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# Comparative RH Maps of the River Buffalo and Bovine Y Chromosomes

N.B. Stafuzza[a] H. Abbassi[b] J.R. Grant[c] E.A. Rodrigues-Filho[a] P. Ianella[a] S.M. Kadri[d] M.V. Amarante[d] P. Stohard[c] J.E. Womack[e] F.A. Ponce de León[b] M.E.J. Amaral[a]

[a]UNESP – São Paulo State University, IBILCE, Dept. Biologia, São José Rio Preto, SP, Brazil; [b]Department of Animal Science, College of Food, Agricultural, and Natural Resource Sciences, University of Minnesota, St. Paul, Minn., USA; [c]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alta., Canada; [d]UNESP – São Paulo State University, Instituto de Biociencias, Dept. Parasitologia, Distrito de Rubião Júnior, Botucatu, SP, Brazil; [e]Texas A&M University, Department of Veterinary Pathobiology, College Station, Tex., USA

**Key Words**
Bovine · Comparative RH map · River buffalo · Y chromosome

**Abstract**
Radiation hybrid maps were constructed for river buffalo and cattle Y chromosomes. A total of 41 cattle-derived Y-chromosome molecular markers were selected and tested with 2 previously described 5,000-rad whole-genome radiation hybrid (RH) panels (river buffalo – $BBURH_{5000}$ and cattle – $BTARH_{5000}$) for generation of maps. Among the initial 41 selected markers, a subset of 26 markers generated PCR products suitable for scoring with the $BBURH_{5000}$ panel. Of these, 19 markers (73%) were distributed in 1 linkage group spanning 341.3 cR. Retention frequencies (RF) for individual markers ranged from 17.8% for *SMCY* to 56.7% for *BTY1*, with an average RF of 37.6%. From the selected markers, 37 generated reliable scores using the $BTARH_{5000}$ panel. The newly constructed BTAY RH map contains 28 markers distributed within 1 linkage group. Twenty-four of these markers had been previously mapped on BTAY using a 7,000-rad cattle-hamster WG-RH panel and 4 markers were mapped for the first time *(ZFY*, *SeqRep*, *RepSeqS4* and *BTY1)*. The length of the BTAY RH map was estimated to be 602.4 cR. Retention frequencies for individual mapped markers ranged from 10% *(INRA126)* to 63.3% *(SeqRep)*, with an average RF of 35.3%. RH marker positions along the Y chromosome were compared between BBUY and BTAY, which revealed differences in the order of some of the markers. The BBUY pseudoautosomal region (PAR) is delineated by 3 BTAY PAR markers (MAF45, TGLA325 and UMN2008). These markers are telomeric in both species but are not found in the same order. Here we have demonstrated the effective use of bovine Y chromosome markers for the development of the first BBUY RH map. Likewise, these set of markers can be used for comparative assessment of Y chromosomes in other members of the Bovidae family.



The Y chromosome in mammals is of special interest because it is paternally inherited and carries species-specific genes involved mainly in spermatogenesis and other male fertility related functions [Lahn and Page, 1997; Skaletsky et al., 2003]. In the Bovidae family, the Y chromosome shows different sizes and morphologies depending on the position of the centromere [Di Meo et al., 2005]. Sex chromosomes share a small homologous region known as the pseudoautosomal region (PAR). The

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M. Elisabete J. Amaral
UNESP – São Paulo State University, IBILCE, Department Biologia
Rua Cristovao Colombo, 2265
São José do Rio Preto, SP 15054-000 (Brazil)
Tel. +55 17 3221 2407, Fax +55 17 3221 2390, E-Mail eamaral@ibilce.unesp.br

PAR behaves like an autosome and recombines during male meiosis.

A radiation hybrid (RH) panel of 90 clones was constructed for river buffalo [Amaral et al., 2007] and recently used to make RH maps for each of the river buffalo autosomes and the X chromosome with the exception of the buffalo Y chromosome [Amaral et al., 2008]. In this study, we used the RH panel to construct a preliminary RH map of the river buffalo Y chromosome (BBUY) using markers derived from the cattle Y chromosome for comparison. In order to compare the BBUY RH map to a BTAY RH map containing a higher number of common markers, we also built a similar resolution RH map for the bovine Y chromosome using the $BTARH_{5000}$ panel [Womack et al., 1997]. Considering that river buffalo and cattle belong to the Bovidae family with an evolutionary divergence estimated in 20 million years [Parma et al., 2004], chromosomal rearrangements and comparison of positions and order of homologous genes are a valuable attempt to enhance our understanding of both genomes.

## Materials and Methods

*Selection of Markers, Primer Optimization and Genotyping by PCR*

Y chromosome markers, including expressed sequences and microsatellites, were selected from published cattle Y-chromosome linkage and RH maps. All BTAY marker primer pairs were tested for PCR amplification in buffalo. Markers that did not generate a PCR product with river buffalo genomic DNA or displayed weak amplification products after PCR amplification were excluded from further genotyping. In some cases new primer pairs were designed based on bovine reference DNA sequences deposited in the GenBank database (http://www.ncbi.nlm.nih.gov/Genbank/). The software program PRIMER3 (http://frodo.wi.mit.edu/cgi-bin/primer3/primer3_www.cgi) was used to design oligonucleotide primers for PCR [Rozen and Skaletsky, 2000]. Details about the selected markers are described in table 1.

The appropriate annealing temperature and amplification patterns for each set of primers were established in preliminary experiments to yield specific amplification of buffalo and/or bovine PCR product in a hamster background. Bovine and river buffalo male and female genomic DNAs as well as hamster DNA were used as templates for amplification to determine their usefulness for RH panel analysis. PCR primers that did not amplify buffalo or bovine DNA and/or amplified multiple PCR products were discarded. Similarly, PCR primers yielding hamster PCR products of similar size to river buffalo or bovine DNA were discarded.

In a parallel study, Liu and Ponce de Léon [unpublished] had isolated BTAY BACs and have carried out BAC end sequencing to develop BTAY BES marker sequences. The most promising, based on their retention frequencies (10 to 30%), of these bovine BES sequences were tested for amplification in male buffalo DNA and only 2 *(P1F4T* and *P2D5T)* were genotyped in the $BBURH_{5000}$ panel. Forty-one markers yielded PCR amplification patterns useful for RH panel analysis. Details about the selected markers are described in table 1.

PCR reactions were performed in a MJ Research PTC-200 thermocycler with thermal gradient software. The markers were scored after amplification of DNA from the $BTARH_{5000}$ [Womack et al., 1997] and $BBURH_{5000}$ panels [Amaral et al., 2007]. PCR amplification solutions included: 10 mM Tris-HCl, 1.5 mM $MgCl_2$, 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, Calif., 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 6 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 both cattle and buffalo RH panels DNA and scored independently in order to avoid discrepancies. Primer pairs that showed ambiguous results were typed a third time.

*Statistical Analysis and Map Construction*

RH maps were constructed using CarthaGene [de Givry et al., 2005]. Linkage groups were defined using a LOD threshold of 5. Of the 26 markers genotyped on buffalo RH panel, 19 were assigned to 1 linkage group, while 28 of the 37 markers genotyped on bovine RH panel were grouped together. The remaining markers were in linkage groups of 2 markers and singletons and were not considered for further analysis. Different markers with compatible retention pattern (double markers) were merged together. A 1,000:1 framework map was created with the grouped markers using the '*buildfw*' command, which constructs a map by an incremental locus insertion method. All remaining markers were then inserted one by one in all possible positions to find the most probable position. These additional markers were placed on the map when the difference in log likelihood between the best position and the second best position was greater than 0.5. Using these criteria, 19 buffalo markers and 28 bovine markers were ordered and assigned to cR positions on their respective maps. Each map was further refined using the flip algorithm to test all possible marker orders within a sliding window of 8 markers. Finally, the polish command was used to test the reliability of the map by displacing each marker in all possible intervals.

*Microsatellite (MS) Isolation and Sequencing*

A set of microsatellite markers developed for the bovine Y chromosome [Liu et al., 2003] were assessed for amplification in buffalo. Between 3 and 5 separate RH panel amplifications were carried out for each marker to determine the repeatability and consistency of the amplification. To assess the level of homology and presence or absence of microsatellite segments in river buffalo PCR products, amplified with BTAY microsatellite primers, these were run in 4% low melting agarose gels. The latter was necessary because the Y chromosome has a high content of repetitive DNA and it was necessary to assess that each amplification product was a single product and not a combination of repetitive fragments amplified by the same primer pair. The corre-

**Table 1.** Summarized information about the selected Y chromosome markers used in this study

| Marker | Primer sequences (5′–3′) or primer source reference | Bovine | | | | Buffalo | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | annealing temp., °C | RF[a] % | map position, cRay | product PCR size | annealing temp., °C | RF[a] % | map position, cRay | product PCR size |
| *AMELY* | Checa et al. [2002] | 57 | 18.9 | 109.3 | <300 | PCR multiple products | | | |
| *BC1.2* | Schwerin et al. [1992] | 65 | 52.2 | excluded | <300 | PCR multiple products | | | |
| *BM861* | Bishop et al. [1994] | 56 | 33.3 | 336.0 | <200 | PCR multiple products | | | |
| *BOV97M* | Williams et al. [2002] | 58 | 53.3 | 461.1 | <200 | 61 | 51.1 | 80.2 | <200 |
| *BRY.1* | Matthews and Reed [1991] | 60 | 52.2 | 518.2 | <300 | 65 | 54.4 | 103.1 | <300 |
| *BTY1* (A18483)[b] | TTAGCAGGAAAGGCCAAAGA CACCTGTAGGAATGCCACCT | 58 | 56.7 | 503.1 | <200 | 58 | 58.9 | 141.4 | <200 |
| *BY39* | Kappes et al. [1997] | 59 | 43.3 | 430.2 | <200 | 61 | 48.9 | 90.1 | <200 |
| *BYM-1* | Ward et al. [2001] | 65 | 20 | 173.1 | <300 | PCR multiple products | | | |
| *EIF1AY* (AV664570)[b] | AGGCGGATCTCGGAAGAC GTGACGACGCACTTGAGG | 65 | 27.8 | excluded | <200 | 63 | 12.2 | excluded | <200 |
| *HEL26* | Barendse et al. [1994] | 60 | 33.3 | 0.0 | <200 | PCR multiple products | | | |
| *INRA008* | Williams et al. [2002] | 58 | 57.8 | 503.1 | 120 | 59 | 47.8 | 93.8 | 116 |
| *INRA030* | Ciampolini et al. [1993] | 65 | 26.7 | excluded | <200 | Weak signal after PCR amplification | | | |
| *INRA057* | Williams et al. [2002] | 65 | 35.5 | 295.3 | <200 | PCR multiple products | | | |
| *INRA124* | Hanotte et al. [1997] | 56 | 23.3 | excluded | <200 | No amplification with buffalo DNA | | | |
| *INRA126* | Vaiman et al. [1994] | 56 | 10 | excluded | <200 | PCR multiple products | | | |
| *INRA 189* | Kappes et al. [1997] | 65 | 20 | 134.4 | <200 | 54 | 22.1 | excluded | <300 |
| *MAF45* | Kappes et al. [1997] | 63 | 32.2 | 36.0 | <200 | 60 | 30 | 331.0 | <200 |
| *PBRR1-0907R* | Liu et al. [2002] | 52 | 34.4 | 234.4 | <300 | 61 | 38.9 | 0.0 | <300 |
| *P1F4T*[b] | TGCCCTACGACAGAATCAGA CCTTCCTCTGGGGTCTTGC | Not genotyped on BTARH panel | | | | | 53.3 | 106.0 | 56 |
| *P2D5T*[b] | GTCTCCAGATTTGTATATGTG TAAGGCGCCTCTTGATGA | Not genotyped on BTARH panel | | | | | 57.8 | 108.3 | 58 |
| *RepSeqS4* (D16357)[b] | TGGGTAGGGTTCTCAACCAG ATGGACAAAGGAGCCTGATG | 64 | 57.8 | 495.8 | <200 | 63 | 45.5 | 174.0 | <200 |
| *SeqRep* (Z31587)[b] | ACATTGACATGCTGCACTCC GTGGTTGCCTTTAGGTGGAA | 60 | 63.3 | 483.9 | <200 | 65 | 38.9 | 57.9 | <300 |
| SMCY (BI538086)[b] | CGAGAGGAGCTAGAGCCAAA GGAGTCAAAGTGGGGAAAGG | 65 | 17.8 | excluded | <300 | 59 | 8.9 | excluded | <300 |
| *SRY-HMG* | Liu et al. [2002] | 65 | 41.1 | excluded | <300 | 59 | 18.9 | excluded | <300 |
| *TGLA325* | Kappes et al. [1997] | 65 | 30 | 73.6 | <200 | 65 | 28.9 | 333.5 | <200 |
| *TSPY* | Jakubiczka et al. [1993] | 58 | 45.5 | 602.4 | <300 | 65 | 56.7 | 106.0 | <300 |
| *UMN0103* | Liu et al. [2002] | 54 | 44.4 | 373.7 | <200 | 54 | 51.1 | 90.1 | <200 |
| *UMN0301* | Liu et al. [2002] | 58 | 27.8 | 228.3 | <200 | PCR multiple products | | | |
| *UMN0304* | Liu et al. [2002] | 60 | 35.5 | 236.8 | 187 | 63 | 51.1 | 97.1 | 213 |
| *UMN0307* | Liu et al. [2002] | 58 | 31.1 | excluded | <200 | PCR multiple products | | | |
| *UMN0504* | Liu et al. [2002] | 64 | 32.2 | 346.9 | <200 | Weak signal after PCR amplification | | | |
| *UMN0803* | Liu et al. [2002] | Not genotyped on BTARH panel | | | 284 | 56 | 17.8 | excluded | 268 |
| *UMN0905* | Liu et al. [2002] | 58 | 26.7 | 57.3 | <200 | PCR multiple products | | | |
| *UMN0910* | Liu et al. [2002] | 58 | 40 | 261.8 | <200 | No amplification with buffalo DNA | | | |
| *UMN0929* | Liu et al. [2002] | Not genotyped on BTARH panel | | | 190 | 56 | 27.8 | 314.8 | 178 |
| *UMN2008* | Liu et al. [2002] | 58 | 28.9 | 65.5 | 140 | 58 | 27.8 | 341.3 | 130 |
| *UMN3008* | Liu et al. [2002] | 56 | 43.3 | 538.2 | <300 | 56 | 27.8 | 239.4 | <300 |
| *XBM451* | Sonstegard et al. [2001] | 65 | 28.9 | 49.2 | <200 | Positive for all $BBURH_{5000}$ cell lines | | | |
| *Yp11_Rep* (E12119)[b] | GCAAAAGACAGACTGGCACA ATGCTGCTTCAGGGAGAAAA | 60 | 40 | 249.4 | <200 | 61 | 40 | excluded | <200 |
| *Y_Probe* (E04509)[b] | CGTGAACGAAGACGAAAGGT TCTCTGTGCCTCCTCAAAGAA | 58 | 18.9 | excluded | <200 | Weak signal after PCR amplification | | | |
| *ZFY* (AJ002270)[b] | CCATCGAATGTGATGAATGTGGG TCCGCATGTGCTTTCTAAGCTCTG | 60 | 22.2 | 123.8 | <300 | 59 | 24.4 | 266.3 | <300 |

[a] RF(%): retention frequency.
[b] New designed primers (in parentheses the corresponding GenBank accession number).

sponding band(s) were excised and purified by QIAquik Gel Extraction kit (Qiagen). The DNA was cloned into a pGEM®-T Easy Vector (Promega, Madison, Wisc., USA). JM109 High Efficiency competent cells (Promega) were used for transformations. Each transformation experiment was carried out in a 100-μl volume and was plated onto duplicate LB/ampicillin/IPTG/X-Gal plates. The cloned fragment of DNA was PCR amplified using the T7/SB6 priming sites of the cloning vector. The resulting PCR products were used as templates for sequencing using the forward and reverse primers of bovine specific marker. Sequencing was carried out at the Advanced Genetic Analysis Center of the University of Minnesota. Sequences were generated and analyzed with the BioEdit 7.0.9 software [Hall, 1999].

## Results and Discussion

We herein present the first RH map for the river buffalo Y chromosome using the $BBURH_{5000}$ panel [Amaral et al., 2007], incorporating markers available on published bovine Y-chromosome linkage [Kappes et al., 1997; Sonstegard et al., 2001] and RH maps [Liu et al., 2002, 2003].

Among the initial 41 selected cattle-derived markers, a subset of 26 markers generated PCR products suitable for scoring with the $BBURH_{5000}$ panel. Failures on PCR amplification were observed with 15 markers. Amplification of multiple PCR products with buffalo DNA were observed in 10 of these discarded markers *(AMELY, BC1.2, BM861, BYM-1, HEL26, INRA057, INRA126, UMN0301, UMN0307* and *UMN0905)* while a weak signal after PCR amplification and failure to amplify were observed in 3 *(INRA030, UMN0504* and *Y_Probe)* and 2 *(INRA124* and *UMN0910)* of the markers, respectively. With exception of 1 marker *(P1F4T)* that also generated amplification with hamster DNA, PCR products were observed only with buffalo DNA. The marker *XBM451* showed amplification in all cell lines and was also discarded.

The remaining 26 markers amplified PCR products suitable for genotyping with the $BBURH_{5000}$ panel. Of these, 19 markers (73%) were distributed in 1 linkage group spanning 341.3 cR (fig. 1).

The RH map is based on a framework map composed of 9 markers. The remaining 10 markers, which did not meet the statistical criteria for a frame marker, were individually inserted to the most probable position. Two markers *(P1F4T* and *TSPY)* were assigned to the same position on the RH map. Six markers *(EIF1AY, INRA189, SMCY, SRY-HMG, UMN0803* and *Yp11_Rep)* were dropped because they could not be included in the framework map or placed with confidence with respect to the framework map. Retention frequencies (RF) for individual markers ranged from 17.8% for *SMCY* to 56.7% for *BTY1*, with an average RF of 37.6%. This value is higher than the previously described RF of 27.3% observed for the whole buffalo genome and the X chromosome [Amaral et al., 2008]. Higher than expected RFs on the haploid Y chromosome have been also previously observed in human [Gyapay et al., 1996; Stewart et al., 1997] and dog [Priat et al., 1998], whose RH panels were also male-derived.

A higher value in the retention frequency was observed in the region of the BBUY RH map between the markers *BOV97M* and *BTY1*. This kind of observation has been described as expected for markers near to the centromeric region [Murphy et al., 1999] or markers with multiple copies on the Y chromosome [Liu et al., 2002]. Further physical characterization of this region should provide useful information to clarify the kind of evolutionary rearrangements that occurred in the river buffalo Y chromosome.

Additional information about mapped markers, including their RF and cR position on the RH map, is compiled in table 1. Three mapped markers *(UMN0304*, *TGLA325* and *ZFY)* previously assigned by FISH to BBUY [Iannuzzi et al., 2003; Di Meo et al., 2005] were used to orient the BBUY RH map.

To compare the BBUY RH map to a BTAY RH map containing a higher number of common markers on both RH maps, we also constructed a similar resolution RH map for bovine Y chromosome using the $BTARH_{5000}$ panel [Womack et al., 1997].

From the selected markers described in table 1, 37 markers generated reliable scores using the $BTARH_{5000}$ panel. The majority of the markers amplified PCR products only with the bovine DNA, except the marker *UMN0307*, which also amplified a PCR product with the hamster DNA.

The newly constructed BTAY RH map (fig. 1) contains 28 markers distributed within 1 linkage group. Twenty-four of these markers had been previously mapped on BTAY using a 7,000-rad cattle-hamster WG-RH panel [Liu et al., 2002, 2003] and 4 markers were mapped for the first time *(ZFY*, *SeqRep*, *RepSeqS4* and *BTY1)*.

Of the 28 markers, 14 were reliably positioned on the framework map, and the remaining 14 markers were placed one by one on their most likely position on the map. The length of the BTAY RH map was estimated to be 602.4 cR (fig. 1). The map was consistently oriented with the cytogenetic map for cattle Y chromosome [Di Meo et al., 2005] with the markers *TGLA325*, *ZFY*,

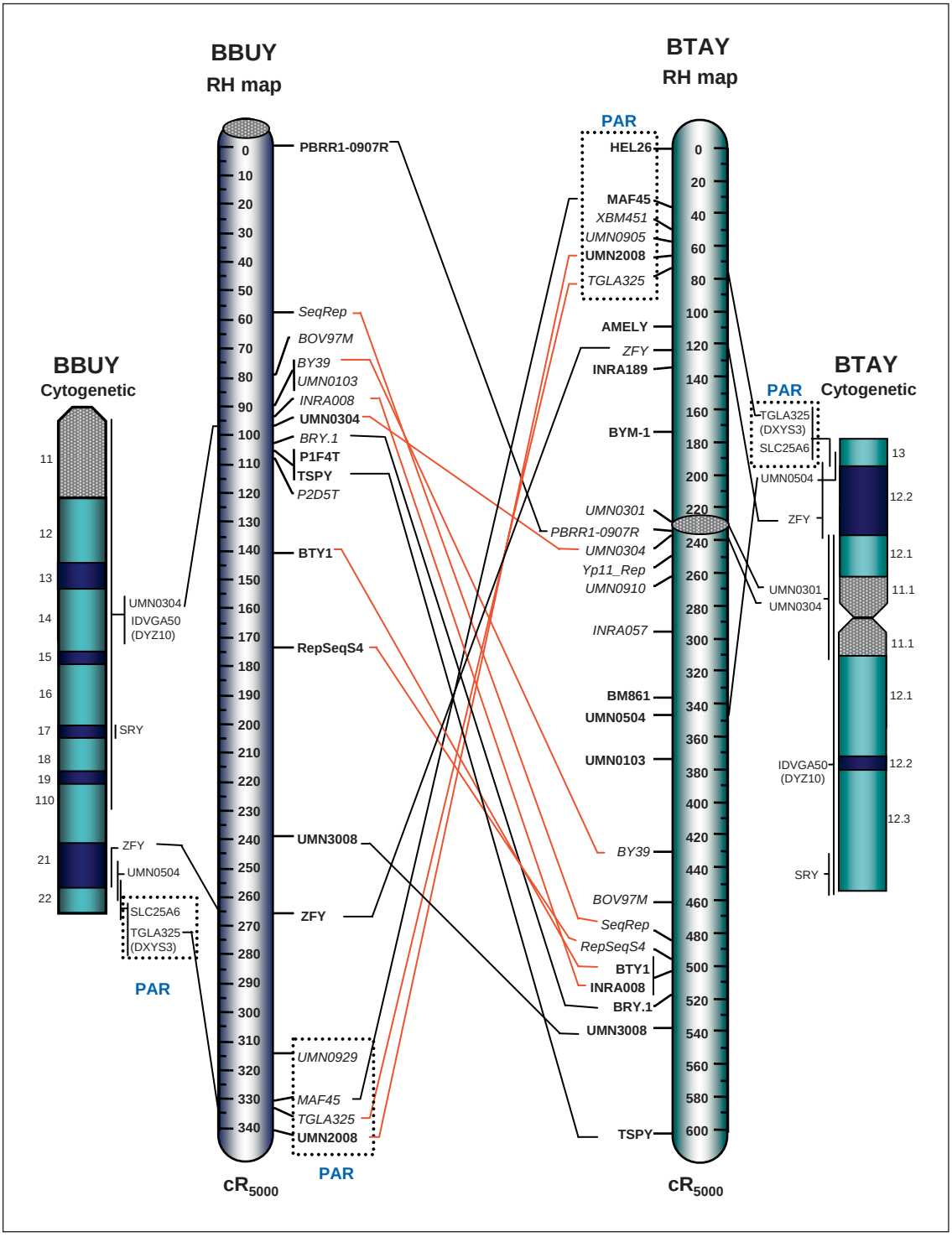


**Fig. 1.** Comparison of the BBUY RH map (left) with the BTAY RH map (right). The cytogenetic ideogram [Di Meo et al., 2005] for the buffalo and the bovine Y chromosomes are represented on the side of each RH map. Framework markers, whose order is better than the second best at least 0.50 LOD units, are in bold font. Markers common to both the BBUY and the BTAY RH maps are joined by black or red solid lines. Solid red lines indicate markers which are oriented sequentially regarding the cattle but inverted in buffalo. A black line also joins those markers on the RH maps that have been physically mapped by FISH to their location on the ideogram [Di Meo et al., 2005]. Positions on both RH maps are in $cR_{5000}$. The distances are shown in each corresponding map. The pseudoautosomal regions (PAR) are indicated in dotted boxes.

**Table 2.** BTAY and BBUY sequence comparisons of some of the BTAY markers used for the construction of the BBUY RH map. Markers in bold are represented on the BBUY RH map. Accession numbers for the buffalo genomic DNA sequences are amplified with bovine PCR primers

| Bovine | | | | Buffalo | | | | Homology |
|---|---|---|---|---|---|---|---|---|
| Name of marker | GenBank accession number | Type of repeat | Size bp | Name of marker | GenBank accession number | Type of repeat | Size bp | |
| ***INRA008*** | X73126 | $(TG)_{16}$ | 120 | ***INRA008BBU*** | GQ273501 | $(TG)_3TC(TG)_3(TC)_3$ | 116 | 87% |
| ***UMN0304*** | AF483758 | $(TAAA)_3TA(CA)_{16}$ | 187 | ***UMN0304BBU*** | GQ273503 | $(TAA)_3(CA)_{15}$ | 213 | 93% |
| *UMN0803* | AF483745 | $(CA)_{4-6}$ CCCTCACACAA$)_6$ | 284 | *UMN0803BBU* | GQ273504 | $(CA)_{3-6}$ $(CCCTCACAC)_4$ [TTA/T$]_5$[CATA] | 268 | 95% |
| ***UMN0929*** | AF483749 | $(CA)_{19}$ | 190 | ***UMN0929BBU*** | GQ273505 | $(CA)_{13}$ | 178 | 89% |
| ***UMN2008*** | AF483746 | $(CA)_2(CA)_{11}G–(CA)_3$ | 140 | ***UMN2008BBU*** | GQ273500 | $(CA)_9CCATACACCT(CA)_5$ | 130 | 90% |

*UMN0301*, *UMN0304* and *UMN0504*. Of the total number of markers genotyped on the $BTARH_{5000}$ panel (37), 9 markers *(BC.12, EIF1AY, INRA030, INRA124, INRA126, SMCY, SRY-HMG, UMN0307* and *Y_Probe)* could not be ordered.

Retention frequencies for all mapped markers ranged from 10% *(INRA126)* to 63.3% *(SeqRep)*, with an average RF of 35.3%. The markers *BTY1* and *INRA008* were assigned to the same cR position on BTAY RH map. Additional information about the markers is presented in table 1. Primer pairs for bovine microsatellites *UMN0929*, *UMN0803*, *UMN0304*, *UMN2008* and *INRA008* amplified river buffalo DNA fragments containing microsatellite sequences (table 2). These markers can potentially be used for parentage analysis and segregation studies.

In general, a lower value in the retention frequency was observed for the markers genotyped in this study, using both RH panels constructed with 5,000-rads, when compared with the values observed for the same markers previously genotyped using a 7,000-rad cattle RH panel [Liu et al., 2002]. For instance, markers *BRY.1, TSPY, BOV97M* and *INRA008* showed, respectively, an RF of 52.2, 45.5, 53.3 and 57.8% using the $BTARH_{5000}$ panel; 54.4, 56.7, 51.1 and 47.8% with the $BBURH_{5000}$ panel, and 67, 70.5, 69.4 and 67.9% with the 7,000-rad panel.

Figure 1 also indicates differences in the order of some of the markers, when BBUY and BTAY RH maps were compared. Considering the differences in morphology of the Y chromosomes relative to the centromere position on both species, acrocentric in river buffalo and submetacentric in cattle, differences in the order of the markers were expected, and may represent the potential breakpoints that occurred during the differentiation of BBUY and BTAY. It is also possible that as more markers are placed on the BBUY RH map, relative positions assigned to the markers may change.

Markers *HEL26*, *XBM451*, *UMN0905*, *MAF45*, *TGLA325* and *UMN2008* on the BTAY RH panel are known to be located on the pseudoautosomal region (PAR) of the Y chromosome, meaning that the selected PCR primers were also complemented with sequences from the bovine X chromosome [Iannuzzi et al., 2000; Liu et al., 2003; Di Meo et al., 2005]. Our BBUY RH mapping results confirmed the previous assignment of the pseudoautosomal region (PAR) to the terminal portion of BBUY [Iannuzzi et al., 2003; Di Meo et al., 2005], where, for the first time 3 markers, *UMN0929, MAF45,* and *UMN2008*, were assigned to this region and compared with the positions of those markers mapped to the PAR region on BTAY.

Considering that a genetic linkage map does not exist for river buffalo, the first radiation hybrid map for the Y chromosome generated in this study provides valuable data for comparative mapping. Increasing the number of genes on the BBUY RH map and comparing their positions with the map locations on BTAY will elucidate the conserved breakpoints between these 2 chromosomes.


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