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A second-generation linkage map of the sheep genome

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Abstract. A genetic map of *Ovis aries* (haploid n = 27) was developed with 519 markers (504 microsatellites) spanning ~3063 cM in 26 autosomal linkage groups and 127 cM (female specific) of the X Chromosome (Chr). Genotypic data were merged from the IMF flock (Crawford et al., Genetics 140, 703, 1995) and the USDA mapping flock. Seventy-three percent (370/504) of the microsatellite markers on the map are common to the USDA-ARS MARC cattle linkage map, with 27 of the common markers derived from sheep. The number of common markers per homologous linkage group ranges from 5 to 22 and spans a total of 2866 cM (sex average) in sheep and 2817 cM in cattle. Marker order within a linkage group was consistent between the two species with limited exceptions. The reported translocation between the telomeric end of bovine Chr 9 (BTA 9) and BTA 14 to form ovine Chr 9 is represented by a 15-cM region containing 5 common markers. The significant genomic conservation of marker order will allow use of linkage maps in both species to facilitate the search for quantitative trait loci (QTLs) in cattle and sheep.

Introduction

Similarity in DNA sequence and microsatellite (ms) locus order among species of ruminant Bovidae were used to develop the current low-resolution genetic map for sheep (232 linked markers; Crawford et al. 1995). Recent genetic maps for cattle (Barendse et al. 1994, 1997; Bishop et al. 1994; Kappes et al. 1997) and goats (Vaiman et al. 1996) developed, in part, with ms of ovine and bovine origin provide further examples of significant homology at individual loci. Information on the similarity of locus order between species is also beginning to emerge (Vaiman et al. 1996). Nineteen ms of ovine origin are included on the IBRP genetic map of cattle (Barendse et al. 1997), 40 on the latest USDA cattle genetic map (Kappes et al. 1997), and 45 on the goat linkage map (Vaiman et al. 1996). In general, locus order appears conserved within the family Bovidae, but discrepancies in linkage group length are apparent (Vaiman et al. 1996), particularly in areas of known rearrangement (Crawford et al. 1995).

A second generation ovine linkage map was constructed primarily with bovine ms. This allowed us to determine whether the degree of similarity in syntenic markers extends to order and interval, in effect creating a framework comparative (linkage) map for the two subfamilies of Bovidae, Bovinae, and Caprinae. Such a map is useful for several reasons. First, using available bovine primers would obviate the expense of developing a large set of random ms of ovine origin. Second, simultaneous construction of linkage maps for the two species, and perhaps even additional closely related species (bison, goat), would be limited only by the degree to which primer pairs would amplify a unique locus across species and the degree of heterozygosity at that locus. Third, numerous aspects of the evolutionary development and divergence of these selected species can be evaluated as additional loci are characterized for marker order and chromosomal location. Finally, the degree to which QTL information is transferable from one species to another within the Bovidae family can be ascertained. The comparative mapping concept of complex phenotypes to orthologous QTL has been clearly demonstrated in cereal grains (Paterson et al. 1995), and comparative analysis among mammalian genomes is progressing (Sonstegard et al. 1997; Sun et al. 1997).

The characterization of >1000 bovine ms loci in sheep was previously reported (de Gortari et al. 1997). In this study, bovine ms were used in a comparative linkage strategy to increase overall coverage and define genetic breakpoints about translocated regions of the sheep genome.

Materials and methods

Data collection. The families used to construct the ovine linkage map have been described previously (Crawford et al. 1995; de Gortari et al. 1997). Briefly, the AgResearch International Mapping Flock (IMF) consists of nine, three-generation full-sib pedigrees with a total of 98 progeny. The USDA reference population (MARC) has 247 backcross progeny produced by mating four F_1 rams (2 Suffolk × Romanov; 1 Rambouillet × Romanov, and 1 Romanov × Rambouillet) to 44 Romanov ewes. Genomic DNA was extracted from white blood cells as described by Miller and associates (1988). Amplification conditions for each primer have been reported (de Gortari et al. 1997). In general, PCR reactions (12 μl) contained 100 ng template DNA, buffer (50 mM KCl, 1.5 mM $MgCl_2$, 10 mM Tris HCl, pH 9.0), 30 μM each of three unlabeled dNTPs, 0.45 μM primer pairs, and 0.35 U Taq DNA polymerase. Radioisotope was incorporated into the PCR product by addition of [α-^{32}P] dATP 0.1 μCi (3000 Ci/mmole) and 3 μM unlabeled dATP. All amplification conditions included an initial denaturing step of 3 min at 94°C, followed by 30 cycles of 1 min at 94°C, 1 min at the annealing temperature, and 1 min at 72°C. Final extension was for 4 min at 72°C. Reaction products were electrophoresed (40 V/cm) on 7% denaturing polyacrylamide gels with a standard M13mp18 ladder and visualized by autoradiography. Some primer pairs were genotyped preferentially across families of informative sires. Primer sequences not previously reported in Crawford and colleagues (1995) and Freking and coworkers (1997) are referenced in de Gortari and associates (1997) or Kappes and collaborators (1997). When two sets of primer pairs for the same locus were genotyped, the locus name first published was used. Genotypes were independently scored twice and discrepancies resolved.

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Data analysis. The linkage map consists of 402 bovine, 101 ovine, and 1 cervine microsatellites. Loci other than microsatellites included 7 ovine RFLP, 2 bovine proteins, 2 ovine proteins, and 4 erythrocyte antigens. Markers were placed into linkage groups based on two-point lod (≥3.0) scores, and the linear order was determined by maximizing the likelihood function within each group by multi-point linkage analysis (CRI-MAP v. 2.4; Green et al. 1990). Markers were added to the linkage groups in decreasing order of informative meioses. Genotypic data from Crawford and colleagues (1995) were merged by genotyping 154 of the markers in both reference populations. Inspection of two-point linkage information and the cattle linkage map were used to identify potential genotypic errors for markers that inflated the linkage group >20 cM. The CHROMPIC option was used to identify unlikely recombination events. Genotypes contributing to these events were amplified and scored a second time to resolve discrepancies and errors. On OAR1, 2, and 7, the linkage groups were divided in order to run the analysis. Common linkage group lengths were calculated from the current map and the USDA MARC cattle map (Kappes et al. 1997), with the two most external common markers used for each linkage group. Three-hundred and seventy of 504 ms (73.4%) are common to the MARC bovine map and the ovine map reported here. Ten additional polymorphic markers with ovine data remain unlinked (lod <3.0; meioses range, 12–261).

Results

Map development. In total, 519 markers were linked (485 intervals) on this second-generation genetic map. The map integrates 262 (51%) markers developed at MARC, with 257 (49%) markers from international sources. The two combined reference populations have the potential to produce 760 informative meioses. The mean number of informative meioses per marker was 197 (range 12–624). The autosomal map spanned ~3063 cM. Individual autosomal linkage groups averaged 19 markers (range 8–48) and 117.8 cM (range 49.2 cM, OAR25 to 298 cM, OAR1), as displayed in Table 1. The X Chr had 22 linked ms covering 126.9 cM (female specific). Average interval between adjacent linked markers was ~6.4 cM with 55.5% of the intervals <5 cM and only 3.8% >20 cM. There were 512 unique loci (Table 1). Five loci were described by two sets of primer pairs for the same microsatellite (TGLA58, OAR3, 79.2 cM; MAP2C, OAR11, 102.3 cM; INRA035, OAR12, 98.4 cM; HMH1R, OAR19, 79.5 cM; BOLA-DRB1, OAR20, 34.9 cM). One locus (HBB, OAR15, 50.5 cM) was described by two sets of microsatellite primer pairs and a protein polymorphism. Nineteen microsatellite markers derived from bovine sequences were mapped to ovine chromosomes (Freking et al. 1997), but not placed on the current bovine linkage map (Kappes et al. 1997). Table 1 also illustrates the species source and type of markers used to construct each linkage group.

Although map resolution remains modest (average interval 6.4 cM) and is likely to remain so for the immediate future, we attempted to identify the number of observed double recombinants within .20-cM intervals in each linkage group. The 17 double recombinants identified suggest that either the error rate was low or at this level of resolution we are not yet able to rigorously identify genotypic errors (Rohrer et al. 1996; Kappes et al. 1997). Figure 1 illustrates the 27 linkage groups of the current map. Additional information (primary sequence, annealing temperature, number and size of alleles, etc.) about each locus may be obtained at http://sol.marc.usda.gov. All 26 autosomes are oriented with respect to the chromosome (top is p arm for OAR1–3 and centromere for OAR4–26) either by direct physical assignment in sheep or indirectly through the homologous bovine chromosome (Kappes et al. 1997; Lopez-Corrales et al. in preparation).

Conservation of microsatellite markers. Genomic conservation among Bovidae allowed extensive use of ms developed in the bovine. Mean heterozygosity of the 519 markers linked in this ovine map was 68.9% when calculated from the eight F_1 sires representing the IMF and MARC pedigrees. However, the mean heterozygosity of a larger sample of bovine-derived autosomal ms in sires of the IMF and MARC ovine families was 45.3% (de Gortari et al. 1997) compared with 60.1% in the sires and dams of the MARC cattle reference population (Bishop et al. 1994). The number of ms in common with a homologous bovine linkage group totaled 370, with a range of 5 to 22 common ms. Twenty-seven of these ms were derived from sheep and the remaining 343 derived from bovine sequences. The common markers span 2866 cM (sex average) in sheep and 2817 cM in cattle. Marker order within a linkage group was consistent between species with limited exceptions. The three metacentric chromosomes in sheep, OAR 1, 2, and 3, are homologous to BTA1 and 3, BTA 2 and 8, and BTA 5 and 11, respectively. The translocation of the telomeric end of BTA9 to BTA14 in sheep (OAR9), previously reported by Crawford and coworkers (1995), is represented by a 15-cM region containing 5 common markers. Figure 2 presents the comparative linkage between BTA9 (the nontranslocated region) and its homolog OAR8. Marker order was inverted only eight times (>2-cM intervals) when the sheep map was compared with the cattle linkage map developed by Kappes and colleagues (1997). The length of the inversions ranged from 3 to 57 cM. The majority of these are probably not true inversions, but result from a low number of coinformative meioses that prevented rigorous ordering of loci. Finally, 6 ms (BMS66, OAR3; BMS719, OAR4; BM3627, OAR7; BM4439, OAR8; BMS2840, OAR16; HEL6, OAR23) mapped to sheep linkage groups other than the expected homolog (OAR23, 12, 2, 15, 5, 1, respectively). This was probably owing to amplification of closely related sequences flanking a second locus,

Table 1. Characteristics of the ovine linkage map.

Chromosome Number	Number of Unique Loci	Linkage Group Length (cM)	Number of Bovine ms	Number of Ovine ms	Number of Other Markers
1	50	298.0	38	11	1[a]
2	40	280.9	32	8	
3	42	293.3	36	7	
4	18	129.2	11	7	
5	17	147.0	14	3	
6	21	144.5	14	3	4[b]
7	19	139.3	18	1	
8	20	111.0	19	1	
9	20	106.8	16	4	
10	14	77.5	8	4	2[c]
11	13	126.1	13	1	
12	17	113.6	18	0	
13	14	128.9	10	4	
14	8	80.3	7	1	
15	16	93.2	16	1	1[d]
16	17	93.7	12	5	
17	22	86.2	13	6	3[e]
18	19	97.0	13	4	2[f]
19	19	81.0	16	4	
20	17	64.3	11	6	1[g]
21	14	68.5	9	4	1[h]
22	14	72.8	12	2	
23	8	51.1	7	1	
24	11	65.9	8	2	1[i]
25	9	49.2	5	4	
26	11	63.5	7	4	
X	22	126.9	19	3	
Total	512*	3,189.7	402	101	16

[a] Ovine protein polymorphism.
[b] Ovine RFLP (2); bovine polymorphism; bovine erythrocyte antigen (EAA).
[c] Ovine RFLP; bovine EAB.
[d] Bovine protein polymorphism.
[e] Ovine RFLP (3).
[f] Bovine EAM; ovine protein polymorphism.
[g] Bovine EAC.
[h] Red-deer (cervine) microsatellite.
[i] Ovine RFLP.
* Six loci represented by more than one marker.

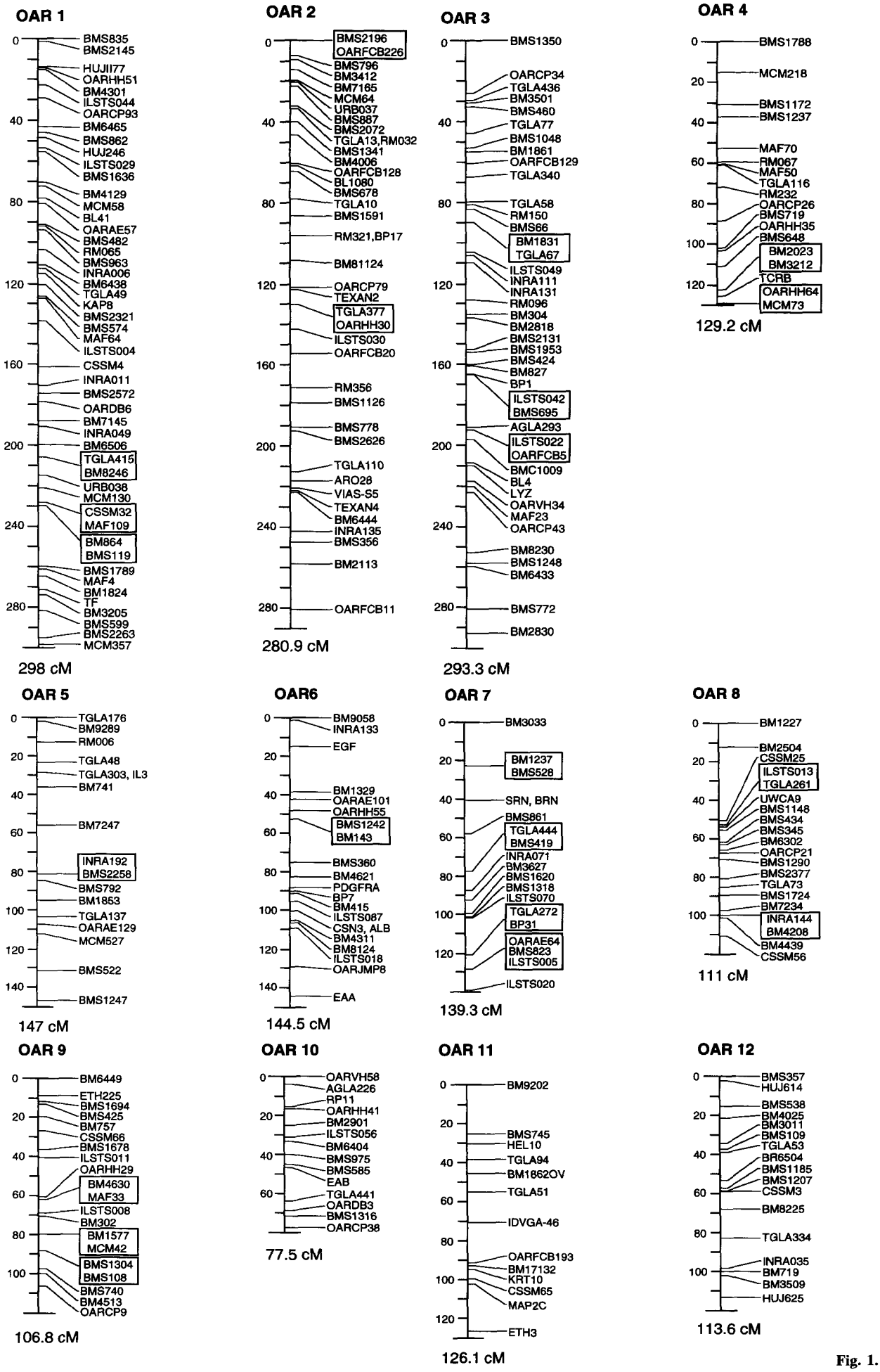
OAR 1
0 BMS835 BMS2145
HUJII77 OARHH51 BM4301 ILSTS044 OARCP93
40 BM6465 BMS862 HUJ246 ILSTS029 BMS1636
BM4129 MCM58 BL41 OARAE57 BMS482 RM065 BMS963 INRA006
80 BM6438 TGLA49 KAP8 BMS2321 BMS574 MAF64 ILSTS004
120 CSSM4 INRA011 BMS2572 OARDB6 BM7145 INRA049
160 BM6506 TGLA415 BM8246 URB038 MCM130 CSSM32 MAF109
200 BM864 BMS119 BMS1789 MAF4 BM1824 TF
240 BM3205 BMS599 BMS2263 MCM357
280
298 cM
OAR 2
0 BMS2196 OARFCB226 BMS796 BM3412 BM7165 MCM64 URB037 BMS887 BMS2072 TGLA13,RM032 BMS1341 BM4006 OARFCB128 BL1080 BMS678
40 TGLA10 BMS1591 RM321,BP17 BM81124
80 OARCP79 TEXAN2 TGLA377 OARHH30 ILSTS030 OARFCB20
120 RM356 BMS1126 BMS778 BMS2626 TGLA110 ARO28 VIAS-S5 TEXAN4 BM6444 INRA135 BMS356 BM2113
160 OARFCB11
200
240
280
280.9 cM
OAR 3
0 BMS1350 OARCP34 TGLA436 BM3501 BMS460 TGLA77 BMS1048 BM1861 OARFCB129 TGLA340
40 TGLA58 RM150 BMS66 BM1831 TGLA67 ILSTS049 INRA111 INRA131 RM096 BM304 BM2818 BMS2131 BMS1953 BMS424 BM827 BP1
80 ILSTS042 BMS695 AGLA293 ILSTS022 OARFCB5 BMC1009 BL4 LYZ OARVH34 MAF23 OARCP43
120 BM8230 BMS1248 BM6433 BMS772 BM2830
160
200
240
280
293.3 cM
OAR 4
0 BMS1788 MCM218 BMS1172 BMS1237 MAF70
20 RM067 MAF50 TGLA116 RM232 OARCP26 BMS719 OARHH35 BMS648 BM2023 BM3212 TCRB OARHH64 MCM73
40
60
80
100
120
129.2 cM
OAR 5
0 TGLA176 BM9289 RM006 TGLA48 TGLA303, IL3 BM741
20 BM7247 INRA192 BMS2258 BMS792 BM1853 TGLA137 OARAE129 MCM527
40 BMS522 BMS1247
60
80
100
120
140
147 cM
OAR6
0 BM9058 INRA133 EGF BM1329 OARAE101 OARHH55 BMS1242 BM143 BMS360 BM4621 PDGFRA BP7 BM415 ILSTS087 CSN3, ALB BM4311 BM8124 ILSTS018 OARJMP8
20 EAA
40
60
80
100
120
140
144.5 cM
OAR 7
0 BM3033 BM1237 BMS528 SRN, BRN BMS861 TGLA444 BMS419 INRA071 BM3627 BMS1620 BMS1318 ILSTS070 TGLA272 BP31 OARAE64 BMS823 ILSTS005 ILSTS020
20
40
60
80
100
120
139.3 cM
OAR 8
0 BM1227 BM2504 CSSM25 ILSTS013 TGLA261 UWCA9 BMS1148 BMS434 BMS345 BM6302 OARCP21 BMS1290 BMS2377 TGLA73 BMS1724 BM7234 INRA144 BM4208 BM4439 CSSM56
20
40
60
80
100
111 cM
OAR 9
0 BM6449 ETH225 BMS1694 BMS425 BM757 CSSM66 BMS1678 ILSTS011 OARHH29 BM4630 MAF33 ILSTS008 BM302 BM1577 MCM42 BMS1304 BMS108 BMS740 BM4513 OARCP9
20
40
60
80
100
106.8 cM
OAR 10
0 OARVH58 AGLA226 RP11 OARHH41 BM2901 ILSTS056 BM6404 BMS975 BMS585 EAB TGLA441 OARDB3 BMS1316 OARCP38
20
40
60
77.5 cM
OAR 11
0 BM9202 BMS745 HEL10 TGLA94 BM1862OV TGLA51 IDVGA-46 OARFCB193 BM17132 KRT10 CSSM65 MAP2C ETH3
20
40
60
80
100
120
126.1 cM
OAR 12
0 BMS357 HUJ614 BMS538 BM4025 BM3011 BMS109 TGLA53 BR6504 BMS1185 BMS1207 CSSM3 BM8225 TGLA334 INRA035 BM719 BM3509 HUJ625
20
40
60
80
100
113.6 cM

Fig. 1.

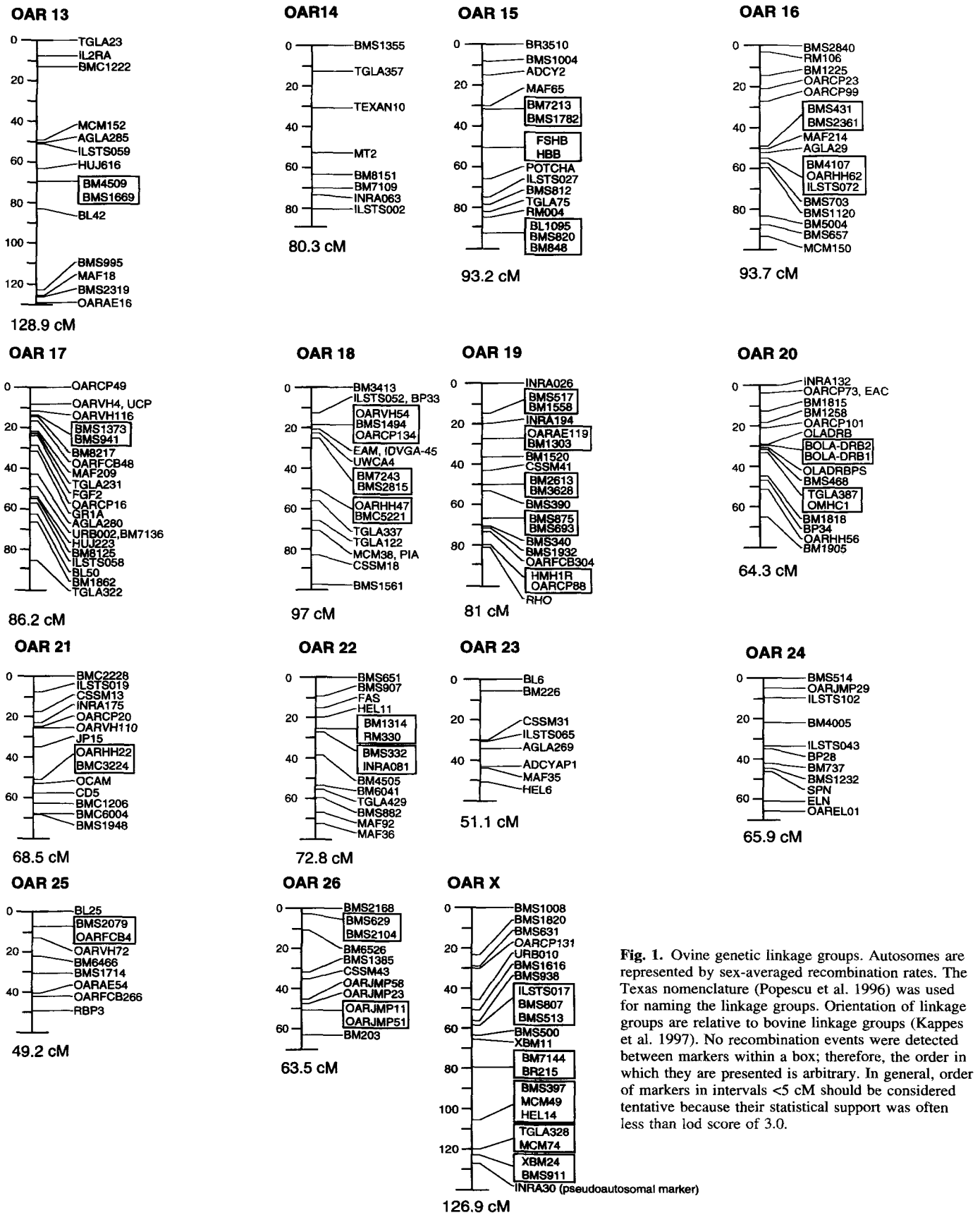

Fig. 1. Ovine genetic linkage groups. Autosomes are represented by sex-averaged recombination rates. The Texas nomenclature (Popescu et al. 1996) was used for naming the linkage groups. Orientation of linkage groups are relative to bovine linkage groups (Kappes et al. 1997). No recombination events were detected between markers within a box; therefore, the order in which they are presented is arbitrary. In general, order of markers in intervals <5 cM should be considered tentative because their statistical support was often less than lod score of 3.0.

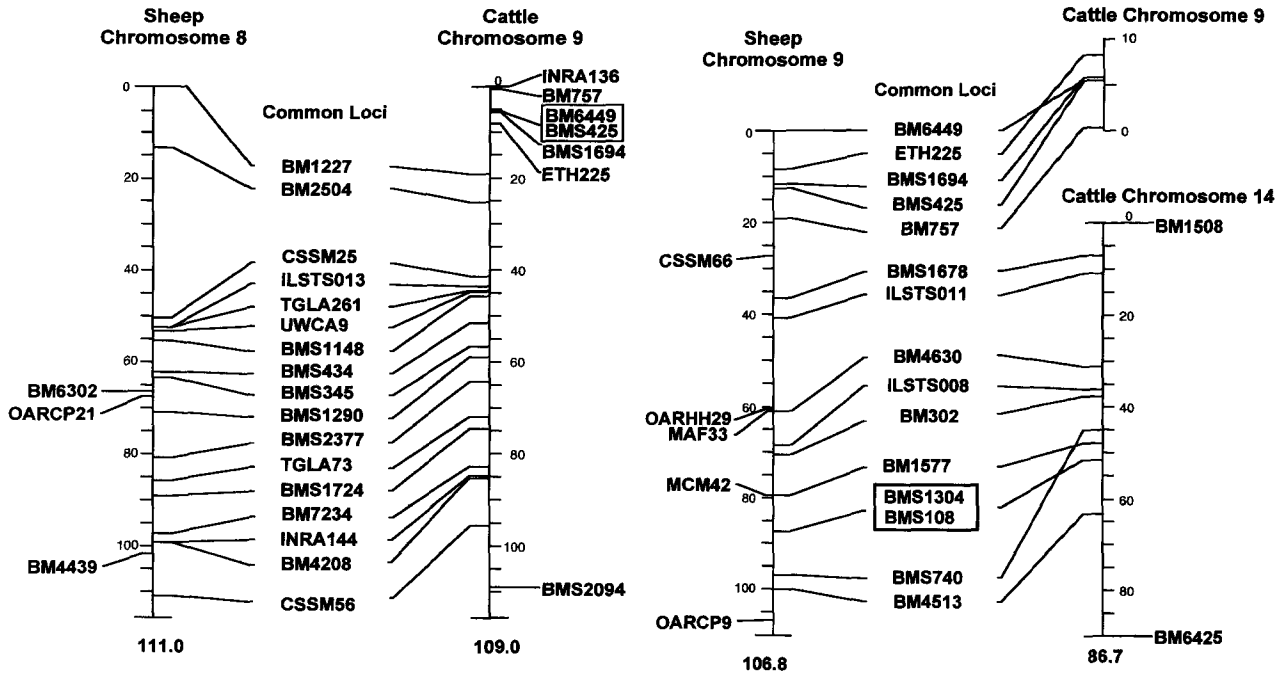

Fig. 2. Current resolutions of the previously reported translocation (Crawford et al. 1995). Ovine linkage groups for Chr 8 and 9 with the homologous bovine linkage groups (Chrs 9 and 14). Loci listed in the center of the linkage groups are common to both maps.

rather than a translocation, because sizes of amplified products were not always consistent across species.

This conservation of marker order and interval is likely to extend to other species within the Bovidae. de Gortari and associates (1997) reported that 67% of bovine primer pairs amplifying a locus in sheep (40% of the 1036 tested) were polymorphic, a value similar to that reported by Vaiman et al. (1996) for the goat. Seventy-seven of 166 (46%) bovine ms that were polymorphic in the goat (Vaiman et al. 1996) are present on the current ovine map.

Discussion

The present map, which includes the genotypes from the IMF flock (Crawford et al. 1995), more than doubles the number of linked ovine markers, increases coverage by ~1000 cM, and consolidates linkage groups to one per chromosome compared with the initial map (Crawford et al. 1995). Our use of bovine ms to construct the initial linkage map for sheep indicated that ~50% of bovine markers were informative, and this information formed the basis for the current map. The ovine map includes 402 bovine primer pairs out of the 504 (80%) linked ms. The current map represents a considerable improvement in resolution (average interval 6.5 cM) and suggests that the overall genetic length of the sheep genome is similar to the bovine genetic length of 2990 cM estimated from 1250 linked markers reported by Kappes et al. (1997). However, the length of the sheep map reported here is less than the length of the bovine map of 3710 cM estimated from 703 linked markers reported by Barendse and coworkers (1997) and considerably less than the bovine genome length (>4000 cM) estimated by Ferretti and associates (1997). Our current estimate of the sheep map length (3190 cM) is closer to the minimum size (~2750 cM) predicted from the Chapman and Bruere (1977) chiasmata data, the estimate for goats provided by Vaiman and coworkers (1996) of 3250 cM including the X Chr, and the chiasmata data of Logue and Harvey (1978) for cattle (~2500 cM) and goats (2485 cM). Chromosome ends are not taken into account in predicting genetic length from chiasmata data; therefore, these values are likely to be biased downward.

At the current level of map resolution, attempts to reduce inflation through continuous checking for genotypic errors with options such as CHROMPIC and comparison of family recombination rates to identify errors at the parental and grandparental level are essential. Direct physical assignment of markers at the ends of individual linkage groups, as reported by Heaton and colleagues (1997) and Lopez-Corrales and collaborates (in preparation), will also help provide a robust estimate of coverage as maps develop.

The genomic conservation between cattle and sheep apparently extends to other members of the Caprinae. Although Vaiman and associates (1996) reported several differences in the location of individual ms between the (male) goat map and cattle and sheep maps, some of these loci were probably the result of amplification of a nonhomologous sequence by heterologous primers, similar to that noted in this report for sheep and cattle. However, in some cases, flanking regions of microsatellites were found by Vaiman and colleagues (1996) to be highly similar when sequenced, yet mapped to nonhomologous chromosomes. This suggests the possibility of a rearrangement(s) between goat and either cattle or sheep. Vaiman and coworkers (1996) discussed the evidence supporting a translocation event from goat Chrs 9 to 14 in relation to bovine Chrs 9 and 14. This translocation event is consistent with the event reported in sheep (Crawford et al. 1995). Markers that are monomorphic in the species in which the markers were developed are still potentially useful in linkage map development of other closely related species. This report describes 19 bovine-derived markers not mapped in cattle. These assignments (in sheep) should be interpreted with caution owing to amplification of closely related flanking sequences as discussed above. As homologous loci, these microsatellites may be of value for future marker development upon identification of regions containing QTL across Bovidae.

Concurrent map-based searches for QTL in various livestock species would be enhanced by the development of comparative maps. Evidence of QTL mapping for similar phenotypes to corresponding homologous locations among different cereal grain species has provided strong evidence to suggest orthologous genes were involved in the evolution of these relevant phenotypes (Pa-

terson et al. 1995). This conservation of gene order provides a biological basis for comparative analysis of complex phenotypes among livestock species. The high degree of genomic conservation and ability of heterologous primers to amplify microsatellite loci that maintain a conserved order yield expectations of similar QTL being identified across species. This expectation has particular relevance toward QTL that display more variability in one species than in another, affecting how easily the QTL can be detected. Complex phenotypic traits such as prolificacy, resistance to disease, feed intake, and carcass composition may be investigated in sheep at less cost and over shorter time frames and still have relevance to genetic variability in cattle.

In conclusion, the current sheep map represents a significant increase in resolution that will ultimately enhance the detection of quantitative trait loci for production traits as well as disease susceptibility. It provides an additional set of bovine markers that will undoubtedly prove useful in the development of a comparative linkage map of the Bovidae and, perhaps, other closely related families within the Artiodactyla.

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