Genet. Sel. Evol. 32 (2000) 441–457

Original article

Cytogenetical anchoring of sheep linkage map and syntenic groups using a sheep BAC library

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(Received 7 September 1999; accepted 14 March 2000)

Abstract – In order to simultaneously integrate linkage and syntenic groups to the ovine chromosomal map, a sheep bacterial artificial chromosome (BAC) library was screened with previously assigned microsatellites using a sheep-hamster hybrid panel and genetic linkage. Thirty-three BACs were obtained, fluorescently labelled and hybridised on sheep-goat hybrid metaphases (2n = 57). This study allowed us, (i), to anchor all linkage groups on sheep chromosomes, (ii), to give information on the probable position of the centromere on the linkage map for the centromeric chromosomes, (iii), to contradict the previous orientation of the ovine X linkage group by the mapping of *BMS1008* on OARXq38. Concerning our somatic cell hybrid panel, this study resulted in the assignment of all the previously unassigned groups to ovine chromosomes and a complete characterisation of the hybrid panel. In addition, since hybridisations were performed on a sheep-goat hybrid, new marker/anchoring points were added to the caprine cytogenetic map.

mapping / microsatellite / sheep / BAC library / FISH

Résumé – Ancrage cytogénétique de la carte de liaison et des groupes de synténie par utilisation d'une banque de BAC ovine. Afin d'intégrer, la carte génétique et les groupes de synténies à la carte chromosomique ovine, nous avons criblé, à l'aide de microsatellites, une banque ovine de chromosomes artificiels de bactéries (BAC). Les microsatellites utilisés font partie de la carte de liaison ovine et ont été localisés précédemment dans notre panel d'hybrides somatiques hamster-mouton. Nous avons isolé 33 clones BAC, marqués en fluorescence et hybridés sur métaphase d'un hybride chèvre-mouton (2n = 57). Les résultats de cette étude ont

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apporté plusieurs informations. Au niveau de la carte génétique, ces localisations ont permis l'ancrage des groupes de liaison sur les chromosomes ovins et de donner la position la plus probable du centromère sur les groupes de liaison correspondant aux chromosomes métacentriques. De plus, pour le chromosome X, la localisation du microsatellite *BMS1008* a permis de corriger l'orientation du groupe de liaison. Au niveau de notre panel d'hybrides somatiques hamster-mouton, ces résultats ont permis d'assigner cytogénétiquement tous les groupes de synténies à un chromosome ovin, aboutissant à une caractérisation approfondie du panel. Enfin, en utilisant des métaphases d'hybride chèvre-mouton pour les hybridations *in situ*, nous avons pu ajouter de nouveaux marqueurs et points d'ancrages sur la carte chromosomique caprine.

cartographie / microsatellite / mouton / banque BAC / FISH

1. INTRODUCTION

The first gene maps established in domestic animals were based on the use of somatic cell hybrid panels from pigs [14], sheep [7,20,34] and cattle [17, 42]. Later on, PCR, in combination with microsatellites, made it possible to construct linkage maps for domestic animals. Linkage maps with variable coverage of the genome are now available for these species: *e.g.* 95% coverage in sheep [12], 95% in cattle [4], 88% in goats [35], 96% in pigs [33] and 50% in horses [24]. We previously described the regional characterisation of a sheep-hamster somatic cell hybrid panel by PCR using primers for genes or microsatellites mainly chosen from sheep and goat linkage maps [39]. Indeed, an essential issue for establishing comprehensive genome maps is establishing a connection between linkage and cytogenetic maps. Such a connection has already been carried out for all linkage groups in goats and cattle by physical mapping of 124 and 38 markers, respectively [13,35]. However, in sheep, integration of linkage and chromosomal maps has not been achieved systematically for all linkage groups. Some chromosomes were intensively studied: for instance, the linkage group for chromosome 6 which includes the Booroola *Fec*B mutation, was assigned to OAR6q33-qter by *in situ* localization of *PDEB6B* gene [23,25]. Similarly, for the chromosome 2 linkage group, *NRAMP1*, a gene controlling infection by intracellular pathogens was localised on 2q41 [26,29]. Linkage groups corresponding to autosomes 11, 12, 16, 22, 23, 25 and 26 were solely assigned using somatic cell hybrid without physical localization and no connection was carried out for sexual linkage groups.

Large insert DNA libraries, recently available for species of agricultural interest, makes it possible to rapidly isolate large clones compatible with Fluorescence *in situ* hybridization (FISH) studies. A sheep BAC library has recently been constructed and organised in a pool/superpool format [41]. Using BACs isolated from this library, we report on the first complete integration of linkage and cytogenetic sheep maps and assignment of all syntenic groups to ovine chromosomes.

2. MATERIALS AND METHODS

2.1. Sheep BAC library

DNA from a ram brain with the genotype VRQ/VRQ (V: valine 136, R: arginine 154, Q: glutamine 171) at the *PRNP* locus was used for the construction of a sheep BAC library which is over three genome equivalents [41]. It contains 90 000 clones distributed in 39 superpools themselves organised in rows, columns, and plate pools. The average insert size has been estimated by Field Inverted Gel Electrophoresis (FIGE) at 123 kb.

2.2. BAC library screening and FISH mapping

The sheep BAC library was screened with microsatellite primers selected from the sheep and goat linkage maps (Tab. I). The addresses of single BAC clones were identified by PCR on 5 μL of DNA from superpools or pools in 10 μL reaction volume, with 0.5 units of Goldstar Taq DNA Polymerase (Eurogentec), in the buffer supplied with 2 mM $MgCl_2$, 2% deionised formamide and 0.2 mM of each dNTP either in a Perkin-Elmer Cetus 9600 or an MJ thermocycler. Minipreps of positive clones were then prepared using previously described procedures [36]. To evaluate the insert size and DNA concentration, BACs were digested with *Not*I and run for 16–18 h on a 1% agarose gel in a FIGE mapper apparatus (Bio Rad) using a ramp time of 5–15 s and 110 V in one orientation and 170 V in the other.

Metaphase spreads were prepared from cells obtained from a primary fibroblast cell culture derived from a 57 chromosome, XX sheep goat hybrid [11]. Induction of R banding was carried out by addition of 5-bromo-2-deoxyuridine to the medium at a final concentration of 10 $\mu g \cdot mL^{-1}$ during the second half of the S-phase [16]. Biotinylation of the BAC DNA (200 ng) was achieved either by random priming or by nick translation in the presence of biotine-11 dUTP as previously described by Bahri Darwich *et al.* [3]. Band identification of the R-banded ovine chromosomes was based upon ISCNDA [19] recommendations and Texas nomenclature [32].

3. RESULTS AND DISCUSSION

Among the 36-microsatellite primer pairs tested by PCR in the sheep BAC library, 34 resulted in amplification and two (chromosome X microsatellites) were not found. Most annealing temperatures were at 55 °C, with some variations at 53, 56, 57 or 58 °C for a better DNA amplification. The number of positive superpools varied, from 1 to 4.

Addresses were determined for 34 microsatellites, leading to the identification of 34 BACs. These BACs were localised by observation of the hybridisation signals on both homologous sheep and goat chromosome pairs (Fig. 1 and Tab. II). One BAC clone was chimerical and displayed two signals on two different chromosomes due to the insertion by the vector of two non-adjacent genomic DNA fragments.

Table I. Microsatellites used to isolate BAC clones.

Locus	Forward primer (5′ → 3′)	Forward primer (5′ → 3′)	PCR product (bp)	Reference primers
BMS1008	CCGATATGTATAGTGTTCCCCT	CCTGGTCAAAAAATTAGAAGGA	120	[38]
BMS1172	TGAACCTGTATGAATTCCCTTC	TACTGAATTTAGGAGCCCTCAG	110	[38]
BMS1232	AGCCTTCAGTCTAGGTCAGGG	TTGCCAAATACGAATAAACGC	160	[38]
BMS1290	TTGGCACTTACTACCTCATATGTT	TTTTCTGGATGTTGAGCCTATT	140	[38]
BMS1304	TCCAAAAACTCAACCTTAGCC	TGATCCCTGGTCTAGAACCTAA	125	[38]
BMS1316	CCTTCATGGAAGAAATTTTGTG	GGAGTTACAGTCCATGGGTTC	120	[38]
BMS1341	CCTACCTACTGCACAGTTTTGC	CTCCCATATAAGTTACCCACCC	130	[38]
BMS1669	CTGCAGGGAACCTAAAGTGC	GCCTATGTTCTGCACACTGC	110	[21]
BMS1678	TCTTCTCTGCACTTTGGTTGC	ATAGCTGACATCCACTGGGC	160	[38]
BMS1948	AACACAGGGAAGTGTGTTTTTAA	GACAGTTTGTGGTGTGGAGAC	90	[38]
BMS2104	TGCCACGTCATCTTTTGAAG	GCAAGTTTGCAGGTTCTATGC	150	[38]
BMS2321	TCACTTCACAAAATACACAATGC	CCAAACTCCATAATCACCACTT	150	[21]
BMS2355	TATGAAGAGGAATGAAGGGAGA	CATTTTCAATGTGAGAGTGTCAA	130	[21]
BMS2815	TGATATTCAAACTCAATGAACCC	CTTGCATATGCTCATCATTATCA	100	[21]
BMS356	ACCTCAGAGATGACGCAAGG	TTGAAGTTTTTGTGCTGTTTGG	100	[38]
BMS360	ACAAAACCACTTTCTTAGCAAACA	CTGGGTCTTCATGGTAGGGA	120	[38]
BMS460	TGCCCCATAGTGTAGTGCTC	GCCAGCAGAGAATTGTAGCA	120	[38]
BMS517	ACTTATGGGTGAGCTCCAGTG	AGCTCTCATTGTCCACTCACTC	200	[38]
BMS522	CTTGCTTACTGCTTGCTATGAA	CCCAACAAAATTTCTGATTCTC	120	[38]
BMS528	CTCACTCCACTGGGCTTCTC	TGTGTTCTCACCTCGACCAC	150	[38]
BMS538	TGCTCAGTTATGCTTGAGAGTC	TCCAAGTTGAGCCTTAGTTCTT	140	[38]
BMS820	CCACTACTTGCCTCAGGGAG	ACAGGACTCTCAAGCATCAGC	120	[38]
BMS882	TAGTGTCCACCAGAGACCCC	CCAAAGACACAGTTTAAAGGGC	100	[38]
BMS963	GGAGGATGAAGGAGTCTTTGG	AATTTACCACAGTCCACCGC	120	[38]
ETH03	GAACCTGCCTCTCCTGCATTGG	ACTCTGCCTGTGGCCAAGTAGG	100	[40]
HUJ625	AGCAGCATGAAGAGAGTCCC	GAGGTCACATACCCATCAAGC	200	[37]
ILSTS65	GCTGCAAAGAGTTGAACACC	AACTATTACAGGAGGCTCCC	100	[22]
LSCV09	CTTTACCTTCTGCTGAATATG	GAAGGCTCATTGGCAATTAAC	200	[35]
MCM150	CCACTTGGAGTGAAAATGAGACA	AGGAAAATCTTCCGGAGCTAAAC	110	[18]
OARCP16	CTGCAATAACCCTTAACCTCTGCTTAC	GTGTGAAGAATAGAGGGCTGGTAGC	110	[10]
OARCP73	AAAACTGAGAAATATTCAGATGCAAC	TAAACGTCCATCAACAGAGGAAGGG	200	[10]
OARFCB04	TTTGAAAATAAGCTGGAGAGGCACAGG	AGGCATTTCCAGTCCACCCCACCC	100	[6]
TGLA231	GCTGCAAAGAGTTGGACAGAACTGAGC	CTCCATTTCCCTTTGGTTTGTAAAGAC	110	[10]

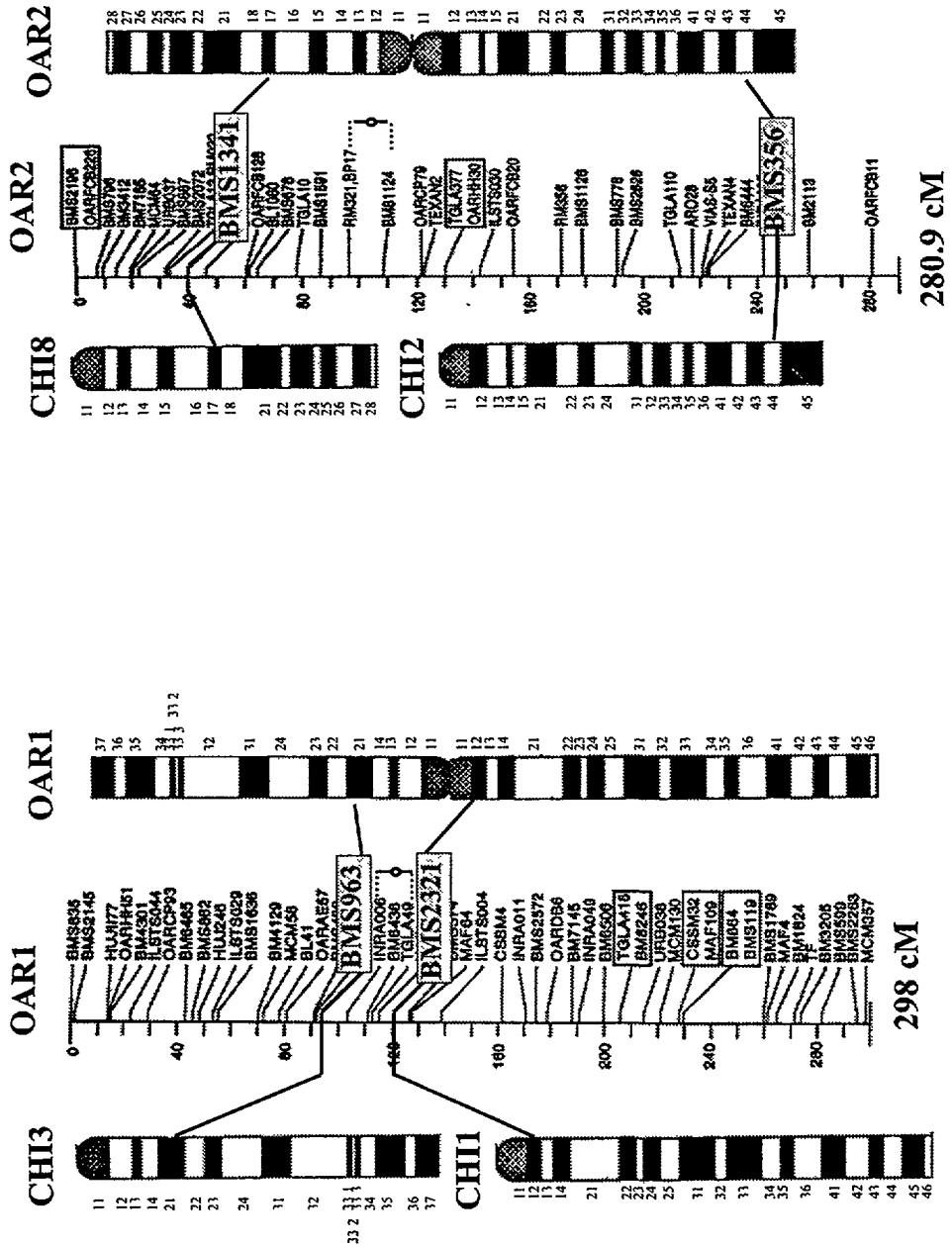

Figure 1. Integration of linkage and chromosomal maps in sheep. The markers analyzed in this study are inside the open grey boxes. The sheep linkage map is from de Gortari [12]. Chromosomes are drawn on the right of each linkage group. Lines connect microsatellites of the linkage group to the chromosomal band. In goats, only the number of the chromosome is indicated except the homologous sheep chromosome 1, 2, 3 and X. Dotted lines indicate previously localised markers used for linkage group orientation. Probable position of the centromere ϕ is indicated for the three sheep metacentric chromosomes. *(continued on the next pages)*

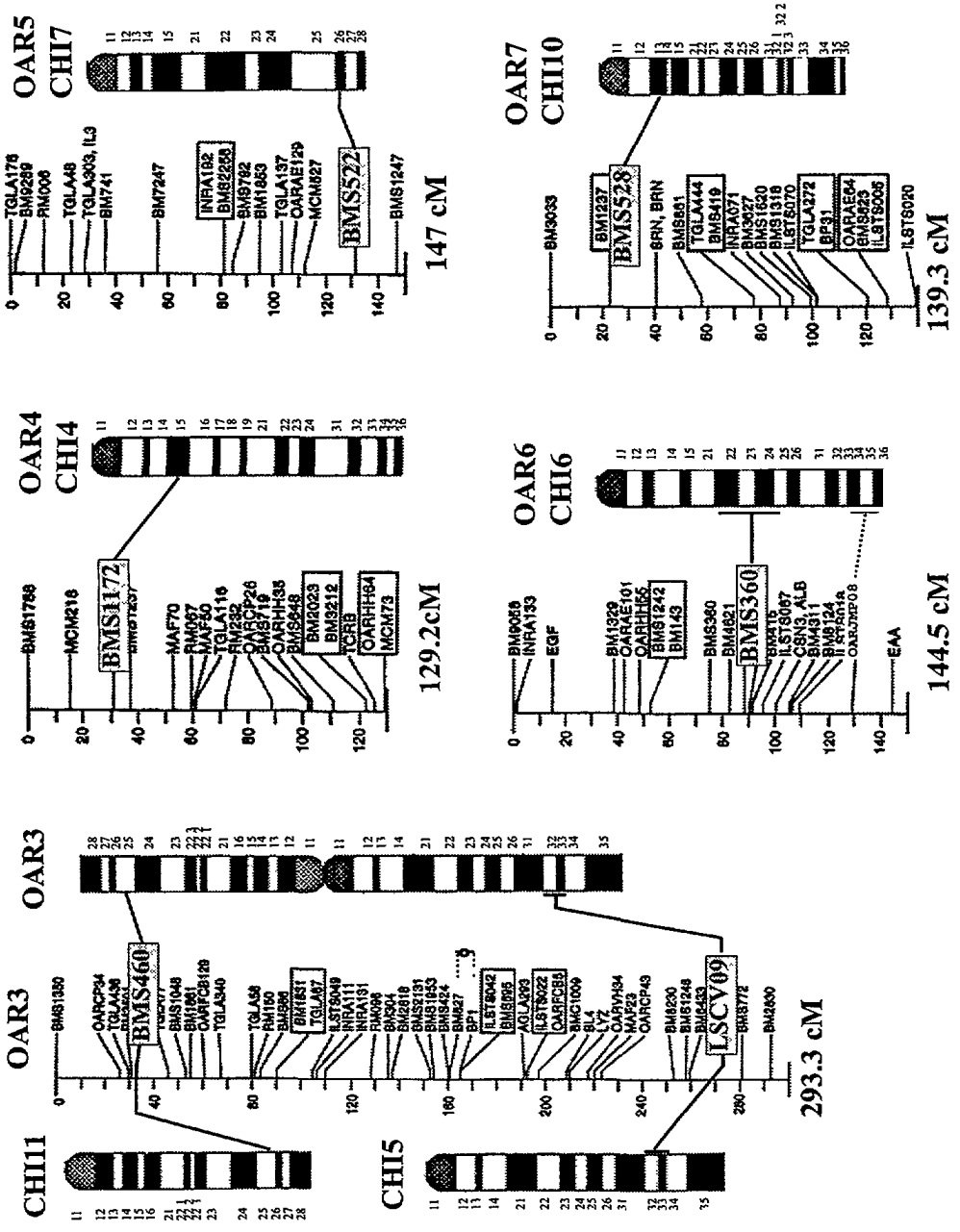

Figure 1. Continued.

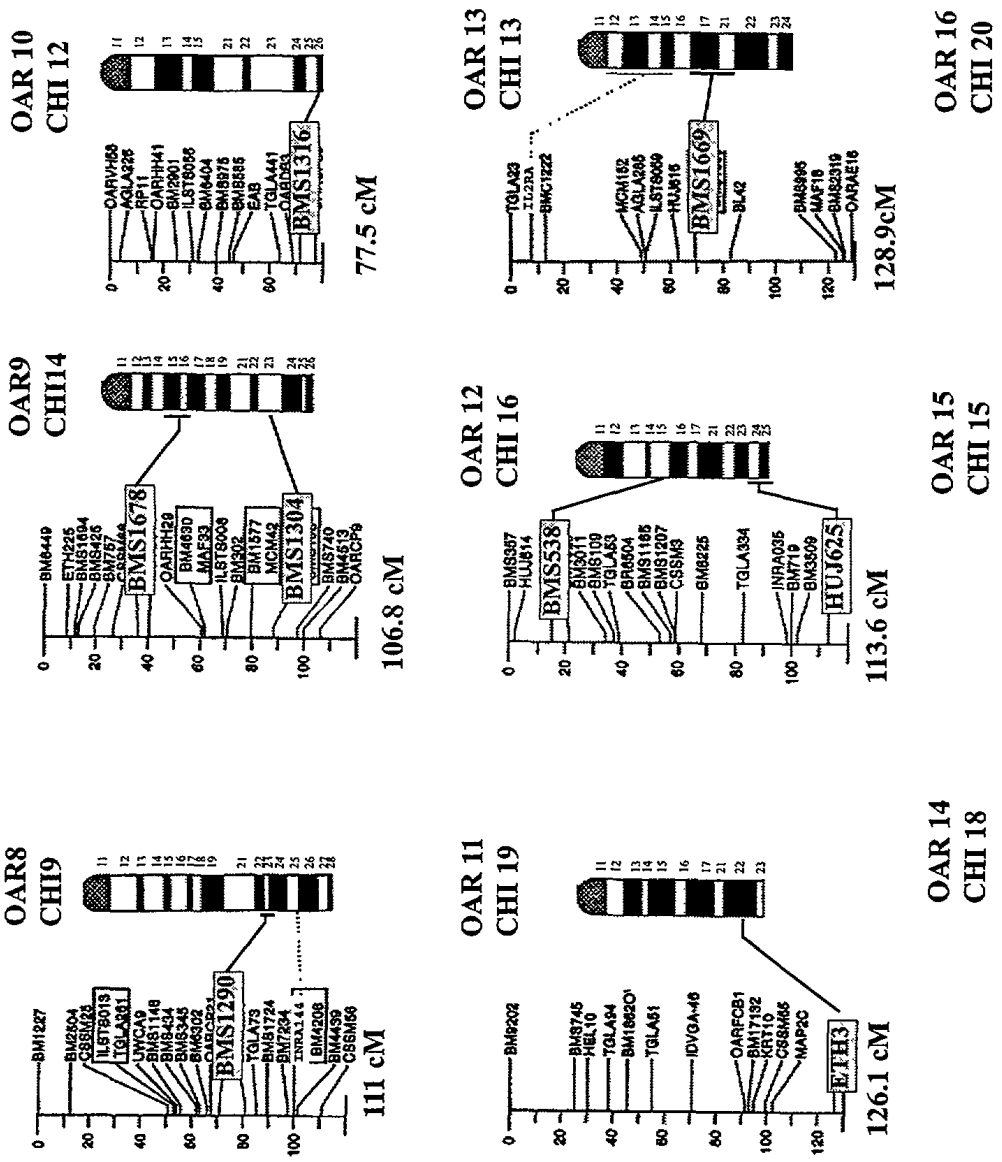

Figure 1. Continued.

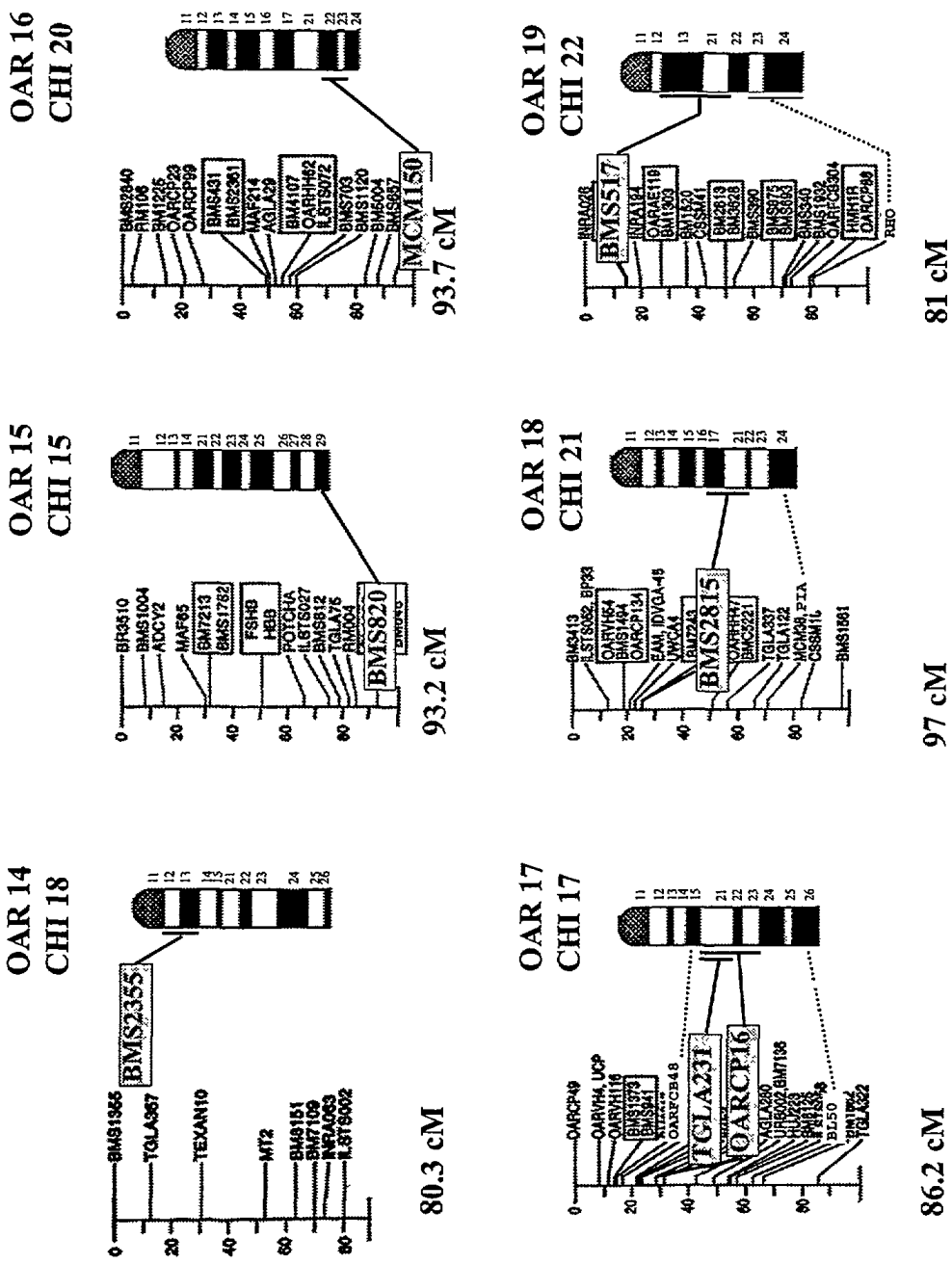

Figure 1. Continued.

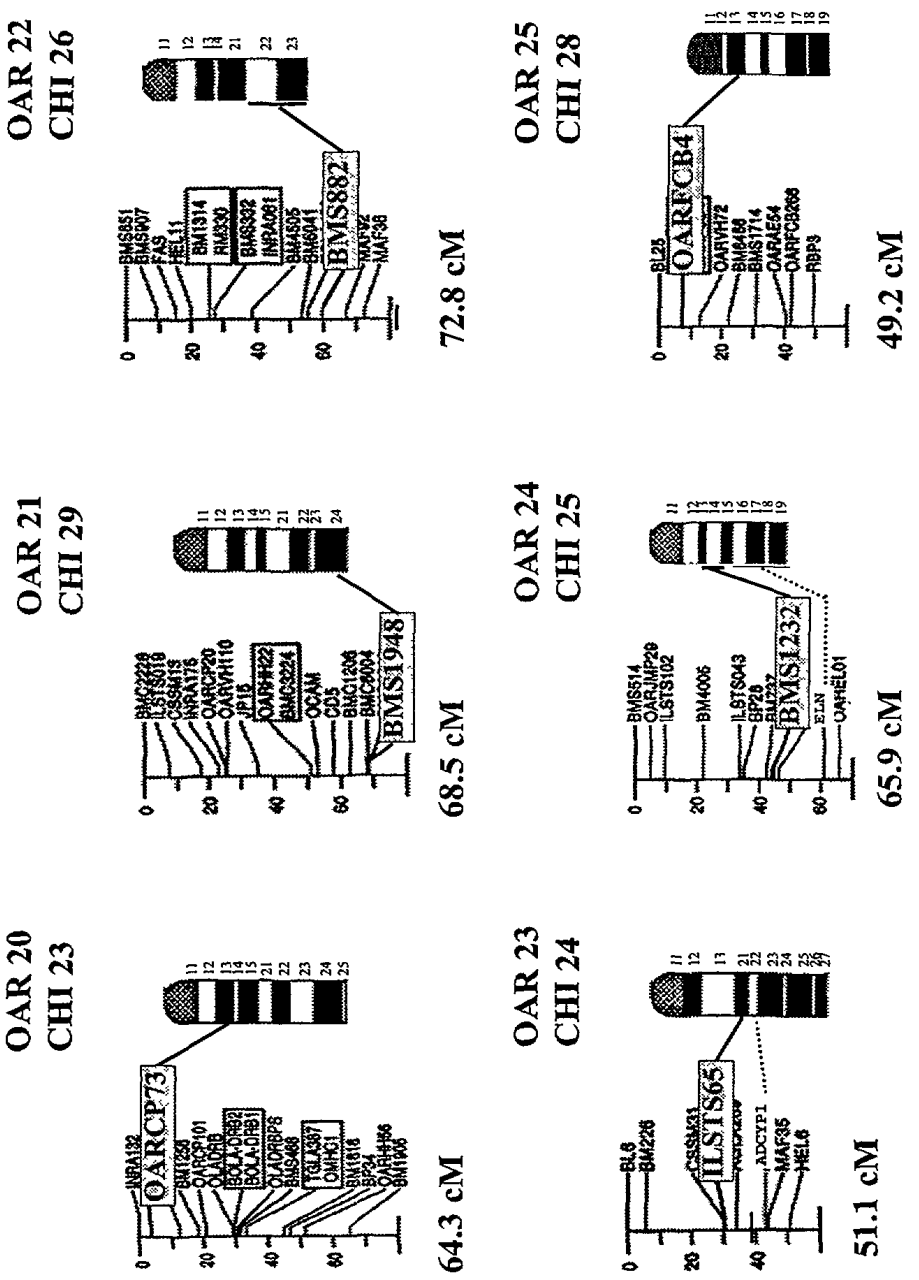

Figure 1. Continued.

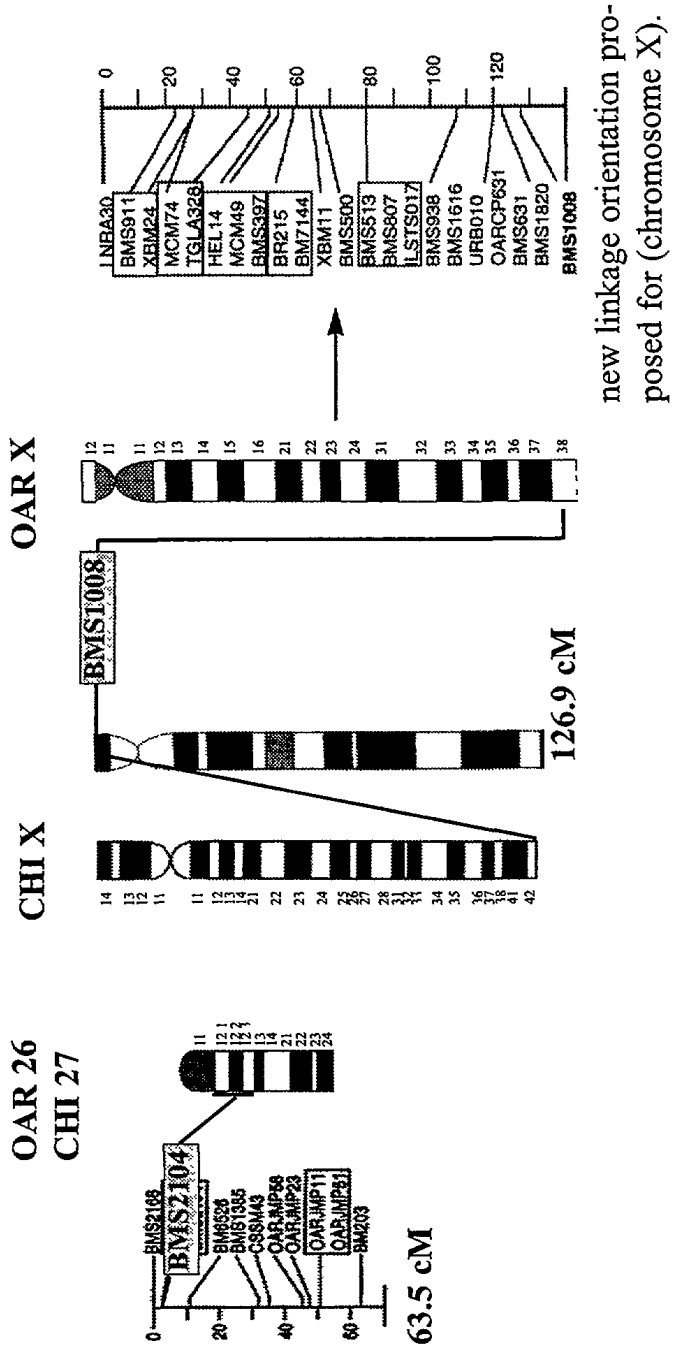

Figure 1. Continued.

Table II. Hybridisation results in sheep and goats; markers used for linkage group orientation.

Markers	Localisation (This study)		Previous anchoring points		
	Sheep	Goat	Markers	Localisation	References
BMS963	1p21	3q21			
BMS2321	1q12	1q12			
BMS1341	2p17	8q17			
BMS356	2q44	2q44			
BMS460	3p25	3q32-33			
LSV09	11q25	5q32-33			
BMS1172	4q15	4q15			
BMS522	5q26	7q26			
BMS360	6q22-24	6q22-24	*OARJMP08*	6q34-35	[28]
BMS528	7q13	10q13			
BMS1290	8q22-23	9q22-23	*INRA144*	CHI9q25	[35]
BMS1304	9q23	14q23			
BMS1678	9q15-16	14q15-16			
BMS1316	10q26	12q26			
ETH3	11q22	19q22			
BMS538	12q15	16q15			
HUJ625	12q24-25	16q24-25			
BMS1669	13q17-21	13q17-21	*IL2RA*	13q12-15	[2]
BMS2355	14q13	18q13			
BMS820	15q29	15q29			
MCM150	16q22-23	20q22-23			
OARCP16	17q21	17q21	*OARFCB48*	CHI17q15	[35]
TGLA231	17q21	17q21	*BL50*	CHI17q26	[35]
BMS2815	18q17-21	21q17-21	*PIA*	CHI 21q24	[35]
BMS517	19q13-21	22q13-21	*RHO*	19q23-qter	[1]
OARCP73	20q13	23q13			
BMS1948	21q24	29q24			
BMS882	22q23-23	26q22-23			
ILST65	23q21	24q21	*ADCYP1*	CHI 24q22	[34]
BMS1232	24q13-14	25q13-14	*ELN*	24q16-qter	[5]
OARFCB4	25q17	28q17			
BMS2104	26q12	27q12			
BMS1008	Xq38	Xq42			

For the goat species, this study resulted in the chromosomal localisation of 33 sheep BAC clones, 29 of them being cytogenetically localised for the first time and seven of them being assigned to chromosome bands not yet defined by any marker. We also confirmed the localisation of *BMS2355* and *OARCP73*, two markers previously assigned on CHI18q12–13 and CHI23q13 respectively [35], and we anchored two genetic markers, *LSCV09* and *HUJ625* on CHI5q32–33 and 16q24–25, respectively.

In sheep, the 26 autosomal linkage groups were anchored to sheep chromosomes by one or two markers. Although the microsatellites *LSCV09* and *BMS2355* have not been genetically localised in sheep, their position on the goat map, close to markers mapped in both species, makes it possible to consider them as anchoring points on the sheep map. For the other autosomes, localisation of microsatellites led to direct anchoring of the sheep genetic and cytogenetic maps.

Linkage groups are unambiguously orientated on sheep chromosomes 1, 2, 3, 9 and 12 by means of the localisation of two microsatellites. However, for OAR17 the colocalisation of two microsatellites *TGLA231* and *OARCP16* gave no indication on the orientation of the corresponding linkage group. However this linkage group was previously orientated in goats by the localisation of *OARFCB48* and *BL50* [35], suggesting a similar orientation in sheep. Linkage groups 4, 5, 7, 10, 11, 14, 15, 16, 20, 21, 22, 25 and 26 were also unambiguously orientated by localising a single microsatellite close to one of the chromosome ends.

Two out of the three X chromosome microsatellites were not found in the BAC library. Since this library was constructed from a ram, sequences from the X chromosome were understandably under-represented. Similar observations were obtained while screening for X-specific sequences from a goat BAC library [30,36]. The localisation of *BMS1008* in the terminal band of Xq arm for both sheep (OARXq38) and goats (CHI Xq42) modifies the published orientation of the X sheep linkage group. Then, based on this result, *INRA30* would probably be localised near the centromere. This *INRA30* microsatellite was found in the pseudoautosomal region (PAR) of the X chromosome in both sheep and cattle [12,31]. In cattle, it was assigned to the distal end of the long arm of the X chromosome at q42-ter [43]. Comparative studies between the cattle and goat X chromosome using bovine X-specific painting probes or *in situ* hybridisation of chromosome X clones have revealed that the PAR is situated in the terminal part of the bovine X long arm and in the tiny short arm of the caprine X chromosome [30, 31]. Our proposition that the *INRA30* microsatellite might be close to the centromere is in agreement with the position of the PAR region in goats and similarly in sheep. Our localisation in sheep and goats is consistent with these results and suggests a similar X chromosome organisation for both species.

The cytogenetic assignation of BACs containing microsatellites made it also possible to predict the centromere position in the linkage groups corresponding to the large ovine metacentric chromosomes 1, 2 and 3. For chromosome 1, the assignment of *BMS963* and *BMS2321* on both sides of the centromere localised it in a small region, less than 30 cM wide. Moreover, comparative linkage mapping data with cattle reduced this interval to less than 10 cM, *i.e.*, between *INRA006* (BTA3) and *TGLA49* (BTA1). Similarly, the centromeres corresponding to OAR2 and OAR3 were in a 10.8 cM interval *i.e.*, between *RM321* (BTA8) and *BM8124* (BTA2) and in a 3.5 cM interval *i.e.*, between *BM827* (BTA11) and *BP1* (BTA5), respectively. The interval distances were calculated from the data available on USDA sheep map through the World Wide Web site (http://sol.marc.usda.gov/genome/sheep).

Table III. Direct assignment of syntenic groups to ovine chromosomes in our sheep-hamster cell hybrid panel.

Syntenic groups Chromosomes	Loci
U1 : OAR12q15	*HUJ614-**BMS538**-FH-PEPC-ENO1-IDVGA68-PGD-HUJ625*
U8 : OAR8q22–23	*INRA127-BM2504-CGA-**BMS1290**-ME1-PGM3*
U9 : OAR1817–21	*MPI–INRA60-INRA103-BMS1494-**BMS2815**-CHRNA7-INRA31-IGHM-MCM38-MCM131*
U13 · OAR21q24	*LDHA-IDVGA07-**BMS1948***
OAR 4q15	*BMS1788-MCM218-**BMS1172**-BMS1237-MAF70-MAF50-MILVET07-OARHH35-BCP-MCM73-OARHH64*
OAR 7q13	*LSCV27-**BMS528**-BMS861-INRA69-NP-CYP19-INRA37-PKM2-ILSTS05-OARAE64*
OAR 9q23	*ETH225-INRA136-ILSTS11-ILSTS08-BM302-**BMS1304**-MCM63-OARCP09*
OAR 10q26	*BMS2252-BMS712-INRA51-EDNRB-BMS585-INRA05-**BMS1316**-TGLA28*
OAR 16q22–23	*BM1225-BMS2361-MAF214-INRA36-LSCV08-BMS1120-**MCM150***
OAR 19q13–21	*INRA26-BM1558-**BMS517**-INRA194-MILVET8-BMS390-BMS875-MCM111-GPX1*
OAR 22q22–23	*BMS651-BMS907-INRA81-**BMS882**-MAF92-MAF36*
OAR 23q21	*TGLA351-BMS2526-CSSM31-**ILSTS65**-MAF35-BMS1332-MCM136*
OAR 24q13–14	*HBA-RM74-BM4005-TGLA40-**BMS1232**-MCM136*
OAR 25q17	***OARFCB4**-IDVGA8-INRA61-TGLA306-MILSTS78-BMS1714*
OAR 26q12	***BMS2104**-BM6526-LSCV40-INRA183-CSSM43-OARJMP58*
OAR Xq38	*DVEPC76-DVEPC14-**BMS1008***

U: unassigned loci. Markers localised by FISH on sheep chromosomes are in bold, other markers were analysed previously [39]. Order of loci within a syntenic group is given according to their position on sheep map or cattle/goat maps.

The cytogenetic localisation of four microsatellites made it possible to assign U1, U8, U9 and U13 on OAR12, OAR8, OAR18, and OAR21, respectively. Moreover, 12 other syntenic groups, previously assigned to sheep chromosomes according to ruminant comparative mapping data, are now directly anchored to ovine chromosomes (Tab. III). Up to now, 130 fragments containing from 1 to 7 markers have been identified in our panel [39]. Among these fragments, 39 containing a marker mapped in sheep were assigned to chromosome regions. The localisation of 52 other fragments has been based on the bovine or caprine cytogenetic mapping because of the chromosome homologies between ruminant chromosomes.

Saturated type II linkage maps are now available for ruminant species, and should be assigned to chromosomal maps in order to evaluate their physical dimension and allows species comparison maps. The main goal of such combined maps is to facilitate the identification of QTL (Quantitative Trait Loci) chromosome regions. In ruminants, QTL search for various traits such as milk production [15], roan coat color [9], muscle hypertrophy [8], or sheep fecundity [27] has already started. Whenever similar regions are detected in humans or in mice, comparative mapping data will help transfer information from the model species to ruminants, based on regionally characterised somatic cell hybrids.

ACKNOWLEDGEMENTS

The authors acknowledge the financial support from the "Projet CMEP 96 MDU 361". Special thanks to Dr Laurent Schibler for providing technical support and advice. We thank Dr Patricia Berthon (Laboratoire de génétique et immunité, INRA, Nouzilly, France) for suggestions and English corrections of the manuscript. Sheep-hamster somatic cell hybrids DNA is freely distributed upon request to K. Tabet-Aoul (tabet@biotec.jouy.inra.fr).

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