Current Status of the River Buffalo (*Bubalus bubalis* L.) Gene Map

S. M. El Nahas, H. A. de Hondt, and J. E. Womack

Ninety-nine loci have been assigned to river buffalo chromosomes, 67 of which are coding genes and 32 of which are anonymous DNA segments (microsatellites). Sixty-seven assignments were based on cosegregation of cellular markers in somatic cell hybrids (synteny), whereas 39 were based on in situ hybridization of fixed metaphase chromosomes with labeled DNA probes. Seven loci were assigned by both methods. Of the 67 assignments in somatic cell hybrids, 38 were based on polymerase chain reaction (PCR), 11 on isozyme electrophoresis, 10 on restriction endonuclease digestion of DNA, 4 on immunofluorescence, and 4 on chromosomal identification. A genetic marker or syntenic group has been assigned to each arm of the five submetacentric buffalo chromosomes as well as to the 19 acrocentric autosomes, and the X and Y chromosomes. These same markers map to the 29 cattle autosomes and the X and Y chromosomes, and without exception, cattle markers map to the buffalo chromosome or chromosomal region predicted from chromosome banding similarity.

The river buffalo is an economically important livestock species in many Asian and Mediterranean countries, and its genetic improvement, especially in reproductive performance and quantity of meat and milk production, ranks high among agricultural research needs of these countries. The majority of important traits in buffalo, as in other farm animals, are polygenic in nature and therefore difficult to isolate and identify at the genome level. However, recent success in mapping quantitative trait loci (QTL) in cattle, pigs, and other livestock species has demonstrated new opportunities for analyzing, and eventually controlling, these continuously distributed traits (Andersson et al. 1994; Georges et al. 1995).

Animal improvement by the genomic approach has been targeted by establishing physical and linkage maps as tools for developing more efficient breeding strategies. Physical mapping includes the use of somatic cell hybrids and in situ hybridization to determine syntenic relationships between loci and to assign loci to specific regions of their respective chromosomes. The establishment of a physical map at the chromosomal level of resolution will facilitate the development of a genetic map, which defines the linear relationship of the loci on the chromosome and estimates the distances between them by frequency of meiotic recombination. Genetic maps will be used to study economically important trait loci. A saturated map of markers, applied to reference families segregating economic traits, will reveal the existence of linkage associations between some of these trait loci and microsatellite markers. Microsatellite markers are easy to identify and often highly polymorphic, and will thus permit marker-assisted selection (MAS) of desirable traits to which they are linked. Some of these marker-trait associations have already been discovered in cattle (Georges et al. 1995).

The close chromosomal relationship between buffalo and cattle is useful in constructing the buffalo genome map. Extensive chromosome arm homology between cattle and river buffalo has been established (Report of the Committee for the Standardization of Banded Karyotypes of the River Buffalo 1994). While the cattle genome consists of 29 acrocentric autosomes plus the X and Y chromosomes, the buffalo genome has 5 biarmed and 19 acrocentric autosomes. Thus the arm number is identical between the species and every arm of the five biarmed buffalo chromosomes has banding similarity to a cattle acrocentric chromosome. Comparative cytogenetics and physical gene mapping have shown that chromosome band identity between closely related species is

From the Department of Cell Biology, National Research Center, Cairo, Egypt (El Nahas and de Hondt) and Department of Veterinary Pathobiology, College of Veterinary Medicine, Texas A&M University, Hwy. 60, College Station, TX 77843 (Womack). Address correspondence to J. E. Womack at the address above or e-mail: jwomack@cvm.tamu.edu.

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a good indicator of genetic homology (Nash and O'Brien 1982) and therefore chromosome banding conservation is predictive of conservation of genetic content. Because of the extensive chromosome conservation between cattle and river buffalo, the cattle physical map can potentially function as a template for developing the buffalo gene map.

The cattle genome is well characterized, with synteny and linkage groups assigned to each chromosome (Masabanda et al. 1996; Mezzelani et al. 1994). Based on banding similarity, the five submetacentric pairs of the buffalo are assumed to originate from fusion of 10 cattle acrocentrics (Report of the Committee for the Standardization of Banded Karyotypes of the River Buffalo 1994). There is no obvious rearrangement of banding pattern in any of the autosomal arms, although the X chromosomes reveal morphologic differences, including the location of the centromere. So far 67 coding genes and 32 DNA segments (microsatellites) have been assigned to river buffalo chromosomes (Figure 1, Table 1). Thirty-nine loci were assigned directly to chromosomes using in situ hybridization, whereas 67 loci were assigned to syntenic groups and to chromosomes using somatic cell hybrids (7 loci were assigned by both methods). These assignments were made in a panel of 37 hybrids resulting from a fusion of the Chinese hamster cell line wg3h with river buffalo lymphocytes (El Nahas et al. 1996b). The investigated markers cover 29 cattle autosomes and the X and Y chromosomes. A marker or a syntenic group was assigned to each arm of the five buffalo submetacentrics plus the 19 acrocentric autosomes and the X and Y chromosomes. Comparative synteny mapping has confirmed the hypothesis that the five submetacentric chromosome pairs of the river buffalo arose by centric fusion of 10 cattle acrocentric pairs, and has also contributed to identifying the nature of the biarmed buffalo chromosome (de Hondt et al. 2000; El Nahas et al. 1997, 1999; Othman and El Nahas 1999). Up to now, no syntenic discrepancies have been found between cattle and buffalo. It should be pointed out here that in 1996, the Texas nomenclature reversed the position of cattle chromosomes 4 and 6 in the Reading Conference (1980) and ISCNDA 89 (1990) nomenclature, taking chromosome 6 as 4 and vice versa. As a result, U13, previously assigned to BTA 4 (Neibergs et al. 1993) and consequently to BBU 7 (El Nahas et

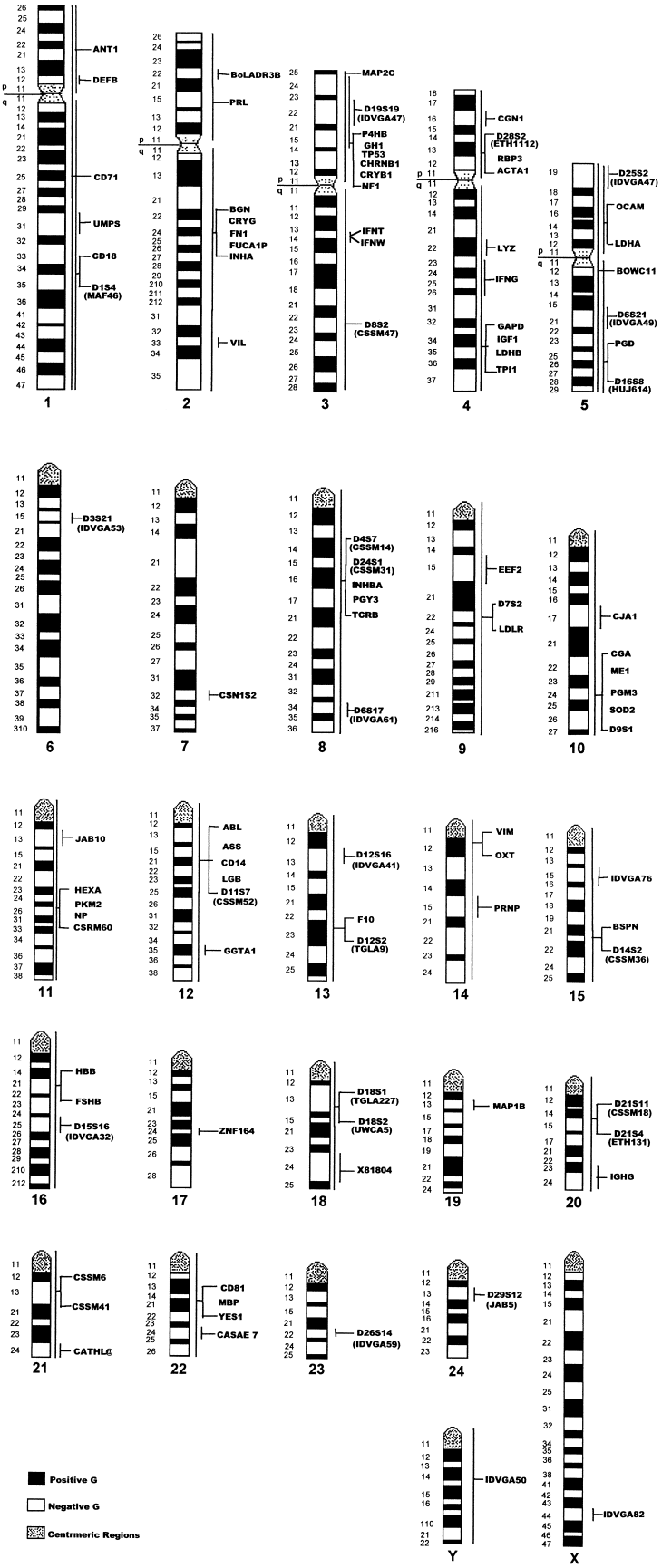

Figure 1. Ideogram of the river buffalo according to the standard G-banded karyotype (Report of the Committee for the Standardization of Banded Karyotypes of the River Buffalo 1994) with physical location of loci referenced in Table 1.

Table 1. Alphabetical list of loci mapped in river buffalo

Locus symbol	Locus name	Buffalo chromosomal location	Cattle chromosomal location	Mode	Reference
ABL1	Abelson murine viral oncogene homolog	BBU 12	BTA11	SR	El Nahas et al., 1996a
ACTA1	Alpha skeletal actin	BBU 4p	BTA28	SR	El Nahas et al., 1996a
ANT1	Adenine nucleotide translocator 1	BBU 1p	BTA27	SP	El Nahas et al., 1997
ASS	Argininosuccinate synthetase	BBU 12	BTA11	SR	El Nahas et al., 1996a
BoLADR3B	Major histocompatability complex class II, DR beta 1	BBU 2p22	BTA23	SP, ISH	de Hondt et al., 2000; Iannuzzi et al., 1993c
BoWC11	Bovine workshop cluster 11	BBU 5	BTA25 or 16	SI	Abou-Mossallem, 1999
BSPN	Brain specific protein η amino chain	BBU 15	BTA14	SP	de Hondt et al., 1997
CSN1S2	Alpha-S2-casein	BBU 7q32	BTA6q31	ISH	Iannuzzi et al., 1996b
CATHL@	Cathelicidin	BBU 21q24	BTA22q24	ISH	Iannuzzi et al., 1998a
CD 14	Antigen CD 14, LPS-binding protein	BBU 12	BTA11	SI	El Nahas et al., 1996b
CD 18	Antigen CD 18, lymphocyte function-associated antigen	BBU 1q	BTA1	SP	de Hondt et al., 1997
CD 71	Antigen CD71, transferrin receptor	BBU 1	BTA1 or 27	SI, SC	El Nahas et al., 1996b; Ramadan et al., 2000
CD 81	Antigen CD81 (TAPA-1)	BBU 22	BTA24	SI	Abou-Mossallem, 1999
CGA	Glycoprotein hormone α-polypeptide	BBU 10	BTA9	SP	de Hondt et al., 1997
CGN1	Conglutinin	BBU 4p16	BTA22q18	ISH, SR	El Nahas et al., 1996a; Iannuzzi et al., 1994b
CHRNB1	Cholinergic receptor, nicotinic, β-polypeptide	BBU 3p15	BTA19	ISH	Iannuzzi et al., 1999
CJA1	Connexin 43	BBU 10q17	BTA9q15-q16	ISH	Iannuzzi et al., 1998a
CRYB1	Crystallin β-polypeptide 1	BBU 3p15	BTA19	ISH	Iannuzzi et al., 1999
CRYG	Crystallin α-polypeptide	BBU 2q	BTA2	SR	El Nahas et al., 1996a
DEFB	Beta-defensin	BBU 1p12	BTA27	ISH	Iannuzzi et al., 1996a
EEF2	Elongation factor 2	BBU 9q15	BTA7q15	ISH	Iannuzzi et al., 1997a
F10	Coagulation factor X	BBU 13	BTA12	SP	Oraby et al., 1998
FN1	Fibronectin	BBU 2q	BTA2	SP	Othman and El Nahas, 1999
FSHB	Beta-follicle stimulating hormone	BBU 16	BTA15	SP	Oraby et al., 1998
FUCA1P	Fucosidase alpha-L-1 tissue	BBU 2q	BTA2	SR	El Nahas et al., 1996a
GAPD	Glyceraldehyde-3-phosphate dehydrogenase	BBU 4q	BTA5	SZ, SC	de Hondt et al., 1991; El Nahas et al., 1993
GGTA1	Alpha-galactosyltansferase 1	BBU 12q36	BTA11q26	ISH	Iannuzzi et al., 1997a
GH1	Growth hormone	BBU 3p24	BTA9q22	ISH	Iannuzzi et al., 1999
HBB	Beta hemoglobin	BBU 16	BTA15q22q27	SP	Oraby et al., 1998
HEXA	Beta-N acetyl glucosaminidase	BBU 11	BTA10	SZ	El Nahta, 1996
IFNG	Gamma interferon	BBU 4q23-26	BTA5q22-q24	ISH	Hassanane et al., 1994
IFNT	Trophoblast interferon	BBU 3q15	BTA8q15	ISH	Iannuzzi et al., 1993b
IFNW	Omega interferon	BBU 3q15	BTA8q15	ISH	Iannuzzi et al., 1993b
IGF1	Insulin-like growth factor 1	BBU 4q	BTA5	SP	El Nahas et al., 1999
IGHG	Immunoglobulin gamma heavy chain	BBU 20q23-25	BTA21q24	ISH	Hassanane et al., 1993
INHA	Inhibin A subunit	BBU 2q	BTA2q36-q42	SP	de Hondt et al., 2000
INHBA	Inhibin beta-A	BBU 8	BTA4q26	SP	Othman and El Nahas, 1999
LDHA	Lactate dehydrogenase A	BBU 5p	BTA29	SZ	El Nahas et al., 1999
LDHB	Lactate dehydrogenase B	BBU 4q	BTA5	SZ, SC	de Hondt et al., 1991; El Nahas et al., 1993, 1999
LDLR	Low-density lipoprotein receptor	BBU 9	BTA7	SP	de Hondt et al., 1997
LGB	Lactoglobulin beta	BBU 12	BTA16q28	SP	Othman and El Nahas, 1999
LYZ	Lysozyme	BBU 4q23	BTA5q23	ISH	Iannuzzi et al., 1993a
MAP1B	Microtubule associated protein	BBU 19q13	BTA20q14	ISH	Iannuzzi et al., 1998a
MAP2C	Microtubule associated protein 2	BBU 3p	BTA19	SP	de Hondt et al., 2000
MBP	Myelin basic protein	BBU 22	BTA24q11-q13.2	SR	El Nahas et al., 1996a
ME1	Malic enzyme	BBU 10	BTA9	SZ	de Hondt et al., 1991; El Nahas et al., 1998
NF1	Neurofibromatosis	BBU 3p13	BTA19q14	ISH	Iannuzzi et al., 1999
NP	Nucleoside phosphorylase	BBU 11	BTA10	SZ	El Nahas et al., 1998
OCAM	Opoid binding and cell adhesion molecule	BBU 5p	BTA29	SP	El Nahas et al., 1999
OXT	Prepro-oxytocin	BBU 14	BTA13	SP	de Hondt et al., 1997
P4HB	2-oxoglutarate 4-dioxygenase, β-polypeptide	BBU 3p24	BTA19	ISH	Iannuzzi et al., 1999
PGD	Phosphogluconate dehydrogenase	BBU 5q	BTA16	SZ	El Nahas et al., 1999
PGM3	Phosphoglucomutase	BBU 10	BTA9	SZ	El Nahas et al., 1998
PGY3	P glycoprotein 3/multiple drug resistance	BBU 8*	BTA4	SR	El Nahas et al., 1996a
PKM2	Pyruvate kinase muscle 2	BBU 11	BTA10	SZ	El Nahas et al., 1998
PRL	Prolactin	BBU 2p	BTA23	SP	Othman and El Nahas, 1999
PRNP	Normal host prion protein	BBU 14	BTA13q17	SP, ISH	de Hondt et al., 1997; Iannuzzi et al., 1998b
RBP3	Retinol-binding protein 3 interstitial	BBU 4p	BTA28	SP	El Nahas et al., 1999
SOD2	Superoxide dismutase	BBU 10	BTA9	SZ	de Hondt et al., 1991
TCRB	T-cell receptor beta cluster	BBU 8*	BTA4	SR	El Nahas et al., 1996a
TP53	Tumor protein p53	BBU 3p21	BTA19q15-q16	ISH	Iannuzzi et al., 1999
TPI1	Triose-phosphate isomerase 1	BBU 4q	BTA5	SZ, SC	de Hondt et al., 1991; El Nahas et al., 1993
UMPS	Uridine monophosphate syntase	BBU 1q31	BTA1q31-q36	ISH	Iannuzzi et al., 1994a
VIL	Villin	BBU 2q33	BTA2q43	ISH	Iannuzzi et al., 1997e
X81804	Zinc finger protein	BBU 18	BTA18	ISH	Iannuzzi et al., 1997b
YES1	Yamagushi sarcoma viral oncogene homolog 1	BBU 22	BTA24	SR	El Nahas et al., 1996a
ZNF164	Zinc finger protein 164	BBU 17	BTA17q24	ISH	Iannuzzi et al., 1997b
COSAE7	DNA segment	BBU 22q24	BTA24q23	ISH	Iannuzzi et al., 1998a
CSRM60	DNA segment	BBU 11	BTA10	SP	de Hondt et al., 2000
CSSM6	DNA segment	BBU 21	BTA22	SP	de Hondt et al., 2000
CSSM41	DNA segment	BBU 21	BTA22	SP	de Hondt et al., 2000
D1S4	DNA segment (MAF 46, ovine)	BBU 1q	BTA1	SP	de Hondt et al., 1997
D3S29	DNA segment (IDVGA 53)	BBU 6q15	BTA3q21	ISH	Iannuzzi et al., 1997a
D4S7	DNA segment (CSSM14)	BBU 8	BTA4	SP	Othman and El Nahas, 1999
D6S17	DNA segment (IDVGA 61)	BBU 8q34	BTA6q32	ISH	Iannuzzi et al., 1997a
D7S3	DNA segment	BBU 9	BTA7	SP	de Hondt et al., 1997
D8S2	DNA segment (CSSM47)	BBU 3q	BTA8	SP	de Hondt et al., 2000

Table 1. Continued

Locus symbol	Locus name	Buffalo chromosomal location	Cattle chromosomal location	Mode	Reference
D9S1	DNA segment (ETH 225)	BBU 10	BTA9	SP	de Hondt et al., 1997
D11S7	DNA segment (CSSM52)	BBU 12	BTA11	SP	Othman and El Nahas, 1999
D12S16	DNA segment (IDVGA 41)	BBU 13q15	BTA12q15	ISH	Iannuzzi et al., 1997a
D12S2	DNA segment (TGLA 9)	BBU 13	BTA12	SP	Oraby et al., 1998
D14S2	DNA segment (CSSM36)	BBU 15	BTA14	SP	de Hondt et al., 1997
D15S16	DNA segment (IDVGA 32)	BBU 16q25	BTA15q25	ISH	Iannuzzi et al., 1997a
D16S21	DNA segment (IDVGA49)	BBU 5q21	BTA16q17	ISH	Iannuzzi et al., 1997c
D16S8	DNA segment (HUJ614)	BBU 5q	BTA16	SP	El Nahas et al., 1999
D18S1	DNA segment (TGLA227)	BBU 18	BTA18	SP	Oraby et al., 1998
D18S2	DNA segment (UWCA5)	BBU 18	BTA18	SP	Oraby et al., 1998
D19S19	DNA segment (IDVGA47)	BBU 3p22	BTA19q17	ISH	Iannuzzi et al., 1997c
D21S4	DNA segment (ETH 131)	BBU 20	BTA21	SP	de Hondt et al., 2000
D21S11	DNA segment (CSSM18)	BBU 20	BTA21	SP	de Hondt et al., 2000
D24S3	DNA segment (CSSM31)	BBU 8*	BTA4	SP	de Hondt et al., 2000
D25S2	DNA segment (IDVGA7)	BBU 5p19	BTA29	ISH	Iannuzzi et al., 1997c
D26S14	DNA segment (IDVGA 59)	BBU 23q22	BTA26q22	ISH	Iannuzzi et al., 1997a
D28S2	DNA segment (ETH1112)	BBU 4p	BTA28	SP	El Nahas et al., 1999
D29S12	DNA segment (IDVGA 71)	BBU 24q13	BTA25	ISH	Iannuzzi et al., 1997a
IDVGA50	DNA segment	BBUY	BTA Y	ISH	Iannuzzi et al., 1998a
IDVGA76	DNA segment	BBU 15q15	BTA14q14	ISH	Iannuzzi et al., 1998a
IDVGA82	DNA segment	BBUXq44	BTAXq34	ISH	Iannuzzi et al., 1998a
JAB10	DNA segment	BBU 11q13	BTA10	ISH	Iannuzzi et al., 1998a

ISH: direct assignment using in situ hybridization; S: indirect assignment using somatic cell hybrids; P: polymerase chain reaction; Z: isozyme electrophoresis; R: restriction endonuclease; I: immunofluorescence; C: chromosomal identification.

* Assignment was corrected after Texas nomenclature (1996) (previously assigned to BBU 7).

al. 1996a) is now assigned to BTA 6 and BBU 8.

A linkage map of microsatellites or other highly polymorphic markers has not yet been established for river buffalo. It appears, however, that cattle microsatellites are conserved in the buffalo genome and map to the chromosomes predicted from similarity of banding patterns. If these conserved microsatellites are polymorphic in river buffalo, genome scans for buffalo QTL can be performed with microsatellites derived from cattle and organized on cattle linkage maps. Studies to determine the relative polymorphic information content (PIC) of cattle microsatellites in buffalo must be done to facilitate the approach. It is also likely that recombination rates between colinear markers will vary in cattle and buffalo gametogenesis. The potential for variation in recombination may be enhanced around the centromeres of the biarmed buffalo chromosomes.

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