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An advanced sheep (Ovis aries, 2n = 54) cytogenetic map and assignment of 88 new autosomal loci by fluorescence in situ hybridization and R-banding

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Summary

Presented herein is an updated sheep cytogenetic map that contains 452 loci (291 type I and 161 type II) assigned to specific chromosome bands or regions on standard R-banded ideograms. This map, which significantly extends our knowledge of the physical organization of the ovine genome, includes new assignments for 88 autosomal loci, including 74 type I loci (known genes) and 14 type II loci (SSRs/microsatellite marker/STSs), by FISH-mapping and R-banding. Comparison of the ovine map to the cattle and goat cytogenetic maps showed that common loci were located within homologous chromosomes and chromosome bands, confirming the high level of conservation of autosomes among ruminant species. Eleven loci that were FISH-mapped in sheep (B3GAT2, ASCC3, RARSL, BRD2, POLR1C, PPP2R5D, TNRC5, BAT2, BAT4, CDC5L and OLA-DRA) are unassigned in cattle and goat. Eleven other loci (D3S32, D1S86, BMS2621, SFXN5, D5S3, D5S68, CSKB1, D7S49, D9S15, D9S55 and D29S35) were assigned to specific ovine chromosome (OAR) bands but have only been assigned to chromosomes in cattle and goat.

Keywords cytogenetic map, FISH-mapping, gene, nomenclature, sheep.

Introduction

Cytogenetic maps, available for several domestic ruminants, are useful tools for studying complex animal genomes and chromosome evolution among bovid species (Piumi et al. 1998; Robinson et al. 1998; Di Meo et al. 2000; 2002; 2005; Iannuzzi et al. 2000a,b; 2001a) and between bovid species and humans (Schibler et al. 1998a; Di Meo et al. 2000; 2002; 2006; Iannuzzi et al. 2000b; 2001a).

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Assignment of individual genes and markers to the physical map allows the identification of rearrangements within conserved chromosome segments that have been designated using chromosome painting probes (Hayes 1995; Iannuzzi et al. 1998; 1999), as well as defines the complex rearrangements that differentiate humans and bovids. Other practical applications of these maps are in clinical cytogenetics, to better define the chromosomal rearrangements and abnormalities that may be involved in abnormal phenotypes (Iannuzzi et al. 2001b; Pinton et al. 2005). Cytogenetic maps are also essential for anchoring linkage and RH maps to specific chromosome regions and to define the order and orientation of linkage groups for which there is poor evidence from the RH and linkage mapping data (Gautier et al. 2002).

Although many loci have been assigned to cattle, sheep and goat genomes by linkage and RH mapping, a relatively small percentage of loci have been physically located to single chromosomal regions or bands. Unfortunately, very
few studies have used both RH and FISH data for confirmation of RH-map construction across whole chromosomes or specific regions (Gautier et al. 2002).

The only cytogenetic map for sheep is available through SheepBase (http://www.thearkdb.org/species.html). This map includes a few well-positioned markers, but uses an old ideogram that differs from that reported in the latest standard chromosome nomenclature (ISCNDB 2001). A more detailed cytogenetic map covering all chromosome regions and constructed on the basis of the latest international chromosome nomenclature (ISCNDB 2001) is still lacking in this very important species.

In this study, a new and advanced cytogenetic map of sheep that contains 452 loci and covers almost all of the chromosome bands (mainly R bands) is presented. The map uses published data and the latest standard chromosome nomenclature (ISCNDB 2001). The map includes 88 loci, including 74 type I loci (known genes) and 14 type II loci (SSRs/microsatellite marker/STSs), assigned by FISH and R-banding for the first time in sheep.

Materials and methods

Synchronized peripheral blood cell cultures and slide preparation steps were carried out as reported earlier (Di Meo et al. 2005). Caprine BACs containing type I and type II loci were identified by PCR screening of the INRA goat BAC library (Schibler et al. 1998a) and have been previously used to build comparative maps between ruminants, pig, horse and humans (Schibler et al. 1998b; Di Meo et al. 2000; 2002; 2006; Iannuzzi et al. 2000b; 2001a; Pinton et al. 2000; Milenkovic et al. 2002; Hayes et al. 2003). Likewise, bovine BAC clones containing type I and type II loci were identified after PCR screening of the INRA bovine BAC library with appropriate primers as described by Eggen et al. (2001). This BAC library was used to construct a first draft of a physical map of the bovine genome and over 26 000 BAC clones of the library were end-sequenced and are thus available as BES (BAC-end sequences) in GenBank (Schibler et al. 2004; 2006). Cattle and goat BAC libraries are available to the entire research community through the GADIE Biological Resources Center (http://www-crb.jouy.inra.fr/BRC/index.html). Table 1 summarizes information about all BAC probes used for this study.

Labelling of probes was done with biotin or digoxigenin with BRL-Gilco and Roche kits respectively. Ethanol precipitation was carried out in the presence of bovine COT-1 DNA or caprine genomic DNA for bovine and caprine BAC clones respectively to suppress repetitive sequences. In situ hybridization, signal detection, chromosome staining, microscope observation and image processing were described before (Di Meo et al. 2005). At least 20 metaphases were examined for each probe. Chromosome identification and band nomenclature for sheep chromosomes followed the R-banded standard ideogram reported in the latest international chromosome nomenclature (ISCNDB 2001). Only loci assigned to specific chromosome bands or regions in the present and previous studies, as well as those reported in SheepBase (Table S1 and references therein), were considered. Symbols of type I and type II loci followed HUGO (http://www.gene.ucl.ac.uk/nomenclature/) and BovMap (http://locus.jouy.inra.fr/cgi-bin/bovmap/intro2.pl) nomenclature respectively. GoatMap data were from http://locus.jouy.inra.fr/cgi-bin/lgbc/mapping/common/main.pl?BASE=goat.

Results and discussion

The frequency of hybridization signals on both chromosomes and chromatids, or on a single chromosome or chromatid, varied between 35% (ASCC3) and 81% (UMPS). All mapped loci were localized on homologous ovine chromosomes and chromosome bands when compared with cattle and goat positions. A few apparent differences between published and expected localizations were due to the banding techniques used in different studies. The data confirmed the high conservation of autosomal chromosomes among the bovid species. Loci FISH-mapped in the present study with locus name and symbol, clone identification and chromosome localization in sheep, cattle, goats and humans are listed in Table 1. Of these loci, 11 (B3GAT2, ASCC3, RARSL, BRD2, POLR1C, PPP2R5D, TNRC5, BAT2, BAT4, CDC5L, and OLA-DRA) have been FISH-mapped in sheep only. An additional 11 loci (D1S32, D1S86, BMS2621, SFXN5, D5S3, D5S68, CSKB1, D7S49, D9S15, D9S55 and D29S35) were assigned to specific sheep chromosome bands but only to whole chromosomes in cattle and goat (Table 1). Ten loci (BRD2, POLR1C, PPP2R5D, TNRC5, BAT2, BAT4, C4B, HSPA1B, CDC5L and OLA-DRA) were assigned to OAR20 extending the physical organization of this chromosome, which contains the major histocompatibility complex of sheep.

The revised sheep cytogenetic map, including loci previously mapped to specific chromosome bands or regions and the loci mapped in the present study on standard R-banded ideograms, is shown in Fig. 1. A total of 452 loci were assigned to specific chromosome bands or regions of sheep chromosomes, of which 291 are type I and 161 are type II, extending the cytogenetic map and density of markers available for this economically important species. These loci are also listed in Table S1, which includes the localization of all FISH-mapped loci in sheep and cattle and/or goat, the bovine syntenic groups and references.

Comparative mapping with human (Table 1) confirms previous comparative mapping data available from BovMap, SheepBase and GoatBase. Alignment of the cytogenetic map locations of loci between sheep, cattle and...
Table 1: Autosomal loci mapped by FISH to ovine (OAR) chromosomal locations.

| Locus symbol | Locus name                                      | Clone  | OAR      | BTA | HSA                  |
|--------------|------------------------------------------------|--------|----------|-----|----------------------|
| D3S32 (ILSTS096) | DNA segment                                   | 0337C071 | 1p13     | 3q  | ————                |
| TCHH (previous alias: THH) | trichohylain                                  | 240D1² | 1p21     | 3q21| 1q21-q23             |
| CDC20        | CDC20 cell division cycle 20 homolog (Saccharomyces cerevisiae) | 13A6¹  | 1p35     | 3q35| 1p34.1               |
| CCT8         | chaperonin containing TCP1, subunit 8 (theta) | 325A10+ 802F11¹ | 1q12.2  | 1q12.2 | 21q21.3–21q22.1     |
| CASR         | calcium-sensing receptor (hypocalciuric hypercalcaemia 1, severe neonatal hyperparathyroidism) | 139D12¹ | 1q31     | 1q31| 3q21-q24             |
| UMP5         | uridine monophosphate synthetase               | 296E8²  | 1q31     | 1q31| 3q13                 |
| AGTR1        | angiotensin II receptor, type 1               | 361C8²  | 1q41dist | 1q42| 3q21-q25             |
| GY1G (previous alias: GYG) | glycogenin 1                                  | 399A5²  | 1q41dist | 1q42| 3q24-q25.1           |
| TFDP2        | transcription factor Dp-2 (E2F dimerization partner 2) | 290G12² | 1q43     | 1q43prox | 3q23         |
| TF           | transferrin                                    | 163H4²  | 2p13     | 8q13| 9p13                 |
| COL6A1       | collagen, type VI, alpha 1                    | 349B11² | 2p17     | 8q17| 9p24                 |
| D1586 (BMS922) | DNA segment                                    | 0533D05¹ | 2p23prox | 8q21dist | 8p21        |
| GALT         | galactose-1-phosphate uridylyltransferase      | 253E10² | 2p27dist | 8q28| 9q33                 |
| VLDLR        | very low density lipoprotein receptor          | 438B7²  | 2q33     | 2q3q | 2q13-q21             |
| SFTPC        | surfactant, pulmonary-associated protein C     | 264F4²  | 2q43     | 2q43| 2q35                 |
| GSN          | gelsolin (amyloidosis, Finnish type)           | 2007C6² | 2q43prox | 4q25prox-q26 | 7p15.3     |
| EN1          | engraved homolog 1                             | 0540C11² | 3p14     | 11q14| 2p13                 |
| SLC11A1 (old alias: NRAMP1) | solute carrier family 11 (proton-coupled divalent metal ion transporters), member 1 | 0078E01² | 3p24     | 11q24dist | 2p23        |
| PAX3         | paired box gene 3 (Waardenburg syndrome 1)     | 337A3²  | 3q24     | 2q43| 2q35-q37             |
| TMEM50A (old alias: SMP1) | transmembrane protein 50A                     | 262H6+  284H5² | 2q45     | 2q45prox | 1p36.11     |
| TGFA         | transforming growth factor, alpha              | 211C11² | 3p14     | 11q14| 2p13                 |
| BMS2621      | DNA segments                                   | 372H08¹ | 3p14     | 11q | ————                |
| SFXN5        | sideroflexin 5                                 | 0904C05¹ | 3p14     | 11  | 2p13                 |
| POMC         | proopiomelanocortin (adrenocorticotropin/beta-lipotropin/alpha-melanocyte stimulating hormone/beta-melanocyte stimulating hormone/beta-endorphin) | 503E3²  | 3p24     | 11q24dist | 2p23        |
| D5S3 (ETH10) | DNA segment                                    | 0356G02¹ | 3q21prox | 5q  | ————                |
| D5S68 (BMS1658) | DNA segment                                    | 0771B05¹ | 3q33     | 5q  | ————                |
| HGF          | hepatocyte growth factor (hepapoietin A; scatter factor) | 217E9²  | 4q22prox | 4q15dist-21 | 7q21.1     |
| NPY          | neuropeptide Y                                | 342C1²  | 4q26prox | 4q25-q26 | 7p15.3     |
| SSBP1        | single-stranded DNA binding protein 1          | 264C10² | 4q34dist | 4q34dist | 7p34      |
| VAV1         | vav 1 oncogene                                | 72E3²  | 5q15prox | 7q15prox | 19p13.2   |
| GM2A         | GM2 ganglioside activator                     | 336E11² | 5q15     | 7q21  | 5                    |
| HSPA4        | heat shock 70 kDa protein 4                   | 544F11¹ | 5q22.1   | 7q22.1 | 5q31.1-q31.2         |
| CSK8071      | DNA segment                                   | 0078E01¹ | 5q22.1   | 7q  | ————                |
| D7S549 (BMS792-D05246) | DNA segment                                  | 0478C12² | 5q22.3   | 7q   | ————                |
| IL12B        | interleukin 12B (natural killer cell stimulatory factor 2, cytotoxic lymphocyte maturation factor 2, p40) | 0006B03¹ | 5q24     | 7q23-q24 | 5q31.1-q33.1     |
| Locus symbol | Locus name                                                                 | Clone | OAR      | BTA    | HSA    |
|--------------|---------------------------------------------------------------------------|-------|----------|--------|--------|
| HADH         | L-3-hydroxyacyl-Coenzyme A dehydrogenase, short chain                      | 232A9 | 6q15prox | 6q15prox | 4q22-q26 |
| D6S29        | DNA segment                                                                | 0980A05 | 6q17    | 6q22   | ————- |
| HMGCR        | 3-hydroxy-3-methylglutaryl-Coenzyme A reductase                            | 39C1  | 7q13prox | 10q12  | 5q13.3-q14 |
| MYH7         | myosin, heavy polypeptide 7, cardiac muscle, beta                          | 86E2  | 7q15    | 10q15-q21 | 14q11.2-q13 |
| MGAT2        | mannosyl (alpha-1,6-)-glycoprotein beta-1,2-N-acetylglucosaminyltransferase| 359E10 | 7q24    | 10q24  | 14q21  |
| SORD         | sorbitol dehydrogenase                                                    | 201F1 | 7q32    | 10q32  | 15q15-q21.1 |
| SPTB         | spectrin, beta, erythrocytic (includes spherocytosis, clinical type I)    | 194B4 | 7q34prox | 10q34prox | 14q24.1-q24.2 |
| TGM1         | transglutaminase 1 (K polypeptide epidermal type I, protein-glutamine-gamma-glutamyltransferase) | 265C8 | 7q34    | 10q34  | 14q11.2 |
| TGFB3        | transforming growth factor, beta 3                                         | 161F12 | 7q34dist | 10q34dist | 14q24 |
| D9S15 (BM2504)| DNA segment                                                               | 0006D02 | 8q14   | 9q     | ————- |
| B3GAT2       | beta-1,3 glucuronoltransferase2 (glucuronosyltransferaseS)                | 60B09 | 8q14    | 9q     | 6q12 |
| D9S16 (CSSM025)| DNA segment                                                              | 016H12 | 8q16    | 9q17-q21 | ————- |
| ASCC3        | activating signal cointegrator1 complex subunit3                          | 914D12 | 8q21.2  | ————- | 6q16 |
| D9S555 (BMS345)| DNA segment                                                               | 0163E12 | 8q22    | 9q     | ————- |
| RARS1        | arginyl-tRNA synthetase-like                                               | 890B11 | 8q24    | ————- | 6q16.1 |
| CYP11B1      | cytochrome P450, family 11, subfamily B, polypeptide 1                     | 115F11 | 9q13    | 14q13  | 8q21-q22 |
| D14S19 (RM180)| DNA segment                                                               | (0517E01)-517G01 | 9q15 | 14q    | ————- |
| D14S47 (BMS1941)| DNA segment                                                              | (0234A01)-239A01 | 9q17  | 14q    | ————- |
| BRCA2        | breast cancer 2, early onset subunit, alpha, type 7                        | 334F1 | 10q15   | 12q15  | 13q12-q13 |
| ACACA        | acetyl-Coenzyme A carboxylase alpha                                        | 42D12 | 11q13   | 19q13  | 17q21 |
| MYH2         | myosin, heavy polypeptide 2, skeletal muscle, adult                        | 120C2 | 11q17   | 19q15-q16 | 17p13.1 |
| LAMC2        | laminin, gamma 2                                                          | 191B7 | 12q23   | 16q23  | 1q25-q31 |
| ITGB1        | integrin, beta 1 (fibronectin receptor, beta polypeptide, antigen CD29 includes MDF2, MSK12) | 132H1 | 13q13dist | 13q13dist | 10p11.2 |
| RAB18        | RAB18, member RAS oncogene family proteasome (prosome, macropain) subunit, alpha, type 7 | 554C8 | 13q15prox | 13q15prox | 10 |
| PSMA7        | prostate-specific antigen (prostate-specific antigen) subunit, alpha, type 7 | 946B2 | 13q22prox | 13q22prox | 20 |
| DPEP1        | dipeptidase 1 (renal)                                                     | 262F4 | 14q13   | 18q13  | 16q24 |
| MC1R         | melanocortin 1 receptor (alpha melanocortin stimulating hormone receptor) | 132F3 | 14q13   | 18q13  | 16q24.3 |
| GNAO1        | guanine nucleotide binding protein (G protein), alpha activating activity polypeptide O | 527F2 | 14q15   | 18q15  | 16 |
| PTGIR        | prostaglandin I2 (prostacyclin) receptor (IP)                             | 276E4 | 14q24dist | 18q24dist | 19q13.3 |
| SLC6A3       | solute carrier family 6 (neurotransmitter transporter, dopamine), member 3 | 72F4 | 16q24   | 20q24  | 5p15.3 |
| IL2          | interleukin 2                                                             | 129G5 | 17q22   | 17q22dist | 4q26-q27 |
| NOS1         | nitric oxide synthase 1 (neuronal)                                        | 208D8 | 17q24   | 17q25  | 12q14-qter |
| COMT         | catechol-O-methyltransferase                                               | 475C7 | 17q26   | 17q26  | 22q11.21-q11.23 |
| MITF         | microphthalmia-associated transcription factor                             | 52G5 | 19q22   | 22q22  | 3p14.1-p12.3 |

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goats confirms the high degree of autosomal chromosome conservation among these bovid species, although some major discrepancies in the location of loci between OAR and BTA (or CHI) were observed (Table S1): TNP1 (OAR2q33-q34, BTA2q42-q43), KRT1 (OAR3q21, CHI5q25), HEXA (OAR7q12, BTA10q15dist), ANK1 (OAR26q17, CHI27q19) and D9S6 (OAR9q24, CHI9q26).

The assignment of D9S6 merits further investigation because OAR9 is currently designated as homologous to CHI14, not CHI9 (ISCNDB 2001). Other minor discrepancies were noted (designated as more than two bands of difference) for D6S29 (OAR6q17, BTA6q22) and C4B (OAR20q22, BTA23q12-q13).

Cattle, sheep and goat autosomes have been arranged using only one common chromosome banding system in the latest chromosome nomenclature of bovid species (ISCNDB 2001), as a result of their high chromosome banding similarities. In addition, all 31 bovine (and ovine/caprine) syntenic groups have been definitively assigned to specific chromosomes on the basis of official marker assignments performed with both G/Q and R-banded chromosomes of cattle (Hayes et al. 2000), as well as in those of both sheep and goat chromosomes (Di Meo et al. 2003). The use of a common chromosome banding system among chromosome of bovid species allows easier comparison of physical maps.

The new cytogenetic map presented here will be a useful tool for further studies on both molecular and clinical cytogenetics of this species. In addition it will allow a better anchoring of linkage (Maddox et al. 2001) and future RH maps by providing independent evidence for the localization and orientation of markers on specific chromosome regions. With few exceptions, all sheep chromosomal bands have at least one locus in the ovine cytogenetic map described here. Use of this cytogenetic mapping data, along with linkage and RH-mapping information, will greatly advance our understanding of the physical organization of the sheep genome and provide a sound platform for local and complete sequencing of the sheep genome.

Table 1 (Continued).

| Locus symbol | Locus name | Clone | OAR | BTA | HSA |
|--------------|------------|-------|-----|-----|-----|
| PBX2P1 (old alias: PBXP1) | pre-B-cell leukaemia transcription factor pseudogene 1 | 130G12^1 | 19q22 | 22q22 | 3q23-q24 |
| BRD2 | bromodomain containing2 | 948D01^1 | 20q13 | ———— | 6p21.3 |
| POLR1C | polymerase(RNA) I polypeptide C, 30 Kda | 237C05^1 | 20q15dist | ———— | 6p21.1 |
| PPP2R5D | protein phosphatase2, regulatory subunit B (B56), delta isoform | 364A09^1 | 20q15dist | ———— | 6p21.1 |
| TNRC5 | trinucleotide repeat containing 5 | 364A09^1 | 20q15dist | ———— | 6pter-p12.1 |
| BAT2 | HLA-B associated transcript2 | 660D10^1 | 20q22prox | ———— | 6p21.3 |
| BAT4 | HLA-B associated transcript4 | 660D10^1 | 20q22prox | ———— | 6p21.3 |
| C4B | complement component 4B | 573A10^1 | 20q22 | 23q12d-q13p | 6p21.3 |
| HSPA1B (old alias: HSP70-2) | heat shock 70 kD protein 2 | 0573C02^1 | 20q22 | 23q22 | 6p21.3 |
| CDC5L | CDC5 cell division cycle 5-like (S. pombe) | 192C02^1 | 20q22 | ———— | 6p |
| OLA-DRA2 | major histocompatibility complex, class II, DR alpha | 589B09^1 | 20q22 | ———— | 6p21.3 |
| D29S35 (BMS1112) | DNA Segment | 0133G06^1 | 21q13 | 29 | ———— |
| LDHA | lactate dehydrogenase A | 0039C07^1 | 21q22 | 29q22 | 11p15.1 |
| DNTT | deoxynucleotidyltransferase, terminal | 169D03^2 | 22q21 | 26q21 | 10q23-q24 |
| PAX2 | paired box gene 2 | 99A10^2 | 22q21dist | 26q21 | 10q25 |
| OAT | ornithine aminotransferase (gyrate atrophy) | 84B5^2 | 22q23 dist | 26q23prox | 10q26 |
| CYB5A (old alias: CYB5) | cytochrome b5 type A (microsomal) | 369C2^2 | 23q12 | 24q12 | 18q23 |
| DSG2 | desmoglein 2 | 312D1^2 | 23q21 | 24q21-q22 | 18q12.1 |
| F11 | coagulation factor XI (coagulation factor 11) (plasma thromboplatin antecedent) | 334A10^2 | 26q15 | 27q15 | 4q35 |

^1 Bovine and caprine BAC clones, as well as comparisons with both cattle (BTA) (BovMap; Hayes et al. 2003) and human (HSA) (HUGO, known genes) chromosome locations are reported.
Figure 1 The new comprehensive sheep cytogenetic map on the latest standard R-banded ideograms (ISCNDB 2001). The 452 loci include 291 type I loci (presented in normal characters) and 161 type II loci (in italics). Also see Table S1. Loci mapped in the present study are reported in bold.
The sheep cytogenetic map
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Supplementary Material

The following supplementary material is available for this article online from http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2052.2007.01598.x

Table S1 Loci assigned to chromosome bands or regions in sheep (OAR), compared to bovine (BTA) and goat (CHI) assignments.