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Report of the First Workshop on the Genetic Map of Bovine Chromosome 23

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Summary

A report of the first workshop on the genetic map of bovine chromosome 23 (BTA23) is given. Five laboratories contributed data from 29 loci, including a total 11586 informative genotypes. The combined pedigrees represented 1930 potentially informative meioses. Eighteen of the 29 loci were common to two or more data sets and were used to construct a framework linkage map of BTA23. Twelve of the 18 could be ordered on the linkage map with a likelihood ratio of greater than 1000:1. Thus, a low resolution consensus map was constructed with a high level of support for order. The sex-averaged, female and male maps span 54·5, 52·7 and 55·8 cM, respectively. Sex-specific differences in recombination frequency were identified for eight pairs of framework loci. Average genetic distance between framework loci on the sex-averaged map is 5·0 cM.

Keywords: bovine, BoLA, chromosome 23, framework map, genetic linkage, major histocompatibility complex

Introduction

Genetic maps may differ in several aspects, including the pedigrees used for map construction, the loci mapped, the statistical evidence for locus order and sex-specific map distances. Although individual linkage maps may differ in the relative genetic distances between loci, a primary concern is agreement in gene order. It is therefore important to compare and integrate available maps to arrive at accurate genetic distances and order of loci. Accurate consensus maps of the bovine chromosomes will be useful guides for future mapping studies, identification of genes affecting economic traits and marker-assisted selection strategies.

Interest in BTA23 stems primarily from the localization of the bovine major histocompatibility complex (MHC) to this chromosome (Fries *et al.* 1986). The bovine MHC (BoLA) is of specific interest owing to its critical role in immunity. Comparisons between the available genetic maps of BTA23, particularly in the MHC region, show major differences in gene order and genetic distances for the genes *DRBP1/DRB3*, *CYP21* and *PRL* (Creighton *et al.* 1992; Barendse *et al.* 1994; Bishop *et al.* 1994; Gwakisa *et al.* 1994; van Eijk *et al.* 1995). It is important to resolve these differences between the linkage maps.

Comparative studies of the bovine MHC have revealed a unique class-II gene organization. By contrast to the MHC of other mammals, the bovine class II genes are divided into two distinct subregions separated by a genetic distance of 15 to 30 centimorgans (cM; Andersson *et al.* 1988; Georges *et al.* 1990; van Eijk *et al.* 1993; Park *et al.* 1995). Definition of the genes contained between the class-II gene clusters and the prospect of identifying an unusual recombination 'hot spot' between the class-II subregions (Andersson *et al.* 1988; Jarrell *et al.* 1995; Park *et al.* 1995) require that dense and accurate maps of BTA23 are available. Furthermore, a framework linkage map of BTA23 would facilitate the identification of putative loci associated with economically important traits. As a first step towards accomplishing these goals a collaborative workshop to examine the genetic map of BTA23 was organized.

Materials and methods

Genotype data from five bovine pedigrees were submitted to the workshop-organizing laboratories at CSIRO and the University of Illinois. All data were submitted in a standardized format for use with the linkage analysis program CRIMAP (version 2.4; Green *et al.* 1990). Each

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data set was analysed independently by both organizing laboratories using the TWOPOINT, BUILD, and FLIPS options of CRIMAP. Standard deviations of pairwise recombination frequencies were calculated according to Ott (1991). Chi-square tests for homogeneity between individual maps, sex-specific maps within data sets and sex-specific framework maps were performed according to Ott (1991). Statistical criteria for the construction of the framework map were as described by Keats *et al.* (1991). Briefly, framework loci were defined as a group of loci for which a locus order had an interval support of ≥3·0 or odds of 1000:1 compared with alternative orders.

Data from the International Bovine Reference Pedigrees (IBRP; Barendse *et al.* 1994), USDA Roman L. Hruska U.S. Meat Animal Research Center Bovine Pedigrees (MARC; Bishop *et al.* 1994) and Texas A&M University Angleton Families (TAMU; J. F. Taylor & S. K. Davis, unpublished observations) were analysed using a sex-specific analysis, whereas data from the Illinois Reference/Resource Families (IRRF; Lewin *et al.* 1994; Ma *et al.* 1996) and the Swedish Agricultural University Pedigrees (UPP; Andersson *et al.* 1988) contained segregation information from males only. The CHROMPIC option of CRIMAP was used to identify and eliminate animals having unlikely multiple recombination events, where unlikely recombination events were defined as those occurring more frequently than would be expected based on the product of the pairwise recombination frequencies (θ)of the loci involved. Data from each laboratory were then combined using the MERGE option of CRIMAP and subjected to analyses as described above; however, only loci common to two or more data sets were used in the analyses.

On July 25, 1994 a workshop coinciding with the 24th Meeting of the International Society for Animal Genetics was held in Prague, Czech Republic. Results of the preliminary analyses were discussed at the meeting. Following the workshop, animals identified as problematic with respect to the number of recombination events were reexamined by the submitting laboratories. Corrected data were resubmitted for the final analyses which were performed at the Urbana laboratory as described above.

Table 1. Locus definition and number of informative meioses for submitted loci.

	Pedigree*					
Locus†	IBRP	IRRF	MARC	TAMU	UPP	Total
BOLA-A	–	153	–	–	42	195
C4	–	–	–	–	15	15
CYP21	413	337	183	–	42	975
D23S7 (UWCA1)	173	123	297	–	–	593
D23S10 (CSSM5)	101	182	–	352	–	635
D23S14 (RM185)	353	217	–	340	–	910
D23S18 (BM1905)	–	–	194	345	–	539
D23S19 (BM1443)	–	–	241	261	–	502
D23S20 (BP34)	–	–	54	–	–	54
D23S21 (BM1818)	–	216	325	–	–	541
D23S22 (BM1258)	–	283	260	264	–	807
D23S23 (RM033)	383	–	63	226	–	672
D23S24 (BM47)	–	216	225	218	–	659
D23S25 (CSSM24)	365	42	–	371	–	778
D23S31 (TAMLS113·3)	–	181	–	126	–	307
D23S36 (BM1815)	–	–	303	–	–	303
D23S37 (SMHCC)	392	–	–	–	–	392
DOB	–	–	–	–	13	13
DQ	–	–	–	–	43	43
DRB3	460	371	–	–	43	874
DRBP1	–	–	312	270	–	582
DYA	–	30	–	–	7	37
EAM	–	–	21	94	–	115
F13A	–	43	–	–	–	43
HSP70-1	–	–	61	–	–	61
LMP2	–	62	–	–	–	62
MOG	141	–	–	–	–	141
PRL	213	121	61	224	–	619
VEGF	119	–	–	–	–	119
Totals‡	3113 (2360)	2577 (2290)	2600 (2182)	3091 (2739)	205 (134)	11586 (10340)

* IBRP = International Bovine Reference Pedigrees; IRRF = Illinois Reference/Resource Families; MARC = USDA Roman L. Hruska U.S. Meat Animal Research Center Bovine Pedigrees; TAMU = Texas A&M University Angleton Families; UPP = Swedish Agricultural University Pedigrees.

† Marker descriptions may be found in one or more of the following references: Andersson *et al.* 1988; Barendse *et al.* 1994; Bishop *et al.* 1994; Shalhevet *et al.* 1995; van Eijk *et al.* 1995; Skow *et al.* 1994.

‡ Number in parentheses are totals for the 12 framework loci.

– = Not typed.

Results

Individual maps

Sex-specific linkage maps were constructed using all reported loci from each data set (Table 1; Fig. 1). Female maps were produced for the IBRP, MARC and TAMU data. Map lengths ranged from 41·1–54·5 cM and were dependent on the loci genotyped by the individual laboratories. Male maps were constructed from all five data sets. The UPP linkage map was limited to seven MHC loci and spanned 14·7 cM. The IBRP and TAMU maps were similar in length to their respective female linkage maps. The MARC male linkage

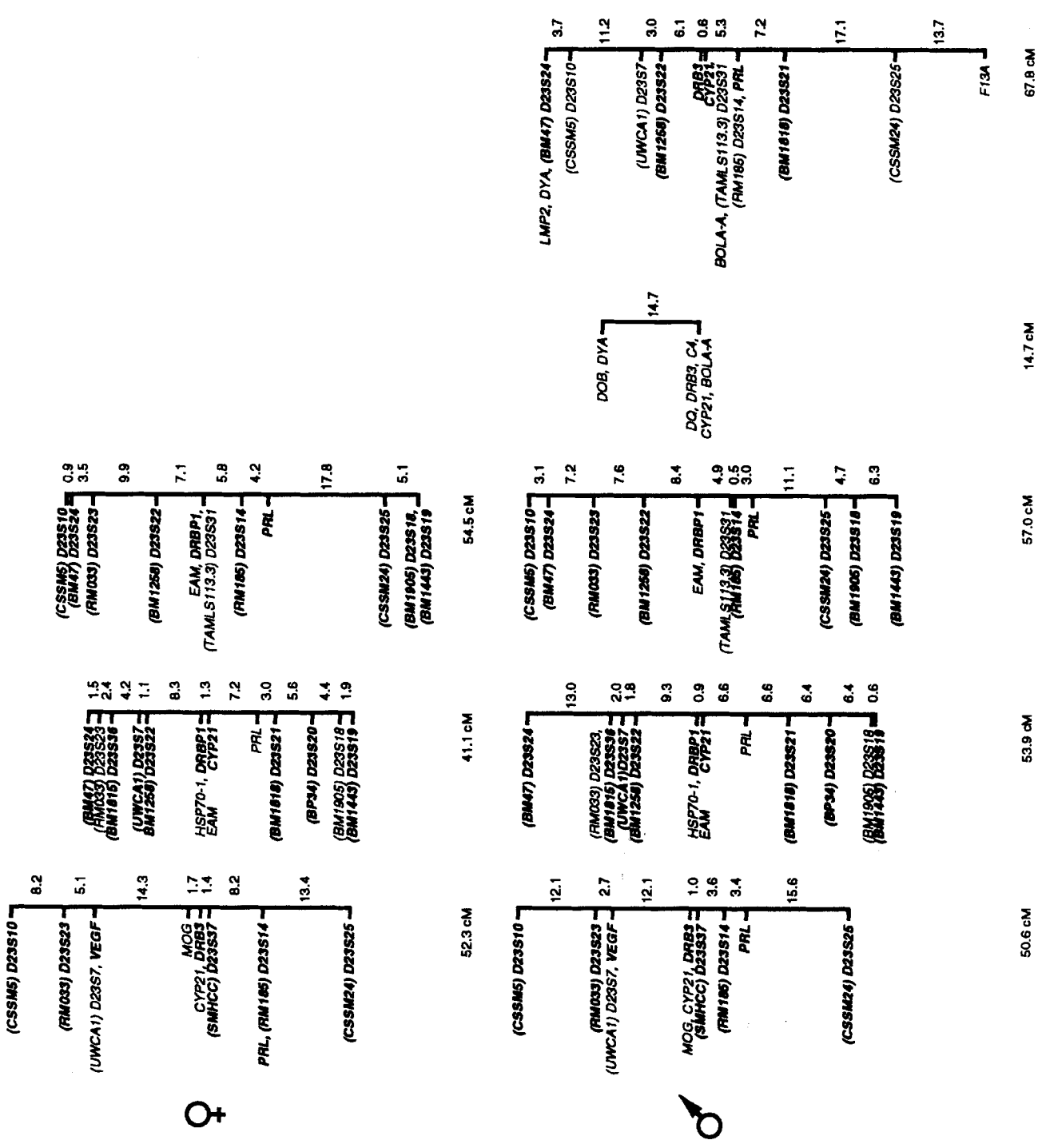

Fig. 1. Genetic maps constructed from analyses of individual data sets. Loci in bold are ordered with likelihood ratio > 1000:1 compared with alternative orders. Maps are aligned at *DRB3* or *DRBP1*.

map was 12·8 cM longer than its female counterpart. The IRRF map was greater in length than all other male maps; however, if *F13A* is excluded, the map spans 54·2 cM between *D23S25* and *D23S24*, similar to the other maps. Tests for homogeneity showed no significant differences in pairwise θ between individual data sets. Tests within the IBRP, MARC and TAMU data sets for homogeneity between sexes revealed significant differences in θ for several intervals (data not shown).

A consensus gene order was reached between maps for loci that were common to two or more data sets. However, a single difference in gene order was identified between the TAMU and IRRF maps. The TAMU gene order is *D23S10-D23S24-D23S22*, whereas the IRRF order is *D23S24-D23S10-D23S22* (Fig. 1). Although statistical support for order in the TAMU map is very strong, support for the IRRF order was sufficient to cause the removal of *D23S10* from the framework map.

Framework map

Combining the individual data sets revealed a total of 29 unique loci submitted by the five participating laboratories (Table 1). Of the 29 loci, genotypes for 18 loci were submitted by two or more laboratories. These 18 loci were used to construct sex-average, female and male framework maps of BTA23. The number of informative meioses for common loci ranged from 37 for *DYA* to 977 for *CYP21* (Table 1). Of the 18 loci, 12 could be uniquely positioned on the linkage map (likelihood ratio > 1000:1; Fig. 2). The sex-average, female and male linkage maps were 54·5, 52·7 and 55·8 cM, respectively (Fig. 2). The average distance between loci on the sex-average map was 5·0 cM.

Sex-specific pairwise θ, standard deviations (SD) and associated LOD scores for the 12 framework loci are given in Table 2. Sex-specific differences in θ were identified for eight pairs of framework loci (Table 2). Two of the pairwise estimates were significantly greater in females while the others were greater in males. The eight intervals that were different between the sexes were consistent with previously identified differences in each of the individual data sets. The two larger female θ were attributable to the IBRP data set (i.e. showed significant heterogeneity between sexes within the data set), whereas two and four of the six larger male θ were influenced by the TAMU and MARC data, respectively.

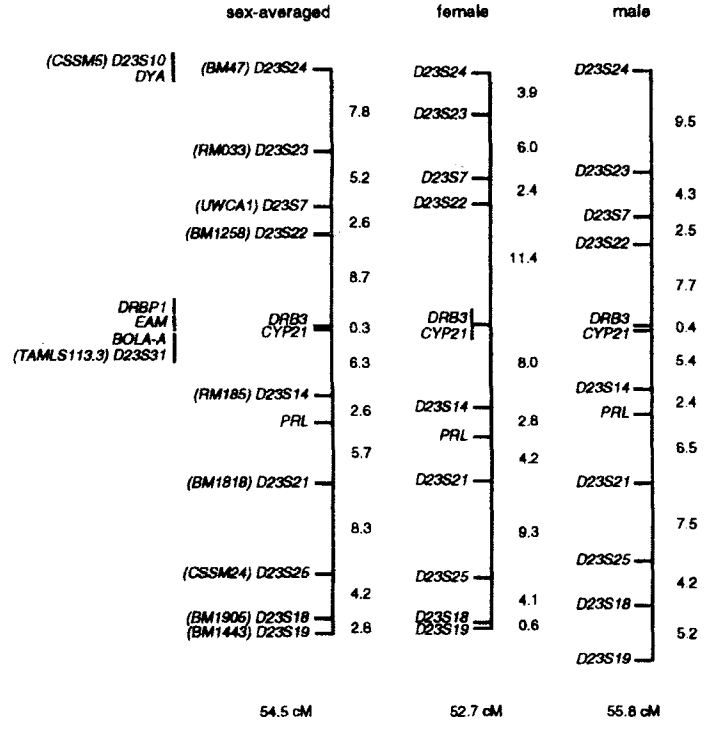

Fig. 2. Sex-averaged, female and male linkage maps of 12 framework loci. The relative locations of 6 additional loci common to two or more datasets are given to the left of the sex-averaged linkage map.

Discussion

Chromosome workshops provide a format to resolve disparities in linkage maps produced by different laboratories. For the human chromosomes, consensus maps have also become an important vehicle for communicating mapping progress to the scientific community as well as providing direction for future mapping efforts. Independently developed linkage maps for most of the bovine chromosomes are currently available, providing impetus for comparison and integration. As a result, the accurate framework linkage maps produced will provide guidance for future research and applications.

Consensus human linkage maps have been constructed from the Centre d'Etude du Polymorphisme Humain (CEPH) pedigrees. In the CEPH collaboration each individual is genotyped in duplicate by different laboratories (Dracopoli *et al.* 1991). The primary advantage of this approach is the minimization of genotyping errors, which increases the accuracy of the map. As a consequence of several independent efforts with different objec-

Table 2. Pairwise recombination frequencies for females (θ_f) and males (θ_m), standard deviations (SD) of θ, maximum LOD scores (Z_{max}) and number of pedigrees contributing to pairwise data for BTA23 framework loci.

Loci	Pedigrees*	θ_f	SD	θ_m	SD	Z_{max}
CYP21-DRB3†	I,R,U	0·00	NE‡	0·01	0·005	167·16
CYP21-PRL	I,M,R	0·04	0·021	0·06	0·012	53·55
D23S7-CYP21	I,M,R	0·14	0·036	0·11	0·021	43·82
D23S7-D23S14§	I,R	0·25	0·063	0·10	0·026	17·29
D23S7-DRB3	I,R	0·09	0·042	0·08	0·018	37·15
D23S7-PRL	M,R,I	0·18	0·051	0·13	0·029	17·28
D23S14-CYP21†	I,R	0·12	0·031	0·07	0·014	60·78
D23S14-D23S25	I,T	0·14	0·019	0·16	0·020	63·21
D23S14-DRB3	I,R	0·10	0·021	0·06	0·014	89·47
D23S14-PRL†	I,R,T	0·04	0·015	0·02	0·008	87·06
D23S18-CYP21	M	0·11	0·060	0·15	0·048	11·03
D23S18-D23S7	M	0·23	0·049	0·33	0·049	6·05
D23S18-D23S14	T	0·25	0·049	0·19	0·027	19·06
D23S18-D23S19†§	M,T	0·01	0·010	0·05	0·014	77·34
D23S18-D23S21	M	0·10	0·030	0·07	0·027	27·63
D23S18-D23S22	M,T	0·30	0·038	0·31	0·031	11·14
D23S18-D23S23	M,T	0·28	0·073	0·35	0·037	3·88
D23S18-D23S25†	T	0·05	0·016	0·05	0·013	67·63
D23S18-PRL	M,T	0·18	0·037	0·19	0·036	17·19
D23S19-CYP21§	M	0·16	0·052	0·34	0·073	7·46
D23S19-D23S7§	M	0·24	0·052	0·41	0·050	4·34
D23S19-D23S14	T	0·26	0·049	0·25	0·039	9·08
D23S19-D23S21§	M	0·07	0·027	0·16	0·035	30·78
D23S19-D23S22	M,T	0·33	0·037	0·33	0·038	8·05
D23S19-D23S25§	T	0·05	0·016	0·12	0·030	43·09
D23S19-PRL	M,T	0·20	0·045	0·26	0·053	9·85
D23S21-CYP21	M,R	0·06	0·038	0·13	0·020	43·13
D23S21-D23S7§	M,R	0·15	0·035	0·25	0·027	22·15
D23S21-D23S14¶	R	NE	NE	0·09	0·022	18·65
D23S21-D23S22	M,R	0·19	0·038	0·19	0·021	32·26
D23S21-DRB3¶	R	NE	NE	0·11	0·023	29·56
D23S21-PRL†	M,R	0·02	0·022	0·04	0·016	29·93
D23S22-CYP21	M,R	0·12	0·037	0·07	0·015	60·78
D23S22-D23S7†	M,R	0·02	0·019	0·02	0·010	70·04
D23S22-D23S14	R,T	0·13	0·035	0·14	0·019	43·60
D23S22-D23S23	M,T	0·10	0·031	0·07	0·025	31·15
D23S22-D23S25	T	0·29	0·042	0·24	0·035	11·40
D23S22-DRB3†¶	R	NE	NE	0·06	0·016	51·67
D23S22-PRL	M,R,T	0·16	0·044	0·11	0·026	29·43
D23S23-CYP21	I,M	0·18	0·033	0·12	0·027	25·21
D23S23-D23S7†	I,M	0·04	0·020	0·02	0·015	32·13
D23S23-D23S14§	I,T	0·27	0·032	0·19	0·021	30·25
D23S23-D23S25	I,T	0·36	0·041	0·31	0·027	9·54
D23S23-DRB3	I	0·17	0·028	0·14	0·024	30·83
D23S23-PRL	I,M,T	0·13	0·051	0·21	0·026	21·08
D23S24-CYP21	M,R	0·14	0·047	0·25	0·026	16·59
D23S24-D23S7	M,R	0·10	0·038	0·14	0·024	29·68
D23S24-D23S14	R,T	0·26	0·050	0·27	0·030	12·33
D23S24-D23S21	M,R	0·28	0·061	0·33	0·029	7·38
D23S24-D23S22	M,R,T	0·09	0·024	0·13	0·018	50·18
D23S24-D23S23†	M,T	0·04	0·019	0·08	0·022	30·62
D23S24-DRB3¶	R	NE	NE	0·20	0·031	11·18
D23S24-PRL	M,R,T	0·29	0·050	0·31	0·042	5·63
D23S25-CYP21	I,R	0·21	0·042	0·17	0·030	17·86
D23S25-DRB3	I	0·22	0·032	0·23	0·033	16·68
D23S25-PRL	I,T	0·15	0·037	0·10	0·017	45·20
PRL-DRB3	I,R	0·09	0·042	0·06	0·016	55·41

* Pedigrees for which data on the locus pair was submitted; I = IBRP, R = IRRF, M = MARC, T = TAMU and U = UPP.
† Adjacent framework loci.
‡ NE = non-estimable.
§ χ^2 for homogeneity between sexes, $P < 0·05$.
¶ no female meioses

tives, bovine consensus maps will probably be constructed using data from different pedigrees genotyped for overlapping sets of loci. An advantage of this type of consensus map is the ability to amass a large number of informative meioses (e.g. Table 1) and thus, not only order the loci but precisely estimate pairwise θ (Table 2). In general, this was true for the BTA23 data. The combined size of five data sets is extremely powerful, having 1930 potentially informative meiotic events. Although the number of pairwise co-informative meioses was far smaller, highly precise pairwise estimates of θ were obtained. In particular, male estimates had smaller associated SD than female estimates. These results were due to the structure of the pedigrees used to construct the map (i.e. large numbers of paternal half-sibs).

The approach of combining several data sets can have limitations. Even with the large number of meioses, only 40 of the 57 pairwise θ were estimated using data from multiple data sets (Table 2). Ideally θ should be estimated using information from more than one data set and from data sets with relatively the same amount of information. A problem associated with estimates from a single data set or when one data set has more information than another is demonstrated in several regions of the framework map. An example is the genetic distance between *D23S18* and *D23S19*. As is clearly shown in Figure 1, the distances between these two loci differ in the MARC and TAMU maps. However, the framework map is overwhelmingly representative of the TAMU data (Figs 1 & 2) although both maps contribute to the estimation of map distance. The TAMU data contains 244 co-informative meioses as compared to the 85 co-informative meioses in the MARC data. Related to this problem is that the θ between some pairs of loci is not directly estimated from any data set, e.g. the recombination frequency between *D23S25* and *D23S21*. Although the IRRF data includes genotype information for both loci, there were no co-informative meioses between them. Exchange of primer pairs between laboratories prior to future workshops should eliminate both of the above problems. Genotyping of the same markers on multiple pedigrees will increase the number of loci that can be placed on framework or consensus maps.

Given the breeding practices used in cattle, genetic improvement is generally influenced more by males than by females. Thus, differences in genetic maps between the sexes may

have implications for their eventual use in marker-assisted selection strategies. Although the lengths of the male and female framework maps of BTA23 are similar (Fig. 2), significant sex-specific differences in pairwise θ were detected in the combined data, addressing the need for determining sex-specific pairwise recombination frequencies. As mentioned previously, sex-specific map differences were directly influenced by the individual data sets. However, common to the three individual sex-specific maps was the general localization of the sex differences. Specifically, increased male recombination was localized towards the telomere, whereas increased female recombination was distributed along the length of the chromosome. These data are consistent with previous observations of differences in θ between the sexes (Dunn & Bennett 1967) and that localization of these differences is also different among the sexes (Dracopoli *et al.* 1991). Differences between the sexes could be due to true differences as a result of variation in θ between pedigrees. However, we cannot rule out the possibility that differences may be due to data errors or weighting of the analysis by one or more of the data sets.

In summary, data from five laboratories were used to construct a framework linkage map of BTA23. Although low in resolution, the genetic distances are accurate and there is a high level of support for gene order that is consistent with the individual data sets. The use of the four major pedigrees in this study to construct future framework and consensus maps of other chromosomes will be very powerful.

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