1). As MS were more polymorphic than RFLPs, we preferred to use MS associated with genes as MS cost less to genotype and required less labor. While only 36 of 44 published MS (DAVIES *et al.* 1992b; JOHANSSON, ELLEGREN and ANDERSSON 1992; ELLEGREN *et al.* 1993; FREDHOLM *et al.* 1993) were scorable in our families, all 36 were informative. Locus name, primer sequences, PCR conditions and number and range of alleles for MS genotyped are presented in Table 1. The average number of alleles observed across all MS was 5.8.

As expected MS were more polymorphic in WC-Chinese sows. The mean level of heterozygosity was 54.4% for WC boars, 65.9% for WC-DU sows and 81.4% for WC-Chinese sows with WC-ME the most heterozygous breedtype (83.9%). Heterozygosity levels of 46–58% within breeds (ELLEGREN *et al.* 1993; FREDHOLM *et al.* 1993) and ~75% in F_1 animals from diverse crosses (COPPIETERS *et al.* 1993; ELLEGREN *et al.* 1993) of swine have been reported. The level of heterozygosity observed in North American breed composite crosses (WC and WC-DU) was similar to what has been observed in *Bos indicus* × *B. taurus* crosses (60–65%) (S. KAPPES and M. BISHOP, unpublished data); humans (63%) (HUDSON *et al.* 1992); and in intraspecific crosses between inbred strains of mice (50%) (DIETRICH *et al.* 1992). The inclusion of WC-

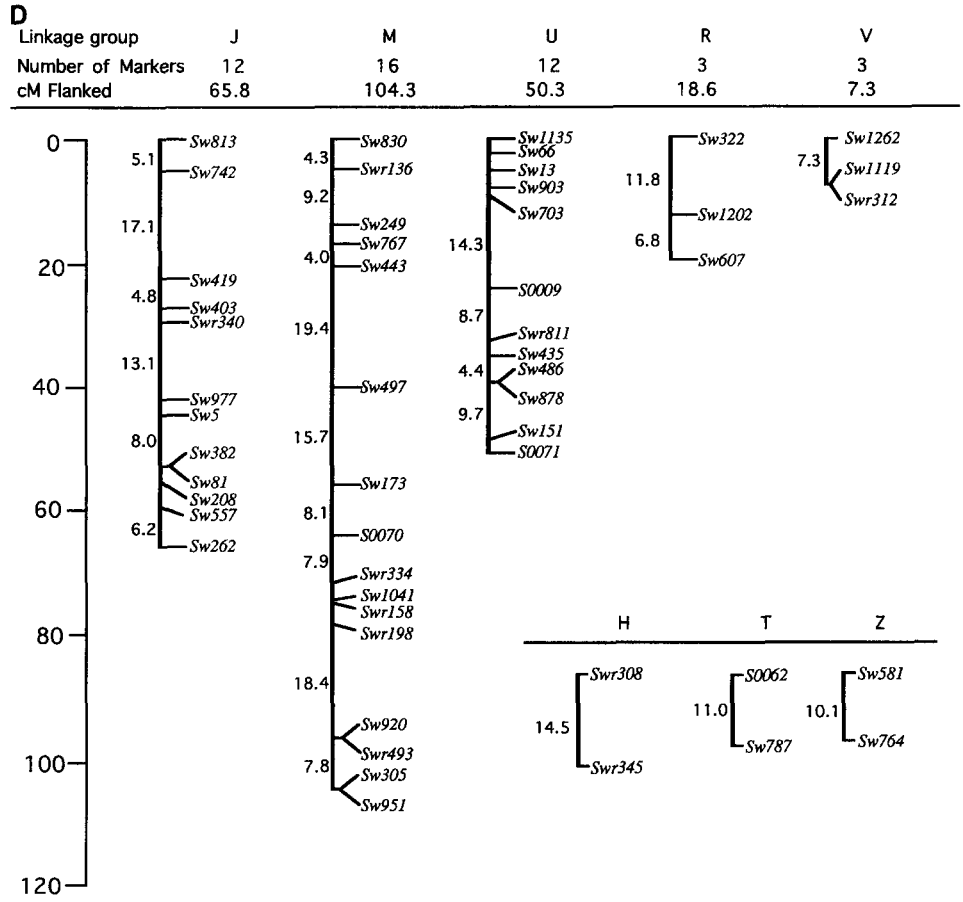

FIGURE 2.—Continued.

Chinese sows accelerated the development of the map as they were nearly as informative as interspecific hybrid mice (90%) (DIETRICH *et al.* 1992).

Only seven RFLPs with previously reported, readily scorable polymorphisms and chromosomally assigned were mapped. All RFLPs developed in our laboratory (analysis of the SLA cluster will be reported elsewhere) for class I (*PD6*) (EHRLICH *et al.* 1987) and class II DQA (HIRSCH *et al.* 1990) and *DRB* (PRATT *et al.* 1990) major histocompatibility loci were informative. Only one band per allele was observed for class I *PD6* (EHRLICH *et al.* 1987) and class II *DQA* (HIRSCH *et al.* 1990) and no more than two bands per allele were found for class II *DRB* (PRATT *et al.* 1990). Restricting probes to regions of genes with low levels of interlocus homology eliminated multilocus hybridization and ensured the observed genetic variability was confined to a single locus. Two alleles of *CASK* (LEVINE *et al.* 1992) also segregated in the population. Glucose phosphate isomerase (*GPI*) was the most informative RFLP (nine alleles present) as the probe sequence is adjacent to an intronic variable number tandem repeat (VNTR) (DAVIES *et al.* 1992a).

Two additional RFLPs were characterized in restriction endonuclease-digested PCR-amplified products. Three restriction enzymes were used for *GH* to maximize the number of informative meioses for this locus (KIRKPATRICK 1992a; LARSEN and NIELSEN 1993). When analyzed as a single locus for the linkage study, no recombinants were detected within the haplotype. Two alleles for *APOB* were detected in our reference population with *Hinc*II (KAISER *et al.* 1993).

Linkage analyses: Markers were placed into putative linkage groups based on two-point linkage estimates (LOD > 3.0). Each set of markers was then aligned based on the linear order that maximized the log likelihood (LOD) from multiple-point linkage analyses. All intervals greater than 20 cM were tested for significance by comparing the LOD of the initial analysis (LOD_M) with the LOD holding the recombination rate of the large interval to 0.5 ($LOD_{0.5}$). Linkage groups were separated by multipoint analysis using CRIMAP 2.4 if the difference ($LOD_M - LOD_{0.5}$) was less than 3.0, thus eliminating spurious two-point linkages. The average number of coinformative meioses observed between all pairs of markers was 73 (range 0–188). As only 60 coinformative meioses are required to detect linkage between markers 20 cM apart with a power of 90% (J. KEELE, unpublished data), most intervals between markers flanking 20 cM or less should be detected. The overall power of detecting linkage was reduced because only two generations of animals were available and without grandparental data the phase of linked markers had to be computed.

Linkage analyses identified 23 autosomal and one *X* chromosomal linkage groups. Idiograms of each linkage group are presented in Figure 2 and distances between markers are proportional to the sex-averaged rate of recombination. One pair of linked markers (*Swr68/Sw983*) is not presented in Figure 2 as no recombinants were observed. Markers are aligned in the order that maximized the LOD. However, marker order within 5-cM intervals should be considered tentative until additional linkage has been established. Linkage group orientation with respect to the centromere and telomere was arbitrary as polymorphic markers physically assigned to chromosomes are currently minimal in the porcine map. The 383 linked markers covered 1997 cM. The average distance between adjacent markers (n = 362 intervals) was 5.5 cM. Sixty-three percent of all intervals were less than or equal to 5.0 cM while only 3.6% of the intervals were greater than 20.0 cM. Individual linkage groups had between two and 32 markers (mean 16) and spanned from 0 to 167 cM (mean 79.5 cM). An additional seven MS were unlinked in the final analyses (*Sw11*, *Swr67*, *Sw413*, *Sw491*, *Sw943*, *S0061* and *S0099*).

Twenty-seven previously assigned polymorphic loci (20 MS and seven RFLP; Table 2) were incorporated into linkage groups anchored to 13 autosomal chromosomes (Figure 2). Five anchor loci are located on chromosome 7 and four on chromosome *6* with the remaining 11 chromosomes having between one and three anchors each. *Kappa-casein* was assigned to chromosome *8* based on the close linkage of the four casein genes (α_{s1}-*casein*, α_{s2}-*casein*, β- *casein* and κ-*casein*) in cattle (FERRETTI, LEONE and SGARAMELLA 1990; THREADGILL and WOMACK 1990) and sheep (LEVEZIEL *et al.* 1991) and the physical assignment of α_{s1}-, α_{s2}- and β-*casein* to porcine chromosome *8* (ARCHIBALD *et al.* 1992). Fourteen linkage groups contained anchor loci. We assigned linkage groups to chromosomes when at least one member of the group had been directly or indirectly assigned to a chromosome (Table 2). Two linkage groups were assigned to chromosome *13*. All five anchor loci for chromosome *7* were members of the same linkage group and all four anchors on chromosome *6* were within one linkage group. The same was true for anchors assigned to chromosome *4*, *8* and *12*. No linkage group could be established for chromosomes *10*, *11*, *16*, *17* and *18*. Informative markers for chromosomes *10*, *11* and *16* have recently been developed but have yet to be published (B. CHOWDHARY, personal communication). Chromosomes *17* and *18* remain bereft of markers (ANDERSSON *et al.* 1993). Four randomly generated markers (*Sw154*, *Sw259*, *Sw707* and *Sw980*) exhibited *X*-linked inheritance in every animal in our reference population and were assumed to be located on the *X* chromosome. One of these *X*-linked markers (*Sw980*) was not significantly linked to the other three (Figure 2). However, *Sw980* was linked to three other markers exhibiting autosomal inheritance. Presumably, *Swr17*, *Sw949* and *Sw973* are located on the pseudoautosomal region of the *X* and *Y* chromosomes. We were unable to assign nine linkage groups containing 54 MS markers to chromosomes. As additional markers for chromosomes *10*, *11*, *16-18* are developed and reported, it is likely that the larger unassigned linkage groups (J, M and U) will be placed on some of these chromosomes.

Our results provide the first assignment of four structural genes and 13 published MS (JOHANSSON, ELLEGREN and ANDERSSON 1992; ELLEGREN *et al.* 1993; FREDHOLM *et al.* 1993) to autosomal chromosomes in the porcine genome. *Diacylglycerol kinase* (*DAGK*) and *IGF1* are assigned to chromosome *5*, *PGHAS* is assigned to chromosome *1* and *OPN* to chromosome *8*. Marker *S0008* is assigned to chromosome *1*, *S0010* to chromosome *2*, markers *S0002*, *S0094* and *S0100* to chromosome *3*, *S0001* and *S0097* to chromosome *4*, *S0005* and *S0092* to chromosome *5*, *S0066* to chromosome *7*, *S0007* and *S0063* to chromosome *14*, and *S0004* to chromosome *15*. We were also able to assign four previously published linkage groups to chromosomes. The linkage group of *S0007* and *S0072* (FREDHOLM *et al.* 1993) (also reported as U6: ANDERSSON *et al.* 1993) is assigned to chromosome *14*. Linkage groups X, XI and XII (U9) (ANDERSSON *et al.* 1993) established in ELLEGREN *et al.* (1993) are assigned to chromosomes *4*, *5* and *3*, respectively.

Coverage of the genome: While the exact size of the porcine genome remains unknown, the presence of only seven unlinked markers in our analyses initially suggests that the 1997 cM reported here covers a majority of the genome. Our results also indicate that there are at least 20 cM between groups that are currently unlinked but located on the same chromosome, *e.g.*, chromosome *13* had two linkage groups detected. There were five more linkage groups than chromosomes identified in this study (24 linkage groups; n = 19). As the unlinked MS are located on chromosomes for which we have other markers, the porcine genome is clearly greater than the 1997 cM reported here; however, if microsatellites are randomly distributed then our data suggest the porcine genome is approximately 2300 cM (J. W. KEELE, unpublished data). Based on length of metaphase chromosomes (ANDERSSON *et al.* 1993), our linkage groups for chromosomes *2*, *3*, *5*, *6*, *7*, *14*, *15* and *X* are not complete. Large gaps are also present in linkage groups, particularly on chromosomes *1*, *7*, *9* and *13*. Marker distribution in the present study was similar to that expected if MS are distributed uni-

TABLE 2

References and chromosomal assignments for anchor loci

Locus name	Type of marker	Chromosome	Type of assignment[a]	Reference
S0082	MS	*1*	LG	ELLEGREN *et al.* (1993)
S0091	MS	*2*	LG	ELLEGREN *et al.* (1993)
APOB	RFLP	*3*	IS	SARMIENTO and KADAVIL (1993) SOLINAS *et al.* (1992a)
S0067, S0073	MS	*4*	LG	FREDHOLM *et al.* (1993)
IFNG	MS	*5*	IS	JOHANSSON *et al.* (1993)
S0003, S0087	MS	*6*	LG	FREDHOLM *et al.* (1992) ELLEGREN *et al.* (1993)
RYR	MS	*6*	IS	HARBITZ *et al.* (1990)
GPI	RFLP	*6*	IS	DAVIES *et al.* (1988) CHOWDHARY *et al.* (1989) YERLE *et al.* (1990)
S0064	MS	*7*	LG	FREDHOLM *et al.* (1993)
TFNB	MS	*7*	IS	CHARDON *et al.* (1991) SOLINAS *et al.* (1992b)
PD6, DQA, DRB	RFLP	*7*	IS	GEFFROTIN *et al.* (1984) RABIN *et al.* (1985) ECHARD *et al.* (1986)
S0069, S0086	MS	*8*	LG	FREDHOLM *et al.* (1993) ELLEGREN *et al.* (1993)
CASK	RFLP	*8*	SA	See text
S0081	MS	*9*	LG	ELLEGREN *et al.* (1993)
S0083, S0090	MS	*12*	LG	ELLEGREN *et al.* (1993)
GH	RFLP	*12*	IS	THOMSEN *et al.* (1990) YERLE *et al.* (1993)
S0084	MS	*13*	LG	ELLEGREN *et al.* (1993)
CH13	MS	*13*	CS	DAVIES *et al.* (1992b)
S0089, ATP2	MS	*14*	LG	ELLEGREN *et al.* (1993)
S0088	MS	*15*	LG	ELLEGREN *et al.* (1993)

[a] Assignment abbreviations are as follows: LG, linkage analysis; IS, *in situ* hybridization; CS, chromosomal specific library.

formly and selected randomly from the genome (WINTERO, FREDHOLM and THOMSEN 1992; DIETRICH *et al.* 1992). As more informative MS derived from cosmid or lambda genomic clones are placed on the linkage and physical maps, MS distribution as well as genomic coverage can be more accurately assessed.

DISCUSSION

We have integrated 334 newly identified MS with 34 MS previously reported, eight MS and seven RFLP associated with type I markers into a skeletal genetic linkage map of the porcine genome. Although comparisons between current linkage results and those previously published are difficult due to the absence of blood typing or serum protein analyses in our study, we were able to compare six intervals in five linkage groups (chromosomes *5*, *6*, *7*, *12* and *14*) where identical markers were used (ELLEGREN *et al.* 1993). Six interval distances were comparable including the distance between the *CRC* (*RYR1*) or malignant hyperthermia locus and *S0087* (chromosome *6*) (ELLEGREN *et al.* 1993). In five additional linkage groups interval distance between identical markers was significantly greater in the present study when compared with that reported by FREDHOLM *et al.* (1993) in a smaller pedigree. The accuracy of marker interval and order will be enhanced as similar sets of markers including erythrocyte antigens and serum proteins are screened across several reference populations.

As the porcine physical map develops, new assignments of genes to chromosomal locations will improve the comparative map between the human, mouse and swine genomes. Our strategy to reduce the randomness of saturating the porcine genome with type II markers is to place more type I markers from established syntenic groups (O'BRIEN *et al.* 1993) in our linkage map and assign porcine cosmid clones containing informative MS by *in situ* hybridization through collaborative efforts. As MS are developed that anchor centromeric and telomeric regions, additional randomly generated MS can be rapidly included into the linkage map, expanding genomic coverage and marker density. A combination of approaches by groups mapping the swine genome should rapidly place a significant number of linked markers on the map. Continued searching of databases will provide type II markers, close to or within type I loci. This overall strategy should provide a saturated linkage

map while yielding a sufficient number of dually mapped loci to accurately assess genomic coverage and chromosomal orientation of linkage groups (FREDHOLM *et al.* 1993).

In summary, the number of MS markers linked in the present swine genetic map will allow us and other investigators to initiate a concerted effort to identify markers which can be used in MAS and provide the frame work for identifying gene(s) that contribute to production efficiency.

The authors wish to acknowledge the contribution of D. B. LASTER whose vision and energy made this effort possible. Thanks to J. WRAY, D. BEHRENS, M. BISHOP, S. KAPPES, R. STONE and S. SUNDEN for helpful discussions, K. SIMMERMAN, R. GODTEL, C. MAHAFFEY and R. SAMSON for technical assistance, S. KLUVER for manuscript preparation, and the MARC swine crew for outstanding husbandry. Special thanks to M. FREDHOLM and L. ANDERSSON for providing primer pairs prior to publication.

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Communicating editor: N. A. JENKINS