A radiation hybrid map of river buffalo (*Bubalus bubalis*) chromosome 1 (BBU1)

M.N. Miziara^a T. Goldammer^b N.B. Stafuzza^a P. Ianella^a R. Agarwala^c
A.A. Schäffer^c J.S. Elliott^e P.K. Riggs^d J.E. Womack^e M.E.J. Amaral^a

^aDepartamento Biologia, UNESP – São Paulo State University, IBILCE, São Jose Rio Preto, SP (Brazil)

^bResearch Unit Molecular Biology, Research Institute for the Biology of Farm Animals (FBN),
Dummerstorf (Germany); ^cDepartment of Health and Human Services, National Center for

Biotechnology Information, National Institutes of Health, Bethesda, MD, Departments of ^dAnimal Science and

^eVeterinary Pathobiology, Texas A&M University, College Station, TX (USA)

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Abstract. The largest chromosome in the river buffalo karyotype, BBU1, is a submetacentric chromosome with reported homology between BBU1q and bovine chromosome 1 and between BBU1p and BTA27. We present the first radiation hybrid map of this chromosome containing 69 cattle derived markers including 48 coding genes, 17 microsatellites and four ESTs distributed in two linkage groups spanning a total length of 1330.1 cR₅₀₀₀. The RH map was constructed based on analysis of a recently developed

river buffalo-hamster whole genome radiation hybrid (BBURH₅₀₀₀) panel. The retention frequency of individual markers across the panel ranged from 17.8 to 52.2%. With few exceptions, the order of markers within linkage groups is identical to the order established for corresponding cattle RH maps. The BBU1 map provides a starting point for comparison of gene order rearrangements between river buffalo chromosome 1 and its bovine homologs.

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As livestock, the river buffalo (*Bubalus bubalis*) plays an important role in the livestock world economy by contributing high quality milk and meat for human consumption. Despite its economic importance, the river buffalo genome is not as intensively studied as other livestock species, such as domestic cattle. Thus, genome mapping of river buffalo remains important for identification of genes affecting economic traits.

The karyotypes of buffalo and domestic cattle appear very similar at the level of chromosome arms. While the cattle genome consists of 29 acrocentric autosomes and a pair of sex chromosomes (X/Y), the river buffalo genome has five biarmed and 19 acrocentric autosomes plus the X and Y chromosomes. According to previous studies and this latest map, all buffalo chromosome arms have homology to single bovine acrocentric chromosomes. Buffalo (BBU) chromosome 1 appears to be a fusion of *Bos taurus* (BTA) chromosome 1 and 27, BBU2 equals BTA2 and 23, BBU3 equals BTA8 and 19, BBU4 equals BTA5 and 28, and BBU5 equals BTA16 and 29 at the cytogenetic level with state of the art banding (El Nahas et al., 1996, 2001; Iannuzzi et al., 2003). All the other chromosomes have a one-to-one correspondence between the two species. Assignment of genes to these buffalo chromosomes to date is consistent with the cytogenetic prediction.

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Request reprints from M. Elisabete J. Amaral
UNESP – São Paulo State University, IBILCE, Dept. Biologia
São José do Rio Preto, SP, 15054-000 (Brazil)
telephone: +55-17-3221-2407; fax: +55-17-3221-2390
e-mail: eamaral@ibilce.unesp.br

Recent reports regarding the river buffalo genome mapping (Iannuzzi et al., 2003; Di Meo et al., 2006) describe a total of 302 loci (180 of type I and 122 of type II) physically assigned to its genome. Of the 302 loci, 256 were mapped by in situ hybridization (254 by FISH), 15 by both FISH and somatic cell hybrid analysis and 33 by using only somatic cell hybrid analysis. BBU1, the largest of the five biarmed chromosomes in the river buffalo genome, has only 13 genes and 10 microsatellites assigned by FISH or somatic cell panel mapping (Iannuzzi et al., 2003; Di Meo et al., 2006). In contrast, the third generation bovine RH map includes 67 markers and 175 markers assigned to BTA27 and to BTA1, respectively (Everts-van der Wind et al., 2005). BTA27 is known to contain economic trait loci (ETLs) influencing clinical mastitis (Goldammer et al., 2004) and both bovine chromosomes contain quantitative trait loci (QTLs) affecting milk yield as well as milk fat and protein content (Polini et al., 2006).

Taking advantage of buffalo-bovine homologies and the extensive resources now available as a result of the bovine genome sequencing project, the goal of this study was to construct the first radiation hybrid (RH) map of BBU1 by utilizing markers chosen from BTA1 and BTA27.

Materials and methods

Sixty-nine markers (including coding genes, ESTs and microsatellites) identified on BTA1 and BTA27 from the previous publications were typed on the RH panel as described elsewhere (Amaral et al., 2007). Most of these markers appeared on at least one of the genome-wide linkage and RH maps (Everts-van der Wind et al., 2004, 2005; Ihara et al., 2004); the original source for each marker is listed in Table 1.

Briefly, PCR reactions were performed in a MJ Research PTC-200 thermocycler with a thermal gradient software. The markers were scored after amplification of DNA from the 90 radiation hybrid cell lines and control buffalo and hamster DNA. PCR mixtures included: 10 mM Tris-HCl, 1.5 mM MgCl₂, 50 mM KCl, pH 8.3 (20°C), 10 mM dNTPs, 0.2 mM each primer, 0.5 unit of AmpliTaq Gold polymerase (PerkinElmer Applied Biosystems, Foster City, CA, USA) and 50 ng DNA in a 10 µl-volume. The PCR conditions were as follows: initial denaturation at 94°C for 10 min, followed by 35 cycles at 94°C for 30 s (denaturation), 50 to 65°C for 30 s (annealing), extension at 72°C for 30 s and a final extension at 72°C for 7 min.

The PCR products were electrophoresed through 2% agarose gels in 1× TBE buffer containing ethidium bromide and photographed under UV light. PCR products were scored as 1 for present, 0 for absent or 2 for ambiguous amplification. All primer sets were typed twice with the RH panel DNA and scored independently in order to increase the accuracy of the results. Primer pairs that showed ambiguous results were typed a third time.

The BBU1 RH map construction was performed by using the software *rh_tsp_map*, version 3.0 (Schäffer et al., 2007) and CONCORDE (Applegate et al., 1998) linked to QSOPT (<http://www2.isye.gatech.edu/~wcook/qsopt/>). We used the maximum likelihood criterion and our framework maps are called 'MLE-consensus' maps because the markers are chosen so that the optimal order is the same for three variants of the MLE criterion that differ in the treatment of uncertain (coded as 2) entries in the RH vectors (Agarwala et al., 2000). The software distribution of *rh_tsp_map* tutorial (ftp://ftp.ncbi.nih.gov/pub/agarwala/rhmapping/rh_tsp_map.tar.gz) includes a tutorial describing the steps that can be used to construct a map for markers typed on a single or multiple panels. For the construction of the BBU1 map, we followed all

the steps from 'Preparing files' through 'Placing additional markers' for making a map, but we did not continue to assign cR-positions to the placed markers because this is a coarse map. Considering the number of markers, linkage groups were made using a pairwise LOD score threshold of 5.5.

Results and discussion

The newly constructed BBU1 RH map (Fig. 1) contained markers distributed within two linkage groups. Linkage group 1 (LG1; spanning 1118.9 cR) included a total of 58 markers (39 coding genes, 15 microsatellites and four ESTs) spanning the entire short arm and extending across much of the long arm, with 47 markers placed as framework and eleven markers placed in bins. The second linkage group (LG2; spanning 211.2 cR) included eleven markers (nine coding genes and two microsatellites) covering the remaining portion of the BBU1 long arm with nine framework markers and two placed in bins.

Of the 69 markers typed on the river buffalo-hamster whole genome radiation hybrid (BBURH₅₀₀₀) panel, *APOD* and *PPP1R2* had the same RH vector and were placed at the same position. Retention frequencies (RF) for all mapped markers ranged from 17.8% (SR140) to 52.2% (BM6438). Additional information about mapped markers including their RF and cR-position on the map is compiled in Table 1.

Because no other river buffalo linkage maps are currently available, we compared the mapped order of the markers from this new BBU1 RH map to the current bovine genome assembly (build 3.1) of chromosomes BTA1 and BTA27. The markers *SLC25A4*, *PLAT*, *BM6526*, *DEFB1*, *KRTAP8*, *SOD1*, *AHSG* from LG1 and the markers *NCK1* and *CRYAA* from LG2 were also compared to their positions previously assigned by FISH (Iannuzzi et al., 2003), serving as anchor markers for the BBU1 RH map. As indicated in Fig. 1, eleven inversions of gene order were observed, including one disagreement with the order of FISH assigned markers and one inversion not supported by the map in Everts-van der Wind et al. (2005).

This first RH map from BBU1, including 48 coding genes and four ESTs, is the starting point for the construction of a high resolution comparative map for this river buffalo chromosome. With our data we were able to generate a large linkage group (LG1) including markers from both bovine homologs (BTA27 and BTA1) spanning most of BBU1. The number of observed disagreements in the gene order among our RH map and the bovine sequence and the river buffalo cytogenetic assignment may contribute to improved maps for buffalo as well as maps for other members of the Bovidae family.

Table 1. Cattle-derived markers mapped to BBU1 based on the BBURH₅₀₀₀ panel, along with their retention frequencies (RF), distances on the RH map, PCR primer sequences, annealing temperatures, GenBank Accessions and UniSTS ID

Marker ^a	Type [*]	RF (%)	Marker position cR	Foward primer (5'-3')	Reverse primer (3'-5')	GenBank Accession	Ref./ UNISTS ID	Tm (°C)
<i>BBU1 linkage group LG1</i>								
SH2D4A	gene	30.0	placed	TGCTGAAACAGATCCTGTCTG	GGACTCCTGTTTTTCCATCG	XM_582664	§	58
PLAT	gene	32.2	0.0	AGACTTTGTCTGCCAGTGCC	CTCTCTGCCGTGCTCCAC	X85800	251598	65
HOOK3	gene	30.0	placed	CTAGGGCAGCAGATCAATGAC	CAGCACAGCCTAAAATGAGC	XM_602978	§	60
THAP1	gene	28.8	placed	AGAAGCTGAAGGAGGTGGTG	CACGCTGGGACTTCGACTAT	NM_001034648	§	58
ADAM2	gene	28.8	20.5	CTCTGCACTCCAGCACCATA	GGGCAATGGCATTGTGTTAAT	NM_174228	§	58
BRF2	gene	31.1	44.6	TGAGCTCGTGGAAGACTCG	CGTCACTGAAGGTGTCTGTA	NM_001015582	§	58
CSSM036	MS	34.4	52.4	GGATAACTCAACCACACGTCTCTG	AAGAAGTACTGGTTGCCAATCGTG	U03827	250971	65
INRA134	MS	34.4	placed	CCAGGTGGGAATAATGTCTCC	TTGGGAGCCTGTGGTTTATC	X73125	250829	59
WRN	gene	35.5	90.8	ACGCCATATATAGCAAGAC	GATCCAAAACAAAGCAAGAA	BE217410	279411	56
DCTN6	gene	32.2	113.4	CGTATGTGGGCAGAAATGTG	GCAGGCAGTCTCCACCATAG	NW_930571	§	58
NRG1	gene	27.7	121.8	ACGGAAAAAGCTTCATGACC	ACCAGCTGCACGTTCTCG	XM_592564	§	58
C8orf79	EST	33.3	139.0	TCTGAAAGTGAACAGCCAGGT	TGACGCCATGAGAGATGATG	AW632623	§	58
CNOT7	gene	38.8	167.5	CCACCCAGTTACAGCATTTGA	GGAATATGTGACCAGACCAGAG	AW289341	278215	64
RM209	MS	33.3	186.4	GTAGAAGTTAGTACTGTCTATCC	CCTCAGAGCCCCATACATTTC	U32921	250931	65
MTNR1A	gene	34.4	placed	TTTCAACAGCTGCCTCAATG	GGAGAGGGTTTGCGTTTAAT	U73327	278796	61
SLC25A4	gene	34.4	199.6	CATTGATTGCGTGGTGAGAA	ATAATGATGCCCTGGACCGA	M24102	^a	65
BM1856	MS	38.8	215.2	GGCCTCAAGTTTCATCCATG	CATCAGCATGAAGCAACCC	G18402	53060	65
ODZ3	gene	33.3	233.8	TGACCAACGTGACATTTCCA	TTGAACCATGGTGTAGAACGA	XM_865074	§	58
CARF	gene	27.7	257.5	AGCACTGCCTCTCAGGTGAC	CGATCCACTTTGTTGTCTGG	XM_590926	§	58
DEFB1	gene	30.0	285.4	GGAAGACAGGAAGGCCTCTGG	CCTCACGTTTTCAGAACCAC	NW_001501821	251704	64
BM6526	MS	37.7	317.3	CATGCCAAACAATATCCAGC	TGAAGGTAGAGAGCAAGCAGC	G18454	28213	65
TGLA179	MS	40.0	placed	CTTTAATCAGCACACAGCTTCCCA	ATATGTGTAGAAAGTTTGGTCAACC	CM000203	251232	65
BMS1001	MS	42.2	327.1	GAGCCAATTCTACAATTCTCTT	AGACATGGCTGAAATGACTGA	G18605	44386	65
DLGAP2	gene	42.2	359.4	CGGACCTCCATCCATCC	CGTCCCTGCTGTCTATGTGG	XM_600714	§	58
CLN8	gene	46.6	369.0	CCCTTCATGTGTCCAATGC	ATCCAGGAGATGCAGGTGAA	XM_609353	§	58
IFNAR1	gene	37.7	441.6	TGAAGATAAGGCAATAATAC	TGAAGAGTTTTTCCAGATAA	BE217555	279374	54
AW267109	EST	45.5	462.7	ATGAAAGTCTTCTGTGCCATGC	TCAGTATTGCCACATGACATGC	AW267109	278038	60
IFNGR2	gene	51.1	472.2	AGACAAAGGCACAGCATTCCAC	GATTTCAAAGGGAGAGCTGGGT	AW289292	278555	60
BM6438	MS	52.2	placed	TTGAGCACAGACACAGACTGG	ACTGAATGGCTCTTTGTGTC	G18435	79562	63
ADAMTS1	gene	45.5	placed	CGACACAAGAGAGGAAAGATGG	CATCACTTTACCCGCTGCTATG	AW428596	277932	60
C21orf45	EST	47.7	placed	CCACCAAGGAAATCCAGCATAC	TATCCAAGTCACCTCCAGGTCA	AW463565	278143	60
KRTAP8	gene	46.6	503.2	TTGCTGAAATACCAAGAGGCA	ATGACAAGAGTCATGAGCATGG	XM_001250875	^b	59
TGLA49	MS	50.0	520.3	GGCAGGACTTCACTCTTTTCA	AGAAAAGGAATAATGAGACAGATTA	CM000177	239049	56
SOD1	gene	35.5	546.7	GTTTGGCCTGTGGTGTAATTGGAA	GGCCAAAATACAGAGATGAATGAA	NM_174615	^c	56
PRSS7	gene	34.4	619.0	CCAAGGTTACACAGAGTGGAT	GGCTTGTGACATGACCTTAC	U09859	278971	65
RM095	MS	41.1	637.5	TCCATGGGGTCGCAAAACAGTGG	ATCCCTCCATTTGTGTGGAGTT	U32918	250928	58
STCH5	gene	38.8	652.8	TGATCTTCAGAACACGTCATAC	GTGAATGAATGTTTGGTGTGAC	AW267080	279153	56
ROB02	gene	27.7	placed	GAATTGGCTGTCTGCATCTG	ACCTTTGTCTGATCAGG	AW653888	279030	50
POU1F1	gene	34.4	710.1	GGCTGAAGAACTAAACCTGGAG	TAGGAGAGCCTATCTGCATTCTG	X12657	278932	52
PROS1	gene	30.0	730.1	GTACAGGTGGATTGTGATGAAG	GAGAGACAAGAGGTAAGAAACA	X12891	278968	52
ESDN	gene	26.6	744.5	ATTGGGCTAGACCGTGCGATA	GGAACCAAGCAGTTAAAGG	AW314878	278348	65
DOC1	gene	33.3	761.6	TTACCAAGACAAAGTTGCAG	CCCTTCCTTATCCGTTTAT	AW289233	278315	58
ALCAM	gene	28.8	placed	CTGGAGAGCAGAACATGGGAAA	TATCCAGGCACATGATCCACTGA	X73801	277962	65
TGLA57	MS	30.0	802.2	GCTTTTAAATCCTCAGCTTGCTG	CGTTCCAAAACCTTTACAATATGTAT	CM000177	250987	56
BBX	gene	34.4	812.9	CCAGTGAAGCGCCCTTTAAT	ACCACATGGACTCACTAGCATC	AW428450	278098	65
LOC151584	EST	30.0	823.6	ACCAATGCTGCCTGCTAACT	ACTCCAGGCCTTGCAATGAAT	AW352867	278663	65
TACTILE	gene	20.0	849.5	TTGTAGACTGCACTGGTGGAAAC	GAGTCCATTTGGAAGTGATCTG	AW289280	279172	65
BMS527	MS	25.5	904.2	TCAGTGAAGCAAGAGAAATATCC	TCCATTCCCTTTGAATATCCC	G18871	65219	60
BM1312	MS	30.0	921.8	CCATGTGCTGCAACTCTGAC	GGAATGTTACTGAACCTCTCCG	G18434	30885	54
BMS4030	MS	30.0	938.8	TGTACCAACACAGGAGCAC	TGACAGAGGGACCCATATCC	G19083	74568	65
CASR	gene	23.3	964.3	CGGTGTGCTTCTGTGGTTAGGT	CAGGCTGTCTGCAAGGTTCAAG	S67307	278154	65
PDIR	gene	24.4	983.6	AACGTGTGTTTGTGCGGAGAATAC	GAAAGTTGACCTGAGTGCAAAG	AW289373	278896	64
TRAD	gene	30.0	1004.7	GCGAGGAAAGGATAAAATC	ACATTTTTCAGTTTCACC	AW353439	279211	62
APOD	gene	26.6	1025.4	GAAGATCCCAAGTGAAGCTTTG	ATCAGCTCTCAGCTCCTTGT	AW357610	277980	51
PPP1R2	gene	26.6	1025.4	GCATCACTGCTGAATTTTCAGAC	GTCAGTGTTCAGTTCTAGCCAA	AW315482	278944	64
BM6506	MS	26.6	1057.4	GCACGTGGTAAAGAGATGGC	AGCAACTTGAGCATGGCAC	G18455	47201	63
AHSB	gene	27.7	1065.9	GTCCCAACTTCTCATCCTTCCA	GGCAAGAGCACTTTCAAAGTC	X16577	277947	60
TLOC1	gene	20.0	1118.9	CATAGCAGTTTCTCTGATCTGA	GTGATCTTTCTACAGCAGTTTC	AW289224	279200	65
<i>BBU1 linkage group LG2</i>								
IL12A	gene	22.2	placed	AAAGTCAAGCTCTGCATCCT	GTTATGAGAGACCTCAGCATTC	U14416	278561	58
SR140	gene	17.8	0.0	TACTACTGCCAGCAGATCCA	CTGCATCTGTAGACCTGTTG	AW289396	279143	58
RNF7	gene	24.4	39.6	CCTGTTCCCTGGTCCAAACTTA	GGAGTTATTGAAGCGGTTCCGT	AW428600	279028	65
FOXL2	gene	25.5	63.0	TCCTCCGGACGACACACTACAA	GAAATGTGAAACCCGGCAGCAG	AW267121	278443	65
CSSM019	MS	23.3	placed	TTGTCAGCAACTTCTTGATATCTT	TGTTTAAAGCCACCAATTATTTG	U03794	251074	59
NCK1	gene	25.5	75.6	CGCTCTCTCTCTGCTCTTAA	TGCAAG2TAAGTAAAGGTGG	AW425735	278818	58
MX1	gene	20.0	109.2	CCGTAGTCTCTGCTGTCTCTTA	GGAATGACCCTTCTACAGTGCT	U88329	278800	65
CRYAA	gene	27.7	134.1	CCTAGAAAGTGGGGATCCAT	GGTCACTCTGAGGCTCTTGCA	NM_174289	^c	64
HLS	gene	27.7	152.7	TGAGCAGTGGCTGCGTTTAT	AACAGCTTCTCCTCCGTGAATC	AW354578	278525	61
CBR1	gene	22.2	168.9	CCCTGAAGTGCAGCAGAAATTG	CCCGTCTTTGTGTCTTCCA	AW461769	278157	61
BMS2263	MS	23.3	211.2	AACCCAGTCAACCAAGCAAG	CACCCAGCCATCACTTC	G18934	2985	65

Genes from chromosome BTA27 are in italics, genes from chromosome BTA1 are in normal. * MS – Microsatellite, EST – Expressed Sequence Tag. § New designed primers from known cattle ESTs. ^a Li and Womack, 1997; ^b Harlizius et al., 1997; ^c Barendse et al., 1994.

Fig. 1. Comparison of BBU1 RH map (centre) with bubaline cytogenetic map (left) and cattle genome build 3.1 for BTA1 and BTA27 (right). The framework markers, whose order is better than the second best at least 0.50 LOD units, are in bold font. Placed markers assigned to the same MLE-consensus map interval are shown in boxes. Markers common to both BBU and BTA maps are joined by a solid line. A black line joins those markers on the BBU1 RH-map that have been physically mapped by FISH to their location on the ideogram (Iannuzzi et al., 2003). Blue lines indicate markers on the BBU1 RH-map with inverted order regarding the cattle maps and the river buffalo cytogenetic map. Comparison of *SLC25A4* on the cytogenetic map with RH map is not shown as this marker is not localized to a band on 1p. The highlighted interval (4 Mb) of BTA1 map indicates the gene order based on Drögemüller et al. (2005) and Wunderlich et al. (2006). *: *SH2D4A*, *DEFB1*, *DLGAP2*, *CLN8*, and *POU1F1* are assigned to contigs unplaced on BTA build 3.1. †: Eighteen markers on RH MLE-consensus map and on the map of Everts-van der Wind et al. (2005) have a consistent marker order between the two maps. Since the map of Everts-van der Wind et al. (2005) supports the marker order of RH map for *PRSS7* and *RM095*, inversion for this pair with BTA 3.1 build is shown in green.

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