

GENETIC AND PHYLOGENETIC STUDIES OF TOLL-LIKE RECEPTOR 5 (TLR5)
IN RIVER BUFFALO (*BUBALUS BUBALIS*)

A Dissertation

by

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ABSTRACT

River buffalo are economically important to many countries and only recently has their genome been explored for the purpose of mapping genetic variation in traits of economic and biologic interest. The purpose of this research is to characterize the genetic and evolutionary profile of Toll-like receptor 5 (TLR5), which mediates the mammalian innate immune response to bacterial flagellin.

This study is comprised of three parts: 1) generating a radiation hybrid (RH) map of river buffalo chromosome 5 (BBU5) where the TLR5 gene is located and building a comparative map with homologous cattle chromosomes; 2) conducting a single-nucleotide polymorphism (SNP) survey of the TLR5 gene to reveal variation within river buffalo and other species; and 3) performing an evolutionary study by inferring phylogenetic trees of TLR5 across multiple taxa and determining the possible evolutionary constraints within the TLR5 coding region.

River buffalo chromosome 5 is a bi-armed chromosome with arms corresponding to cattle chromosomes 16 and 29. A BBU5 RH map was developed using the previously published river buffalo RH mapping panel and cattle-derived markers. The RH map developed in this study became an integral part of the first river buffalo whole genome RH map.

Genetic variation of the TLR5 gene was evaluated in a small domestic herd of river buffalo. Sequencing of the TLR5 coding region and partial associated 5'- and 3'- untranslated regions yielded 16 novel SNPs. Six SNPs were identified as non-synonymous with one predicted to potentially code for a functionally altered product.

For the evolutionary study of the TLR5 coding region, phylogenetic trees were inferred based on TLR5 variation across multiple orders and another for artiodactyla. Species that are closely related to river buffalo appear to have undergone negative selection in TLR5 while those that diverged from river buffalo earlier may be retaining alleles that river buffalo are removing from the population.

In conclusion, putative chromosomal rearrangements were identified between river buffalo and cattle, the variation that was uncovered in the TLR5 coding region could potentially lead to differential immunity across species, and there appears to be some evolutionary flexibility in the DNA sequence of the TLR5 coding region.

DEDICATION

To my mother, brother, and sister. You're the best.

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CHAPTER I

INTRODUCTION

Economic and Research Comparisons of Cattle and Buffalo

Cattle are the predominant livestock species in the United States and many parts of the world, where the sheer number of head illustrates their importance both economically and socially. Worldwide, the number of cattle was estimated to be about 1.4 billion in 2010 (FAO, 2012). Thirty-six percent of the cattle population reside in the Americas (North and South), with 94 million produced in the United States of America. Thirty-three percent of cattle are found in Asia, twenty percent in Africa, and the rest spread across Europe and Oceania (FAO, 2012). These numbers are important factors in the investment in scientific research worldwide, as the sheer volume of cattle consumes many resources in terms of time, money, and energy. Because cattle are dominant among the ruminant agricultural species, they are also the predominant ruminant livestock species in terms of research investment.

Cattle have also served as model organisms in several areas of biomedical research. Cattle and other large animal models have proven useful in the areas of modern vaccination programs (smallpox), reproduction technologies (in vitro embryo production, sperm conservation, and artificial insemination), and neurodegenerative disease (bovine spongiform encephalopathy), to name a few (Polge *et al.*, 1949; Foote, 1982; Barquet & Domingo, 1997; Hasler, 1998; Dalton *et al.*, 2001; Watts *et al.*, 2006).

As a consequence, cattle genetic resources have been developed in the biomedical research community as well as in the agricultural research community.

The economic burden on producers of livestock is immense and failure to efficiently manage production, breeding, and disease can devastate an industry. It is for this reason that the potential for possible outbreaks of diseases, such as bovine respiratory disease, brucellosis, and bovine spongiform encephalitis, to name a few, cause lasting harm to a region after an outbreak even years after the issue has been resolved. As an example, if foot and mouth disease is found within the population, that country is prohibited from exporting livestock (USDA, 2012). Thus, host response to pathogens remains an important area of genetic research in cattle and other livestock species.

It is useful to examine cattle statistics in the context of other economically important livestock. While cattle reign supreme and impact the economies of many nations, water buffalo are also economically important to many regions of the world, particularly Asia. Ninety-seven percent of the water buffalo population, or about 188 million head, reside in Asia. Two percent of water buffalo are found in Africa. The remaining populations of water buffalo are spread across Europe, the Americas, and Oceania (FAO, 2012). Despite the fact that there are more head of cattle worldwide than there are water buffalo, more people worldwide rely on water buffalo for a larger variety of activities. Not only are water buffalo utilized as a food source, as both dairy and meat, they are also used for draught power in many parts of the world because they are capable of moving heavier loads than cattle (Michelizzi *et al.*, 2010).

Because water buffalo, specifically river buffalo, are an important livestock species worldwide, understanding and examining their genetics can potentially have a positive impact on the agricultural productivity of many developing nations. Studying the genetics of river buffalo also has the potential to benefit the cattle industry through comparative studies because of their close evolutionary relationship. Therefore, the focus of this research is the river buffalo and the genetics of Toll-like receptor 5, a gene of importance to the innate immune system of mammals.

Water Buffalo: Economic and Production Importance

Water buffalo are a member of the order Artiodactyla, sub-order Ruminantia, family Bovidae, sub-family Bovinae, tribe Bovini (Borghese & Mazzi, 2005). The tribe Bovini includes the following genera: *Bos*, *Bison*, *Bubalus*, and *Syncera* (MacEachern *et al.*, 2009). Water buffalo is a single species, comprised of two economically important sub-species: river buffalo, *Bubalus bubalis bubalis*, and swamp buffalo, *Bubalus bubalis carabanesis* (Michelizzi *et al.*, 2010). River buffalo have been differentiated into breeds, while swamp buffalo largely remain as a single breed (Michelizzi *et al.*, 2010). The wild Asian buffalo (*Bubalus bubalis arnee*) is also considered a sub-species of water buffalo, but it is on the IUCN's (International Union for Conservation of Nature and Natural Resources) endangered species list as there are estimated to be less than 4,000 left in the wild and their population is rapidly declining (IUCN, 2011). Buffaloes, as a whole, are not to be confused with the American bison (*Bison bison*). It is common, especially in

the United States, for the two names to be used interchangeably, but they are separated on the genus level.

The two sub-species of water buffalo are used for different tasks. River buffalo are most often used as a meat and dairy source, while swamp buffalo are best used for draught power. Water buffalo are able to better utilize less digestible feeds for growth and nourishment than cattle, which make them particularly valuable to developing countries (Michelizzi *et al.*, 2010). The small producer is able to use and sustain buffalo as a food source and for draught power while utilizing cheaper food sources, thus requiring fewer economic resources.

Buffalo meat also has advantages as a food source. It is lower in saturated fat than beef and pork (Borghese, 2005a). In addition, buffalo meat has, so far, not been linked to mad cow disease (Borghese, 2005a).

While milk production for the buffalo lags significantly behind cattle dairy breeds, buffalo milk has higher total solids (18-23 percent) than cattle (13-16 percent) (FAO, 2000). Buffalo milk also has high casein to total protein ratio (81-84 percent) as opposed to cattle milk (78 percent) (Tripaldi *et al.*, 1997; Tripaldi *et al.*, 2003). The general demand for buffalo milk is also increasing. Fourteen percent of the buffalo milk that is produced in Italy is exported to Germany, France, the UK, Switzerland, the US, and Japan (Borghese, 2005b).

Anecdotally, water buffalo are healthier, on average, than cattle. Their wallowing behavior, which is due to the fewer number of sweat glands, exposes them to a large variety of pathogens. Though water buffalo are afflicted by many of the same pathogens

as other large ungulates, cattle in particular, disease effects on the animal and productivity are sometimes not as apparent as in cattle (Fagioli *et al.*, 2005).

Despite the many advantages that water buffalo boast, their reproductive efficiency is sub-optimal. Female water buffalo also express estrus weakly, so artificial insemination techniques have not had the impact they have generally had on cattle breeding and management programs (Barile, 2005).

This study focuses on the immunology of river buffalo, specifically the gene coding Toll-like receptor 5, which is important to innate immunity as it functions in recognizing broad motifs in pathogens or pathogen-associated molecular patterns (PAMPs) in mammals. Studying innate immunity is important because a poorly functioning immune system can negatively impact animal health which in turn can lead to monetary loss for producers.

Buffalo Genetics: Asiatic and African

To properly understand the important differences as discussed in the previous section (nutritional, fertilization, and hardiness disparities) between river buffalo and other large ungulates, these differences need to be examined first on a genetic level. There are two main species of buffalo: Asiatic (*B. bubalis*), which has two sub-species, the river (*B. b. bubalis*) and swamp (*B. b. carabanesis*) buffalo; and African, which is comprised of cape buffalo (*Syncerus caffer caffer*) and African forest buffalo (*Syncerus caffer nanus*). Cytogenetically, river buffalo have 50 chromosomes. River buffalo have 19 pairs of autosomal acrocentric chromosomes, 5 pairs of metacentric or

submetacentric autosomal chromosomes, and X and Y chromosomes (Iannuzzi, 2007). Swamp buffalo diverge from river buffalo in that they possess a diploid number of 48 chromosomes. This difference between river and swamp buffalo is the result of a river buffalo chromosomal fusion between *B. bubalis* (BBU) 4 and BBU9 in swamp buffalo (Iannuzzi, 2007; Amaral *et al.*, 2008). Hybrids between the two sub-species are possible, but the resultant offspring possess 49 chromosomes and may suffer from reduced fertility (Iannuzzi, 2007).

Bos taurus are also different from water buffalo in that they possess 60 chromosomes, 29 acrocentric autosomal chromosome pairs and the X and Y chromosome pair (Zimin *et al.*, 2009). To further illustrate the genetic differences between river buffalo and cattle, river buffalo have 5 bi-armed chromosomes, the remaining chromosomes cytogenetically correspond to *Bos taurus* acrocentric chromosomes (Amaral *et al.*, 2008). The fusion of BTA chromosomes 1 and 27 form BBU chromosome 1, BTA2 and BTA23 form BBU2, BTA8 and BTA19 form BBU3, BTA5 and BTA28 form BBU4, and BTA16 and BTA29 form BBU5 (El Nahas *et al.*, 2001; Iannuzzi *et al.*, 2003). River buffalo x cattle hybrids have not been observed, but inter-species fertilization is possible *in vitro* (Kochhar *et al.*, 2002).

In contrast, African buffalo have more chromosomes than their Asian counterparts. Cape buffalo have 52 chromosomes, with four being bi-armed. African forest buffalo have 54 chromosomes, with three being bi-armed. Crosses between Asian and African buffalo have not been reported and are unlikely to succeed owing to the fact

that they share no bi-armed chromosomes, which would yield unbalanced chromosome numbers in possible offspring (Iannuzzi, 2007).

Innate immune genes are not well studied in river buffalo. There have been studies performed in river buffalo describing the differential expression of TLR5 in river buffalo (Vahanan *et al.*, 2008), but to the best of the author's knowledge, no further discussion about possible evolutionary origins for the differential expression within river buffalo. This research represents the first detailed investigation of the TLR5 gene in river buffalo.

Toll-Like Receptor (TLR) Characteristics

The *Drosophila melanogaster* protein, Toll, was discovered by embryologist Christiane Nüsslein-Volhard of the Max Planck Institute in Tübingen, Germany in an analysis of mutations in fruit flies. In 1985, she saw abnormal fly larva in which the ventral portion of the body was underdeveloped. The protein product of the Toll gene was found to cause ventralization, and normal functional activity of Toll is necessary for dorsoventral polarity in the fly (Steward & Nusslein-Volhard, 1986). It is said that when researchers saw this, they were so surprised that they shouted in German, "Das war ja toll!" which translates as "That's weird!" (Hansson & Edfeldt, 2005). There seems to be some dispute as to the proper translation of "toll". German-to-English dictionaries indicate that "toll" can mean amazing, fantastic, great, wonderful, mad, crazy, or wild.

Building upon this study, it was reported that Toll not only controls dorsoventral polarity, but also has a role in the immune defense in *D. melanogaster*. It was discovered that flies with mutated Toll did not survive fungal infection. Toll activation triggers an NF- κ B cascade, which mounts the defense against fungi. The association with host defense became clearer based on the fact that the protein that induces ventralization, Spätzle, also initiates the NF- κ B cascade. Spätzle is the binding ligand for Toll (Lemaitre *et al.*, 1996).

The first reported cloning of the mammalian homologue of Toll, now called Toll-like receptors (TLR), occurred in 1997. Researchers were able to show that the pathway is conserved between *Drosophila* to humans. It was also discovered that the human homologue, which is known to be Toll-like receptor 4 (TLR4) had the ability to induce both adaptive and innate immunity. The construction of a constitutively active mutant determined that TLR induces NF- κ B activation in a comparable way as ligation of the interleukin (IL)-1 receptor, which is analogous to *Drosophila* Toll (Medzhitov *et al.*, 1997).

The members of the TLR family are type I transmembrane proteins and are evolutionarily conserved between insects and mammals (Anderson, 2000). They tend to recruit other intra- and extracellular proteins to the TLR-MyD88 complex, which initiates signaling cascades and will be discussed later in this chapter (Takeuchi *et al.*, 2000). Mammalian Toll-like receptors are expressed in neutrophils, monocytes, macrophages and dendritic cells (Akira *et al.*, 2001; O'Mahony *et al.*, 2008). Many TLRs are also

expressed on epithelial cells since the epithelial layer is the first point of entry for pathogens (Iwasaki & Medzhitov, 2004). They are also major players in cell death, innate-adaptive immunity crosstalk, and inflammatory conditions (Hansson & Edfeldt, 2005).

Toll-like receptors function within the innate immune system and recognize pathogen-associated molecular patterns (PAMPs). Toll-like receptors generally function as homodimers, but a few also form heterodimers. Ten TLRs have been identified and sequenced in humans and bovids, with thirteen found in the mouse (Kawai & Akira, 2006). Toll-like receptor 2 (TLR2) forms a heterodimer with TLR1 to recognize diacyl lipopeptides and another heterodimer with TLR6 to recognize triacyl lipopeptides (Kawai & Akira, 2006; Kurokawa *et al.*, 2012). TLR3 forms a homodimer to recognize double-stranded ribonucleic acid (RNA) (Alexopoulou *et al.*, 2001; Kawai & Akira, 2006). TLR4 forms a heterodimer to recognize bacterial endotoxin (Poltorak *et al.*, 1998; Kawai & Akira, 2006). TLR5 forms a heterodimer to recognize bacterial flagellin (Hayashi *et al.*, 2001; Kawai & Akira, 2006). Toll-like receptor 7 and TLR8 recognize single-stranded RNA (Hemmi *et al.*, 2002; Heil *et al.*, 2004; Kawai & Akira, 2006). TLR9 forms a homodimer to recognize unmethylated CpG islands (Hemmi *et al.*, 2000; Kawai & Akira, 2006). Toll-like receptors 1, 2, 4, 5, and 6 are located on the cell surface, while TLRs 3, 7, 8, and 9 are located within the cell on specialized organelles (Kawai & Akira, 2006).

The Toll-like family of receptors has been catalogued in water buffalo using reverse transcriptase PCR (RT-PCR). Mononuclear cells express all TLRs except TLR1.

Neutrophils express all TLRs except TLR3. The spleen, liver, and lungs express all TLRs. The heart lacked only TLR10 expression, while the kidneys expressed only TLRs 2, 5, 7, and 9. The uterus expressed all TLRs except TLRs 1, 3, 4, and 6, and the ovaries expressed all TLRs except TLR1 (Vahanan *et al.*, 2008). TLRs 2, 5, 7, and 9 were represented in all tissues surveyed. These TLRs are stimulated by lipoprotein, bacterial flagellin, single-stranded RNA, and unmethylated CpG islands respectively.

A comparable expression profile study was performed in goat using quantitative real-time PCR (qPCR). Data were normalized to glyceraldehyde phosphate dehydrogenase (GAPDH). Tissues surveyed included the lung, skin, uterus, jejunum, lymph node, spleen, and peripheral blood mononuclear cells (PBMNC). A threshold of greater than or equal to 0.5 was used to determine whether there was high expression. All tissues expressed all TLRs. Lungs expressed high levels of all TLRs except TLR4 and TLR10. The skin expressed high levels of TLRs 5, 6, and 7. The uterus expressed high levels of all TLRs except TLRs 3, 4, and 10. The jejunum expressed high levels of all TLRs except TLRs 3, 4, and 10. The lymph nodes expressed high levels of all TLRs. The spleen expressed high levels of all TLRs except TLR4 and TLR10. Finally, PBMNC expressed high levels of all TLRs except TLR10 (Tirumurugaan *et al.*, 2010). TLRs 1, 5, 6, and 7 were both expressed in all tissues and met the threshold of highly expressed.

The expression profile for TLRs has also been catalogued for humans using qPCR (Zarembek & Godowski, 2002). For direct comparison, only the tissues that the two studies have in common will be discussed. The study used expression levels for the spleen to normalize data. The heart, ovary, spleen, liver, lungs, kidney, and peripheral

blood leukocytes (PBLs) express all TLRs. To compare the goat and human expression profile studies that utilized qPCR, I arbitrarily used the goat metric of 0.5 to determine what can be considered “highly expressed” in humans. By using the 0.5 threshold, no TLR could be considered highly expressed in the heart; TLR5 is the only TLR highly expressed in the ovaries; TLRs 3, 5, and 7 were highly expressed in the kidneys; PBLs highly expressed all TLRs except TLRs 3, 7, 9 and 10; no TLRs were considered highly expressed for the liver; the lungs highly expressed TLRs 1, 2, 3, 5, 7, and 8; and the spleen highly expressed all TLRs.

The expression (in terms of presence or absence) differential between humans and water buffalo could be due to the fact that Vahanan *et al.* 2008 did not perform qPCR; therefore, it is possible that TLR expression in the buffalo was so low that presence or absence could not be detected by agarose gel electrophoresis, but would be detected by real-time PCR. In addition, river buffalo samples were collected from the slaughterhouse so animal health would not have been definitively known, which might also be a source of discrepancies between expression profiles.

It can be concluded that diverse TLR representation will generally be found in tissues that are involved in immunity such as lymph nodes and PBLs or those tissues that are generally the sites of invasion (expected to encounter microbes) such as the skin, gut and the lungs.

Toll-Like Receptor 5 (TLR5)

While the family of Toll-like receptors is of great interest and value to immunology in general, this study specifically focuses on TLR5, which recognizes bacterial flagellin. Bacterial flagellin allows bacteria to be motile. Bacterial flagellin has four domains that are connected: D0, D1, D2, and D3. The N-terminal begins at D0 and goes through D1, D2, and D3. Then the C-terminal begins by following N-terminal D3 with D2 and D1 and ends in D0 (Yonekura *et al.*, 2003). Toll-like receptor 5 features a leucine-rich repeat (LRR) domain that serves as the recognition site for bacterial flagellin, a transmembrane domain, and the Toll-like/interleukin-1 (IL-1) receptor (TIR) domain, which is on the inside of the cell and transduces the cytokine storm to activate the immune response (Letunic *et al.*, 2009). Toll-like receptor 5 activity is stimulated by the N-terminal D1 domain on flagellin, but it also requires the D2-D3 and the C-terminal D1 domain (Andersen-Nissen *et al.*, 2005). TLR5 signals through MyD88, which has an N-terminal death domain, a C-terminal Toll/Interleukin-1 receptor (TIR) and a short connecting linker (Bonnert *et al.*, 1997). The intracellular TIR domain of TLR5 engages the TIR domain of MyD88 to initiate the signaling cascade for an effective immune response (Figure 1.1) (Cell Signaling Technologies, 2012). Toll-like receptor 5 is active in the urinary tract, the respiratory tract, and the intestinal tract of the river buffalo (Andersen-Nissen *et al.*, 2007; Vijay-Kumar *et al.*, 2007; Morris *et al.*, 2009).

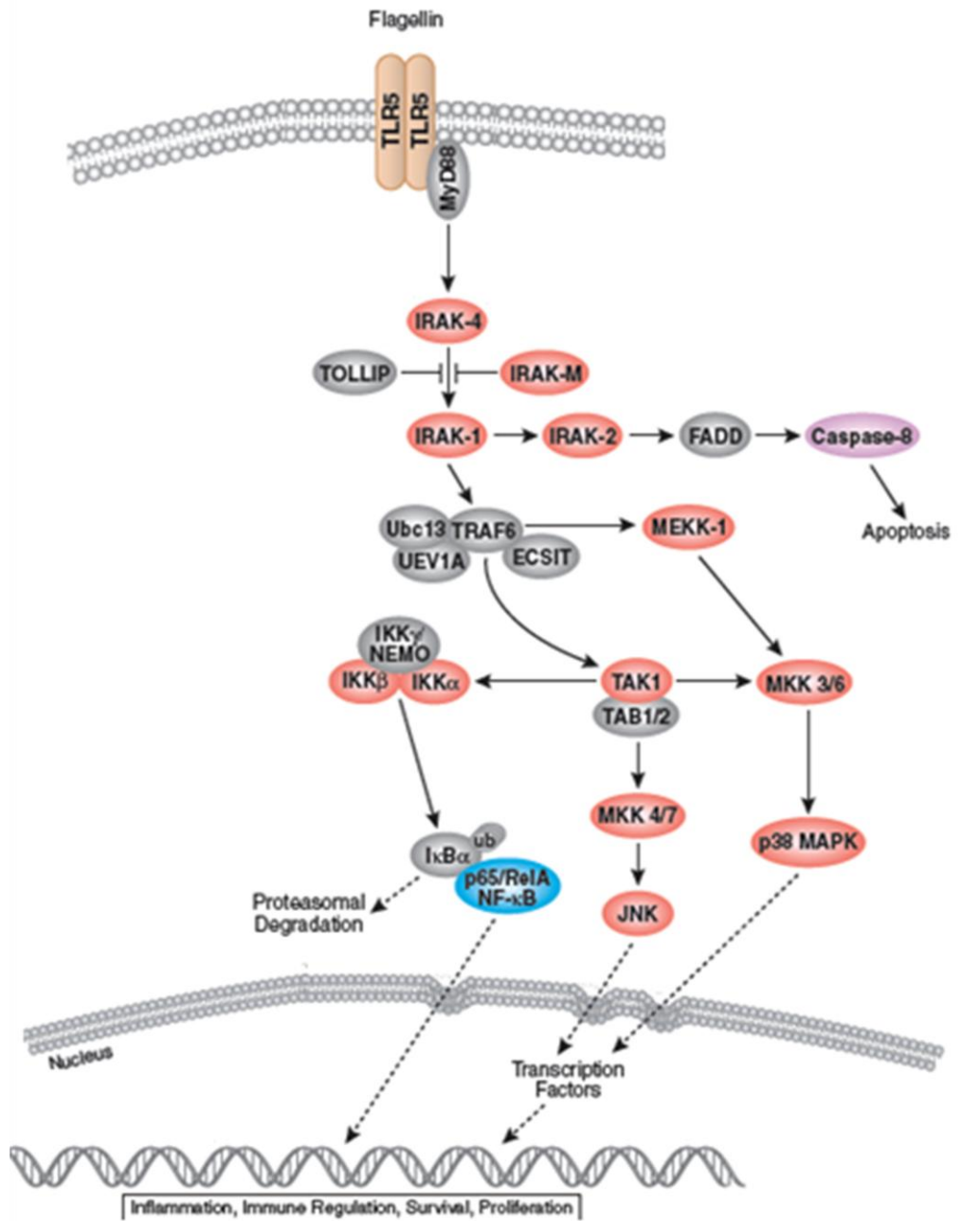


Figure 1.1 Toll-like receptor 5 (TLR5) signaling. TLR5 has three domains: extracellular LRR domain that recognizes bacterial flagella of gram negative and positive bacteria, a transmembrane domain that allows it to cross the cell membrane, and the intracellular TIR domain that interacts with the TIR domain of MyD88 to begin the immune response against flagellated bacteria.

Modified from Cell Signaling Technologies® www.cellsignal.com

What happens in the absence of TLR5 gene expression is paramount to elucidating functionality and importance of TLR5 in regards to innate and adaptive immunity. Knock-out mice were developed to answer this question (Andersen-Nissen *et al.*, 2007). Mice without TLR5 activity have a reduced ability to manage their commensal load; therefore they suffer from an increased burden of commensal bacteria (Andersen-Nissen *et al.*, 2007). Generally, within the gastro-intestinal tract flagellated bacteria, both helpful and harmful, will be found. Examples of pathogens that stimulate TLR5 activity are *Escherichia coli*, *Salmonella typhimurium*, *Pseudomonas aeruginosa*, and *Listeria monocytogenes*. In addition to a decreased ability to maintain a balanced commensal load, TLR5 knockout mice were shown to develop spontaneous colitis. Though they appeared to be healthy and there were no observable phenotypic alterations to their small intestines, they tended to be smaller than their age-matched, sex-matched wild type littermates. Rectal prolapse, enlarged spleens, exacerbated gut pathology in *Salmonella* gastroenteritis, and reduced ability to begin the signal cascade (Figure 1.1) when TLR5 is stimulated were also common in these mice (Andersen-Nissen *et al.*, 2007).

Toll-Like Receptor 5 and Ipaf

The immune system as a construct of human health is riddled with complex relationships between large numbers of system actors. Even when researchers reduce the size and scope of study from the two arms of the immune system (innate and adaptive) and focus on one arm, the complexity remains. This dissertation focuses on TLR5,

which is heavily involved in innate immunity as stated previously. Because the innate immune system is vast and complex, the TLR family works in conjunction with other innate immune actors. One example of this cooperation is between the TLR family and the NLR (Nod-like receptor) family. Specifically this section discusses how TLR5 works with its NLR counterpart, Ipaf.

Toll-like receptors are found on the cell surface, or they localize on specialized cell organelles. Invaders such as *Yersinia pseudotuberculosis* have developed ways to evade TLRs by passing through the endothelium and infiltrating the cytosol, where TLRs are not present and cannot initiate a cytokine cascade (Cossart & Sansonetti, 2004). In response to a pathogen's ability to infiltrate the cytosol, organisms have developed a countermeasure: the Nod-like receptor family, which are cytosolic pattern recognition receptors (PRRs).

Like TLRs, NLRs possess a leucine-rich repeat (LRR) domain that forms the ligand-binding site, which is the feature that allows the NLR (and TLR) to recognize and bind a particular PAMP (Fritz & Girardin, 2005). The first NLRs to be discovered were NOD1 and NOD2, which recognize the products resulting from the degradation of peptidoglycan (PG) (Fritz & Girardin, 2005). Peptidoglycan is a major component of gram positive cell wall and is only a thin layer in the periplasmic space of gram negative bacteria (Fritz & Girardin, 2005). Specifically, NOD1 responds to dipeptide D-Glu-*meso*-DAP that is found in most gram-negative bacteria and a few gram positive bacteria (*Bacillus* spp.) and is a naturally occurring product of peptidoglycan degradation. Some members of the NLR family, which include NOD1 and NOD2, induce tumor necrosis

factor (TNF), Interleukin-6 (IL-6), and IL-12 (Kobayashi *et al.*, 2005). Other family members, including Ipaf, induce caspase-1, which acts upon IL-1 β and IL-18. These two cytokines require a signal from a TLR to begin transcription and translation of their precursor, and then an NLR to induce caspase-1 to activate their processing and secretion functions (Sahoo *et al.*, 2011). Such a combined response provides the immune system the ability to detect flagellated bacteria both outside and inside the cell and serves to lessen the impact of a key evasion tactic of microbes.

Toll-like receptor 5 and Ipaf work together to recognize bacterial flagellin. Ipaf responds to intracellular threats that possess both flagellin and specific virulence factors, while TLR5 recognizes extracellular bacteria flagellin only (Miao *et al.*, 2007). Redundancies, such as this one, ensure that there are numerous checkpoints (if one fails) to detect and neutralize invasion by microbes. It also demonstrates the complexity of the system and reveals potential targets of therapeutics.

Evasion of Toll-Like Receptor 5

As with many biological processes, there is adaptation on both sides of the equation between pathogen and host. Adaptation represents the constant struggle to come to equilibrium that will allow both pathogen and host to successfully propagate. It is generally accepted that the mitochondrion began as an infectious agent. The circular nature of mitochondrial DNA and its mode of replication and propagation are clues that provide evidence that it more than likely began as an infectious agent. Mitochondrial presence within organisms is an example of how, over time, an organism will adapt to

best ensure its own survival. In this case, the host received an efficient means of energy production, and the pathogens, mitochondria, successfully incorporated themselves into their preferred host, thus ensuring their continued survival (Cavalier-Smith, 1987). The Toll-like family of receptors and its agonists are no different.

Many infectious organisms have devised ways to evade TLR5 stimulation. The general concept of the innate immune system is to recognize broad classes of motifs. The response is consistent. The innate immune system can prime adaptive immunity so that the host can eventually tailor a response to infection. Because the innate immune system recognizes broad motifs (PAMPs), it is particularly difficult for a pathogen to change or mutate these motifs to evade detection (Andersen-Nissen *et al.*, 2005). Usually, such changes result in the reduced ability to successfully invade and infect a host (Andersen-Nissen *et al.*, 2005).

However, there are examples of organisms that have successfully found ways to evade the system. Members of the alpha and epsilon (based on ribosomal RNA sequence) proteobacteria (all gram negative) possess flagellin not recognized by TLR5 despite being motile organisms. These organisms were able to successfully mutate the TLR5 recognition site. This class of bacteria also seems to have a compensatory amino acid change within the flagellin monomer surface that results in retention of filament formation (Andersen-Nissen *et al.*, 2005). Notable members important in human disease are: *Campylobacter jejuni* (rod-shaped, non-spore forming, epsilon class, found in animal feces, infection leads to enteritis); *Helicobacter pylori* (helix-shaped, epsilon class, found in stool or vomit and has been found in saliva; causes chronic low level

inflammation of stomach lining and has been strongly associated with gastric ulcers and stomach cancer); and *Bartonella bacilliformis* (rod-shaped, transmitted by sandflies; causes acute Carrion's disease or chronic Verruga Peruana). In addition, successful evasion may also result in an asymptomatic carrier-state, which is a boon to bacteria as it almost ensures successful proliferation within populations (Andersen-Nissen *et al.*, 2005).

Previous studies have also shown other evasion tactics besides mutating the TLR5 recognition site. *Listeria monocytogenes* is able to down-regulate flagellin expression at 37°C (Kathariou *et al.*, 1995). *Escherichia coli* and *Pseudomonas* spp. also down-regulate their flagellin during the process of biofilm formation, which aids bacteria survival in hostile environments; and, as evidenced by *P. aeruginosa* infection, can allow bacterial species to evade host detection and exhibit resistance to antimicrobials (Costerton *et al.*, 1999; Prigent-Combaret *et al.*, 1999; Whiteley *et al.*, 2001).

Other Functions of Toll-Like Receptor 5

Toll-like receptor 5 also has many other roles in addition to recognizing bacterial flagellin. Toll-like receptor 5 has been proven to be an important actor in autoimmune disease, such as Crohn's disease (Gewirtz *et al.*, 2006). However, there are conflicting data as to the nature of the role TLR5 plays in mediating response in the disease. Crohn's is a disease of the gastrointestinal tract. Some data suggest a link between Crohn's disease and an adaptive immune response against flagellin, but there are also

data that suggest the problem is in the innate immune response. Toll-like receptor 5 is also an attractive target for immunotherapies because it has been linked to protective functions, e.g. increased TLR5 in humans resulted in elevated antibody production against some *E.coli* flagella (Hugot *et al.*, 2001; Lodes *et al.*, 2004; Hawn *et al.*, 2005; Sitaraman *et al.*, 2005; Gewirtz *et al.*, 2006; Strober *et al.*, 2007; Vijay-Kumar *et al.*, 2007; Vijay-Kumar *et al.*, 2008).

Discussion of Crohn's disease is important because of a similar disease in livestock called Johne's disease, which causes a chronic inflammation of the intestines. *Mycobacterium avium paratuberculosis* (MAP) is the causative agent of Johne's disease (Pierce, 2009). Numerous studies have attempted to link MAP with Crohn's disease. However, while there is some evidence that MAP is involved with Crohn's disease, it is still not widely accepted as the causative agent (Scanu *et al.*, 2007; Pierce, 2009; 2010). Regardless, large animal models of Johne's disease can serve to elucidate the etiology of Crohn's disease, especially in light of the fact that there is evidence of MAP being present in some Crohn's patients and that both Crohn's and Johne's disease are associated with immune dysregulation (Scanu *et al.*, 2007; Mendoza *et al.*, 2009; Pierce, 2009; 2010).

Toll-like receptor 5 engagement modulates tumor development and growth in the mouse xenograft model of human colon cancer (Rhee *et al.*, 2008). In the study, expression of MyD88 or TLR5 was stably knocked down in human colon cancer cells. The lack of expression of MyD88 or TLR5 resulted in enhanced tumor growth and inhibited tumor necrosis, whereas TLR5 activation by a bacterial flagellin solution that

was administered by researchers around the tumor site increased tumor necrosis (Rhee *et al.*, 2008). Thus, TLR5-dependent signaling could be a potential immunotherapeutic target to modulate colonic tumors.

Toll-like receptor 5 also has a role in the innate immune response to acute *Pseudomonas aeruginosa* pneumonia (Morris *et al.*, 2009). *P. aeruginosa* is an opportunistic pathogen and a leading cause of hospital-acquired pneumonia. TLR5 is highly expressed in human and murine lung tissue by airway epithelial cells, neutrophils, and alveolar macrophages. TLR5 signals through MyD88, which is an adapter protein and is key to pathogen clearance (Morris *et al.*, 2009).

Research Goals

The water buffalo, due to its economic and social importance to a large portion of the world's population, is an organism that is in need of enhanced research efforts to improve its health and productivity. The river buffalo was specifically chosen for this study, as opposed to the swamp buffalo, because of its prominence with producers. Within the context of improved animal health, TLR5 was chosen as a gene of potential importance because of its role in the innate immune system.

This study is comprised of three parts: 1) generating a radiation hybrid map of river buffalo chromosome 5 (BBU5) where the TLR5 gene is located and building a comparative map with homologous cattle chromosomes; 2) conducting a single-nucleotide polymorphism (SNP) survey of the TLR5 gene to reveal variation within river buffalo and across multiple species; and 3) performing an evolutionary study by inferring a phylogenetic trees of TLR5 across multiple taxa and across bovids and determining the possible selective constraints within the coding region of TLR5 over a segment of evolutionary history.

The mapping effort produced a map of an entire chromosome in a species for which whole-genome sequence is not yet available. The goal of the SNP study was to explore the extent of genetic variation in this gene in breeding populations of river buffalo. While a comprehensive SNP chip for buffalo awaits an investment in sequencing, the identification of SNPs in putative candidate genes for host-resistance might provide a first step in the study of association of genetic variation with disease phenotypes.

A SNP chip of candidate genes could reduce the time and monetary investment in association studies since it would only be necessary to sequence DNA across targeted genes and not across the whole genome. The SNP survey afforded the opportunity to evaluate Toll-like receptor 5 within an evolutionary context. By expanding the number of species, the divergence over time of sequences for the TLR5 gene could be observed and adaptive changes in the gene between species could be postulated. Understanding the genomic differences between species (chromosomal rearrangements, sequence variability, and evolutionary departures) provides avenues of future study.

The goal of this research was to highlight some of those differences in river buffalo and to put that into context with other species by constructing an RH map to reveal possible rearrangements between river buffalo and cattle, examining sequence variation and haplotype and protein domain coding structure in the TLR5 gene, and performing a phylogenetic analysis across multiple species based on this single gene of importance in innate immunity.

CHAPTER II
A RADIATION HYBRID MAP OF RIVER BUFFALO (*BUBALUS BUBALIS*)
CHROMOSOME 5 (BBU5)

Introduction

There are approximately 194 million river buffalo (*Bubalus bubalis*) in the world (FAO, 2012). While economically important to many countries, roughly 97 percent of the river buffalo population are located in Asian countries, where it is used for food, fuel, fertilizer, and as draught power (FAO, 2000). Buffalo milk is higher in total solids (protein, fat, minerals) than cow milk; and the meat is also leaner than beef (Tripaldi *et al.*, 1997; FAO, 2000; Tripaldi *et al.*, 2003). Buffalo also have the ability to grow better on less digestible feeds than cattle (Tripaldi *et al.*, 1997; FAO, 2000; Tripaldi *et al.*, 2003).

Despite the fact that the river buffalo is economically important to many Asian countries and in other parts of the world, only recently has its genome been explored for the purpose of mapping genetic variation in the traits of economic and biologic interest. There are few genetic resources available for river buffalo other than the somatic cell and cytogenetic maps (El Nahas *et al.*, 1996; Iannuzzi *et al.*, 2003). Consequently, comparative mapping and exploration of genetic variation in river buffalo is lagging behind other livestock (Womack, 2005).

To generate a radiation hybrid (RH) panel, fibroblast cells from river buffalo were lethally irradiated at 5000 centiRays (CrR) to fragment chromosomes and were

then fused with Chinese Hamster cells, which are thymidine kinase deficient (Cox *et al.*, 1990). The degree of chromosomal fragmentation is dependent on how much the cells were irradiated and determines the resolution of resultant maps. The newly fused cell line was then grown in selective medium that contained hypoxanthine, aminopterin, and thymidine (HAT) so that only cells that contained donor chromosomal fragments were able to grow (Cox *et al.*, 1990). Clones of hybrid cells were then picked and propagated (Cox *et al.*, 1990). A radiation hybrid mapping panel of 90 clones was constructed for river buffalo using the above method (Amaral *et al.*, 2007) and was kindly provided for use in the current study by other students and staff in the J.E. Womack Laboratory at Texas A&M University. The utility of the panel was previously demonstrated by deriving RH maps of chromosomes 3 and 10, 6, and 1 (Amaral *et al.*, 2007; Miziara *et al.*, 2007; Stafuzza *et al.*, 2007). In this current study, this RH panel was used to construct a map of river buffalo chromosome 5 (BBU5), which is included in the recent publication of the first generation river buffalo whole-genome radiation hybrid map (Amaral *et al.*, 2008). This study seeks to describe the chromosomal arrangement of BBU5 via constructing a radiation hybrid map since a comprehensive map of this chromosome has not been previously produced.

Cattle (*Bos taurus*, BTA) and river buffalo (*Bubalus bubalis*, BBU) chromosomes can be matched arm for arm at the cytogenetic level. However, the river buffalo has five bi-armed chromosomes, which appear to be fusions of single-armed cattle chromosomes. The fusion of BTA chromosomes 1 and 27 form BBU chromosome 1, BTA2 and BTA23 form BBU2, BTA8 and BTA19 form BBU3, BTA5

and BTA28 form BBU4, and BTA16 and BTA29 form BBU5 (El Nahas *et al.*, 2001; Iannuzzi *et al.*, 2003). Even though chromosome 5 is the smallest of the bi-armed chromosomes, previous mapping of 10 potentially economic important quantitative trait loci (QTL) markers to BTA16 and BTA29 make BBU5 a potentially important chromosome for traits of biologic and economic interest.

Materials and Methods

The RH map of BBU5 was generated using cattle-derived markers (Table 2.1). Three markers were chosen that had been previously placed on the river buffalo cytogenetic map to aid in the orientation of the RH map (Iannuzzi *et al.*, 2003). Other markers were chosen based on their place on cattle chromosomes 29 and 16 (Jann *et al.*, 2006). Markers were amplified from DNA from a panel of 90 RH cell lines, plus a river buffalo control and hamster DNA by PCR using PE Applied Biosystems GeneAmp® PCR System 9700 and Techne Touchgene® Gradient TC-512 in 96-well PCR plate. Markers were initially optimized by performing a gradient PCR across cattle, river buffalo and hamster controls to find the optimal annealing temperature that would allow for the best possible amplification from cattle and river buffalo but not hamster DNA. Each 10 µl PCR contained the following: 50 ng DNA, 1.5 mM MgCl₂, 0.2 mM each of dNTP, 0.2 mM each of the forward and reverse primer (Table 2.1), and 0.5 U of AmpliTaq Gold DNA polymerase (Applied Biosystems). The gradient PCR reaction was as follows: initial denaturation for 10 s at 94°C, followed by 35 cycles of 30 s at 94°C, 30 s at 58°C Δ 17°C, and 30 s at 72°C, with a final extensions of 5 min at 72°C for 35

cycles. Gradient PCR reactions were conducted on the TouchGene TC-512 (Techne) thermocycler. The resulting amplicons were electrophoresed through an ethidium bromide (EtBr) stained 2% agarose gel in 1X TBE buffer and viewed under ultraviolet transillumination to visualize the bands. Optimal primer temperatures were assessed via success of amplification of the template. The criteria were strong bands with the appropriate band size with no smear or extra bands at other band sizes and no amplification of the negative control.

After the annealing temperature was optimized for the primers, a PCR was carried out using the radiation hybrid panel DNA as the template and the appropriate annealing temperatures for each primer as determined above. The PCR program was as follows and was performed using the ABI GeneAmp PCR 9700 (Applied Biosystems) or the TouchGene TC-512 (Techne) thermocycler: initial denaturation for 10 s at 94°C, followed by 35 cycles of 10 s at 94°C, annealing temperatures ranging from 54°C to 65°C depending on the data from the gradient PCR, 30 s at 72°C, and a final extension of 5 min at 72°C, with a final hold of 4°C.

The resulting amplicons were electrophoresed through a 2% agarose gel in 1X TBE buffer and markers were scored (1 for a strong positive, 2 for an ambiguous result, and 0 indicated a negative) independently. All markers were typed twice across the RH panel DNA and scored at least twice. Discrepancies were resolved by a third repetition. Retention frequencies were then calculated by dividing the number of positives by the number of clones across the panel.

To compute the RH map, the software packages `rh_tsp_map` 3.0 and CONCORDE were used with the maximum likelihood criterion (MLE) (Agarwala *et al.*, 2000; Applegate *et al.*, 2006; Schaffer *et al.*, 2007). The map was constructed according to the steps given in the `rh_tsp_map` tutorial as previously described (Miziara *et al.*, 2007). However, the pairwise LOD score threshold for making linkage groups was increased to 7.0 because the increasing number of typed markers makes spurious high LOD scores between markers on different chromosomes more likely to occur.

Table 2.1

Cattle-derived markers used to construct the BBU5 RH map.

Marker	Type	RF (%)	Location (cR)	Tm (°C)	Forward Primer (5'-3')	Reverse Primer (5'-3')	UniSTS ID	Accession
ILSTS081 ²	MS	34.4	0.0	57	AGTCAGACAACGACTGTGCG	TTTCGAACAGGCTTTTGGGG	16092	L37276
S68957 ³	GENE	35.6	31.13	57	CTTCCCTTGAGATGCCAGAG	CTTCCCTTGAGATGCCAGAG	278462	S68957
BMC6004 ²	MS	35.6	46.8	55	GATTCCCTGATAGAAATGGCA	GGTGAGATGAGGATGCGATC	46306	G19099
RME33 ²	MS	40.0	80.26	53	TTAGAGGCACCACCTAACGG	GCTTCTCAGTTGTTCTGCC	U15435	251429
AW461519 ³	EST	41.1	92.6	57	GGGAGAAGAAAAGGCATTC	GGTCTGTGGTCCCCTTACA	278070	AW461519
BZ932751 ³	EST	41.1	138.7	65	GGCGGCAACGAGTCTGG	AGAGCGGGAGGTGGTGGTC	477149	BZ932751
BMC3224 ²	MS	38.9	148.49	56	CCATCACTGCTATTCTACCTCC	CACAGCCAATTTCTGATTTCA	279690	279690
RM040 ²	MS	34.4	158.55	58	TGGAGGACTACAATCCATGAGG	TAAGTGCAGTAAGATGCCATGG	251356	U10386
BZ900418 ³	EST	33.3	183.57	61	GCTGGCAGGTGTGGGTGTTT	GTCGGATTCTCCCTCTGACCACA	477145	BZ900418
BZ905352 ³	EST	27.8	209.71	57	TGTCTTTTCAGAGTATCATCACCC	TTCAACCATAGGCAACTTCAA	477143	BZ905352
BMS1600 ²	MS	34.4	226.22	55	TGTGGGAATCTGAAGCTCTATAT	GACATGACTGAGCAACTTTTACC	75448	G18676
BZ946384 ³	EST	37.8	233.71	58	CAGGAAAGACTGAGCAGTAAGTG	AATAGCCTTCACTTTGCCTTAC	477140	BZ946384
BZ933262 ³	EST	41.1	263.44	57	ATCCTCAGGCTTTTATCTTTGTG	AGATTCTATGAGCTGATAAGTC	477137	BZ933262
ILSTS089 ²	MS	40.0	Placed	60	AATTCCGTGGACTGAGGAGC	AAGGAACTTTCAACCTGAGG	6537	L37239
BMC8012 ^{1,2}	MS	41.1	283.52	57	AATTCATGCACAGAGGACC	GATTCCAGAAAGTTCCCCCA	6526	G18773
BZ951039 ³	EST	44.4	306.57	57	TGGCAATGATTACAGGTGCATT	TTGAAAAGCACAACCTCATATTC	477131	BZ951039
ILSTS019 ²	MS	46.7	Placed	58	AAGGGACCTCATGTAGAAGC	ACTTTTGGACCCTGTAGTGC	251117	L23492
BZ901563 ³	EST	43.3	318.22	60	CTTAGTCAAGTCTACCACACA	AACCTTTTCTCCAGGCAG	477130	BZ901563
ILSTS057 ²	MS	41.1	Placed	58	GGAACTGTTCTAAGAAGTGG	TGCTGTTTCTTCTATGTGGG	51298	L37265
BZ930457 ³	EST	41.1	337.78	60	GTCTTCAAGTGCCAAATCCA	ACTTTCTCCATAGTTGCCTGTA	477127	BZ930457
CC447793 ³	EST	45.6	347.35	57	GATGTGTTTTGGTGAAGAAGCAGAG	TGAGACAAATGAGAATATGCAGGTG	477125	CC447793
BZ919428 ³	EST	51.1	369.74	63	TGATGGTCTCTTGCTCAGGATGG	GGGCTGAATGGCTCTTTGTTCTG	477123	BZ919428
BZ919809 ³	EST	54.4	376.6	57	CCATTGCCAGATTCAGTCTCATC	AGATCCTCAAGCAGTGTGATGG	477121	BZ919809
BZ938148 ³	EST	48.9	Placed	57	AGTAAGATAATGCCACAGCTTCTAC	AGGCAAATAGAATGCAATGCAAATC	476360	BZ938148
BMS357 ²	MS	50.0	412.66	57	TCCAAACAAGTCTTCTATTTACC	CCAAATAATTGCTGGTCAGG	65755	G18845
AW267148 ³	EST	45.6	432.35	57	ACTTTGTCTTCTGGAAATTAGC	ACTTCAACCTCGTGGGAATTAG	278204	AW267148
HUJ614 ^{1,2}	GENE	45.6	441.81	63	CGCCAGGCATGGTGAAGTCG	CCCAGCACAGTACAGGCTGC	250838	M93653
BZ951725 ³	EST	37.8	471.01	57	TTAACTAGGCTTCAGGCAATG	TAGGTCAAGTTGTTAGCCAGTAAC	476365	BZ951725
BZ948508 ³	EST	32.2	Placed	57	TATTCTTACACAGTATGCAGTATTC	TTGGTTGCTTATTGCTCAGG	476368	BZ948508

Table 2.1 continued

Marker	Type	RF (%)	Location (cR)	Tm (°C)	Forward Primer (5'-3')	Reverse Primer (5'-3')	UniSTS ID	Accession
CC562100 ³	EST	33.3	508.8	57	TGCTCACTCATGCTATCACTTCTCC	ACTGGCAAAGCTGGTCTCTTCTAAC	476371	CC562100
BM121 ²	MS	30.0	Placed	58	TGGCATTGTGAAAAGAAGTAAA	ACTAGCACTATCTGGCAAGCA	73368	G18420
BZ944687 ³	EST	27.8	550.27	63	CCTGCTGCTTGAAGTGCCACAG	ACTGACACCACTGCTCTGCTGAC	476373	BZ944687
BZ950494 ³	EST	24.4	581.77	58	TTGGCACTTGCACAACCTGAATG	GAATGGTCATTGAGCACACAGAAAG	476375	BZ950494
AW289394 ³	EST	36.7	614.81	58	GGGTTGTTACATTCCGTGTCAG	CTGAAATGAAGTGCAGGGCTAC	278430	AW289394
TLR5	STS	36.6	627.62	58	CATCTGTTATAAGAAAGCCCAGA	TATTGAGAAACCAGTCAACATCC	519115	444870
AW461592 ³	EST	40.0	667.93	57	ACTTTCACGTGTCGGTTTCC	TTGCACATTTTAAAAGCACCC	278075	AW461592
BZ945895 ³	STS	34.4	692.050	57	AGATGCTTGCTCAAACAAACTGTG	AGATGCTTGCTGTAACCTCACTTTGG	476386	BZ945895
CSSM003 ²	MS	31.1	705.33	55	GTACCTTAAGGTCAAGGGCTTCT	TGGGTCCAATTGAGAATCTTCATG	251063	U03786
AW289372 ³	GENE	31.1	721.84	60	GGCCTCAACCAAATACAAGC	GTACGGTTACTTGATGCGTG	279203	AW289372
BZ952478 ³	EST	30.0	735.49	65	CGGACAGCGGAGCGGTGAG	CTTCTCTGACCAGCCGTCCAG	476395	BZ952478
IDVGA26 ^{1,2}	MS	17.8	772.85	57	TGAGGACTCAACCCACATTTTG	AAAGAGTGCAACGGGAAAGTG	251442	X85045
BZ910068 ³	EST	20.0	844.43	54	AACCTCATGCTCGCTAACTCAATAC	TCTTACACATCACTCAGTTCCTTGC	476408	BZ910068
BM1706 ²	STS	28.9	877.32	58	ACAGGACGGTTTCTCCTTATG	CTTGCAGTTTCCCATAACAAGG	7959	G18460
INRA048 ²	MS	24.4	894.95	58	CTGTCCCTCAGTAAACAAGTCG	AAGCTAAAGTAGCAGGGAAG	251130	251130
BMS462 ²	MS	24.4	920.28	60	TGCAGACGGGAGAAAAGC	CTCACTTCCTCCTCAGGTGC	71420	G18864
AW482289 ³	GENE	24.4	932.09	51	CCCACCAATGAATAATCTTATGCC	AAAGCTAACACAGAGTCTTCGTAG	278825	AW482289

RF- Retention Frequency, EST- Expressed Sequence Tag, MS- Microsatellite, STS- Sequence Tagged Site

¹FISH mapped markers

²Ihara *et al.* 2004

³Jann *et al.* 2006

Results and Discussion

Using the BBURH₅₀₀₀ panel, a RH map was constructed for river buffalo chromosome 5, a bi-armed chromosome orthologous to cattle chromosome 29 and 16 as shown by chromosome banding and fluorescent in-situ hybridization (FISH) mapping (Iannuzzi *et al.*, 2003; Amaral *et al.*, 2007).

Retention frequencies (the proportion of radiation hybrids that contain donor chromosome fragments) for individual markers ranged from 17.8% (IDVGA26) to 54.4% (BZ919809) as shown in Table 2.1 and graphically in Figure 2.1. Fifty markers predicted to be on chromosome 5 from their location on the cattle map were initially analyzed; however, three of these markers (TGLA45, TGLA35, and BM6121) were dropped during the early stage of making linkage groups because they did not achieve a sufficient two-point LOD score with any other marker. All other markers achieved a sufficient two-point LOD score and formed a single linkage group. Radiation hybrid mapping is affected by the density of the map. Marker density and proximity affects marker placement in relation to other markers since RH mapping depends on statistical association between chromosomal fragments and prospective markers. Therefore, if a segment of the chromosome is not densely or adequately populated with markers, then the software cannot form a statistical association between markers, which can result in a marker being “placed” or “framed”.

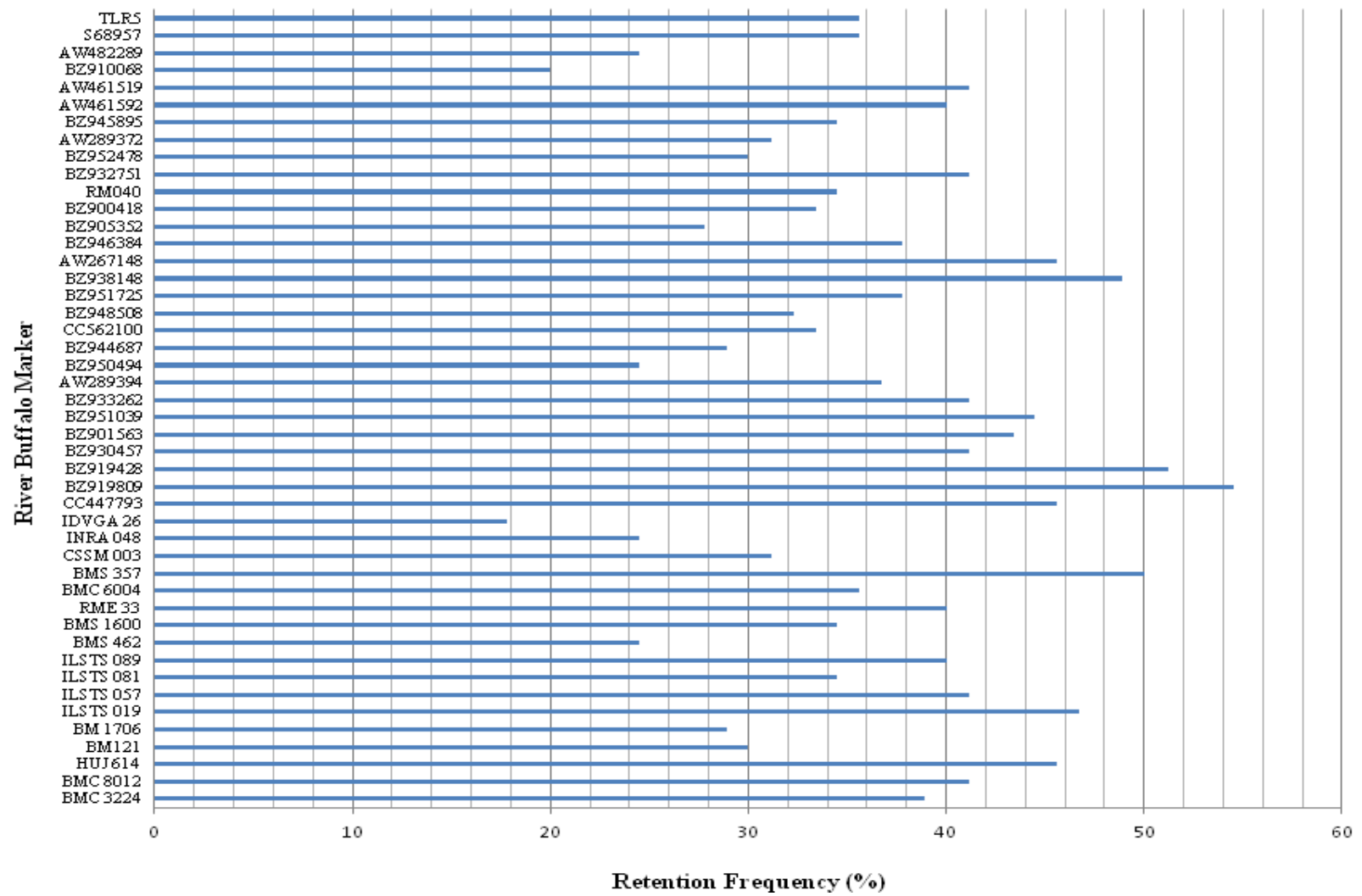


Figure 2.1 Retention frequencies for the 46 river buffalo markers used in this study.

Placed markers are in the area, but the exact location of “placed” markers cannot be confirmed due to the sparsity of other markers or the low pairwise LOD scores. Framed markers can be confidently placed on the map, however. Increasing the density of markers can change marker order since dense areas have markers that can be more strongly associated with each other due to proximity and association with chromosomal fragments that were initially generated on the RH panel. The high LOD score threshold prevents spurious associations between markers. River buffalo chromosome 5 is the only bi-armed chromosome that formed a single linkage group as shown in both the recently constructed whole-genome RH map (Amaral *et al.*, 2008) and the RH map constructed with fewer markers in this study (Figure 2.2).

Three markers that were mapped to the cytogenetic map (BMC8012, HUI614, IDVGA26) corresponded to their respective counterparts on BBU5. This map was oriented consistently with the cytogenetic map for river buffalo and the latest cattle RH map (Iannuzzi *et al.*, 2003; Jann *et al.*, 2006). Two of the three markers mapped on the cytogenetic map flanked the centromere and confirmed our predicted orientation of the RH map based on the hypothesis of centromere fusion of the two homologous cattle chromosomes. Of the 46 markers, 39 were positioned on the MLE-consensus (a.k.a. framework) map, and the remaining 7 markers were placed in their most likely interval between two consecutive markers on the MLE-consensus map. The MLE-consensus map is estimated to be 932.1 cR in length.

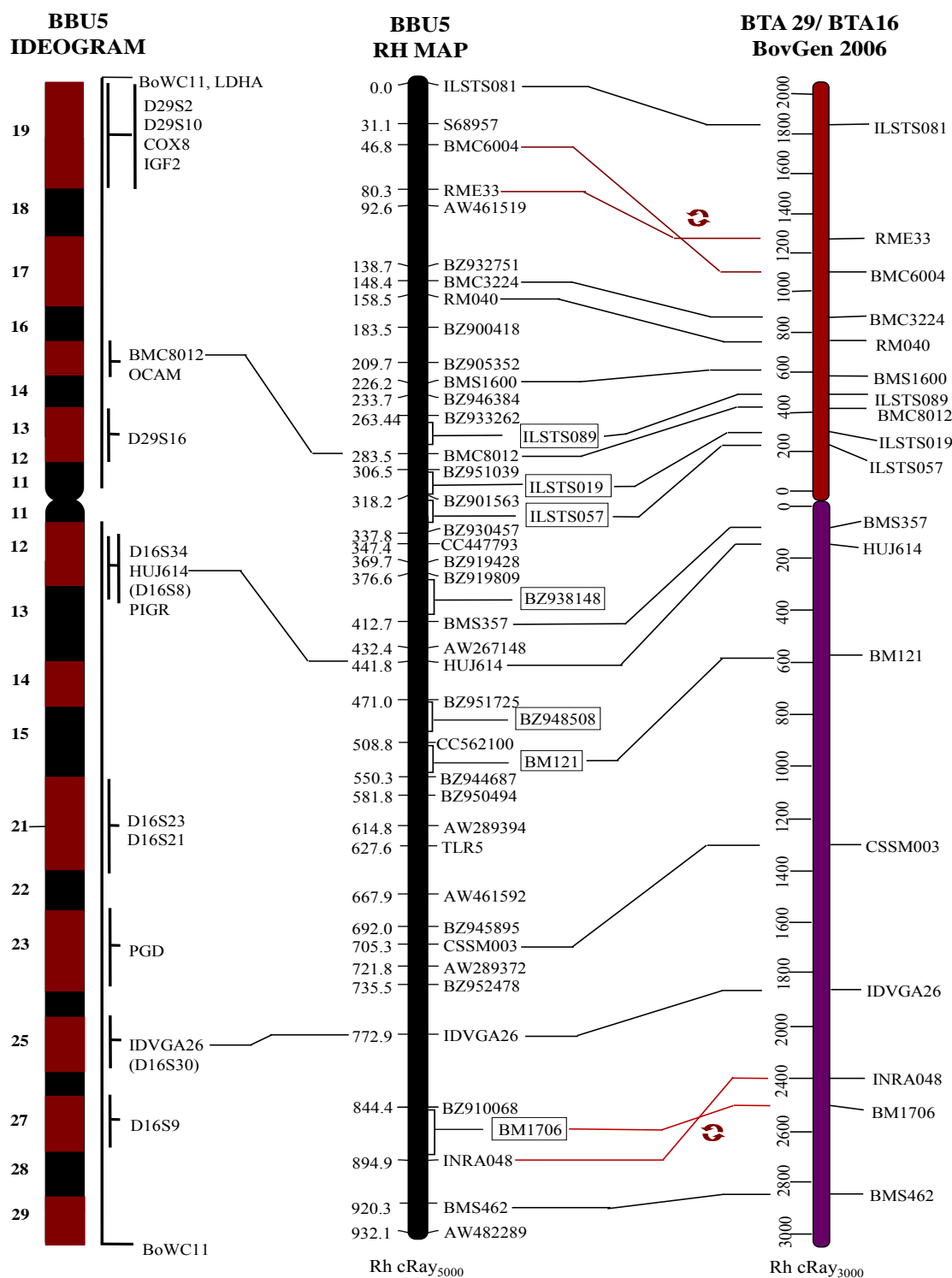



Figure 2.2 Comparison of the river buffalo chromosome 5 RH map. BBU5 RH map (center) with the buffalo cytogenetic map (left) and the bovine chromosomes 29 and 16 BovGen 2006 map (right). Framework markers are in black. Placed markers are boxed. Markers are connected to their counterparts by solid black lines. Inverted markers are denoted by a  symbol.

Two predicted inversions (BMC6004 and RME33, BM1706 and INRA048) were observed in marker orientation compared to the cattle BovGen 2006 map (Figure 2.2). Additionally, the generated RH map was compared to the 2004 MARC genetic linkage maps of BTA 29 and 16 (Ihara *et al.*, 2004). The linkage map also showed the same marker orientation as the BovGen map (data not shown). The recent river buffalo whole-genome (WG) RH map maintains the BMC6004 and RME33 inversion (Amaral *et al.*, 2008). The BM1706 and INRA048 inversion is not maintained. BM1706 is a placed marker so its location was subject to change with increased markers in the region and the WG RH map increases the marker density of that region.

Cattle chromosomes 29 and 16 are rich in quantitative trait loci (QTL) (<http://bovineqtlv2.tamu.edu/index.html>), suggesting that river buffalo chromosome 5 might be a candidate chromosome for corresponding buffalo QTL (Figure 2.3). The following cattle QTLs were confirmed by genetic analysis (whole genome scans that included half-sib families, backcrossing, and crossbred analysis) or by candidate gene studies.

Carcass quality (marbling score) and meat tenderness, carcass yield (hot carcass weight, retail product yield, and live weight), milk protein (protein yield) and milk yield, and weaning weight have been mapped on cattle chromosome 29 (Casas *et al.*, 2000; Smith *et al.*, 2000; MacNeil & Grosz, 2002; Casas *et al.*, 2003; Kim *et al.*, 2003; Viitala *et al.*, 2003). Hot carcass weight, live weight, meat tenderness, milk protein, retail product yield, and weaning weight were mapped in cattle to regions corresponding to the RME33/ BMC6004 inversion on the generated river buffalo RH map (Figure 2.2).

Similarly, carcass quality (marbling score), and carcass yield (fat depth, dressing percentage, hot carcass weight and live weight) were identified on cattle chromosome 16 (MacNeil & Grosz, 2002; Casas *et al.*, 2004). Fat depth was mapped to the region containing BM1706 (MacNeil & Grosz, 2002). BMS1706 is inverted with INRA048 on the generated RH map (Figure 2.2); however, as previously discussed, the inversion is not maintained on the WG RH map (Amaral *et al.*, 2008).

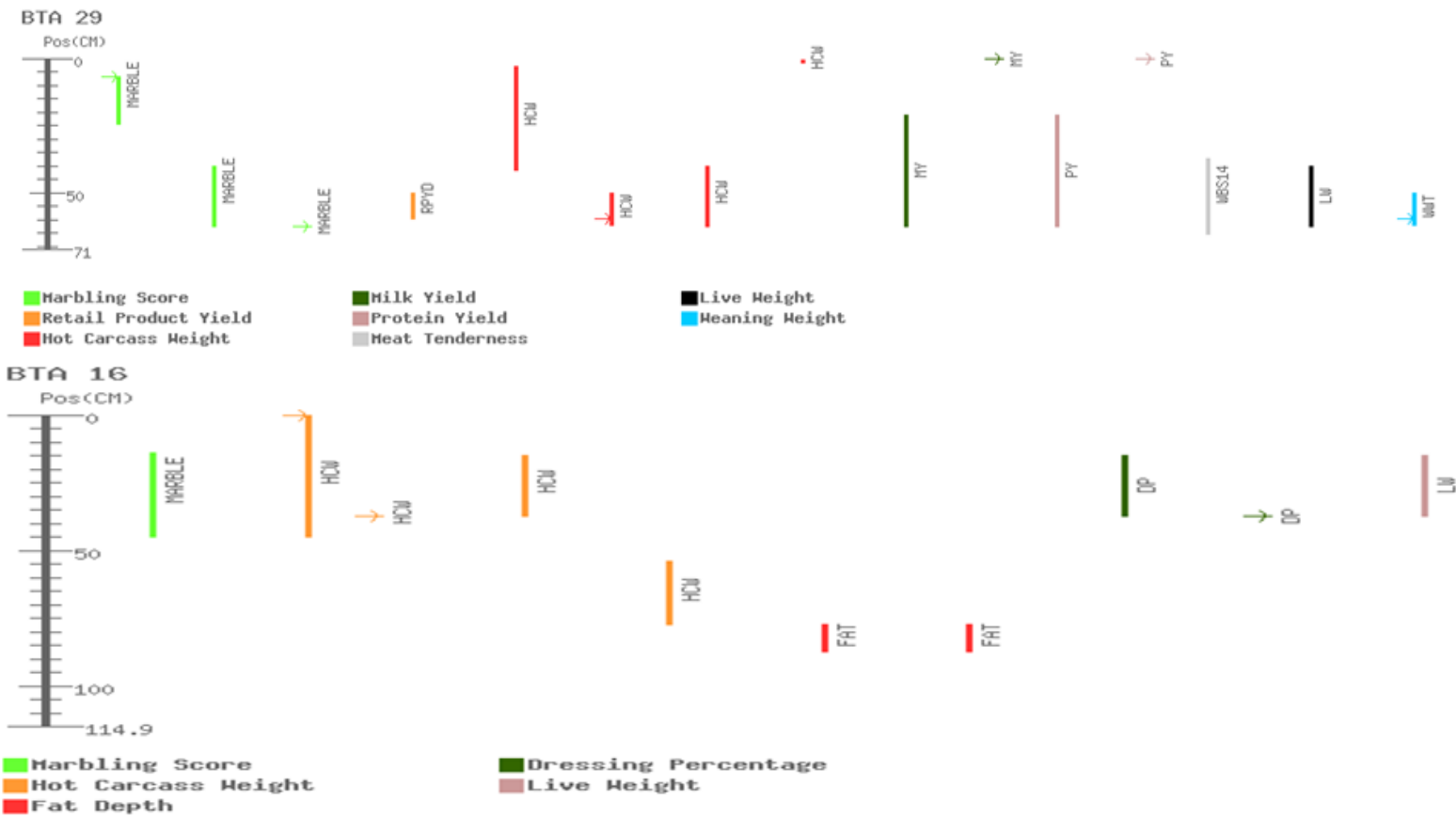


Figure 2.3 Cattle QTLs associated with BTA29 and BTA16. Figure generated using the Bovine QTL Database (<http://bovineqtlv2.tamu.edu/index.html>).

It is not guaranteed that a QTL in cattle will be a QTL in river buffalo but comparative studies are useful in illustrating differences that provide a starting point for investigators. Comparative studies that have identified a QTL in one species have been utilized to begin investigation in another: milk yield and composition QTL polymorphism comparisons of indicine cattle and riverine buffalo to taurine cattle (Tantia *et al.*, 2006), blood pressure QTLs in rat compared to the corresponding regions in human (Garrett *et al.*, 2001), and comparative mapping of porcine chromosome 7 for QTLs compared to multiple vertebrates (Demars *et al.*, 2006). The rearrangement suggested by the RH map presented here and observed in the WG RH map can be confirmed by sequencing the region, which would also serve to further elucidate the region for studies such as for polymorphisms and to identify other genes that may be in the region.

Chromosomal rearrangements, in this case an inversion, have the potential to separate a gene and the regulatory elements that are associated with it. This also serves to change gene order and introduce possible regulatory elements that have the potential to impact gene expression. In this case, possible QTLs in river buffalo have been rearranged, but other genes in that area that have not been identified yet could also be impacted.

The predicted inversion observed on the RH map generated in this study may be a reason for certain performance differences (discussed in Chapter I) between *Bos taurus* and *Bubalus bubalis*.

Because river buffalo are a major source of food and draught power in the world, and due to their close evolutionary relationship with cattle, mapping and comparing their genome to that of cattle provides important information for both species. The generated RH map shows two regions of possible rearrangements with corresponding cattle chromosomes. It is interesting that cattle QTL for two traits, milk protein and muscle fat, that are different from river buffalo are in regions marked by rearrangements. This region might impact QTL expression in river buffalo via a change in gene expression, the discovery of candidate genes, and/or due to sequence differences once candidate genes are revealed in comparison to *Bos taurus*. Other cattle QTL have been mapped to the two cattle chromosomes comprising BBU5, making it an important chromosome for future study in the river buffalo.

CHAPTER III

POLYMORPHISM AND HAPLOTYPE STRUCTURE IN RIVER BUFFALO (*BUBALUS BUBALIS*) TOLL-LIKE RECEPTOR 5 (TLR5) CODING SEQUENCE*

Introduction

The innate immune system of vertebrates evolved as the first line of host defense against pathogens, is evolutionarily conserved, and has the ability to prime acquired immunity (Akira *et al.*, 2001). The innate immune system, unlike its adaptive counterpart, does not learn from each invasion of pathogen. The recognition of broad categories of motifs enables the innate immune system to recognize a multitude of pathogens with no prior exposure necessary. In addition, pathogens cannot easily evade the innate immune system via mutation due to the fact that these broad motifs are basic to pathogens and such changes have the potential to negatively impact a pathogen's ability to invade, infect, and successfully colonize the host organism (Medzhitov, 2001; Andersen-Nissen *et al.*, 2005). Toll-like receptors (TLRs) are important components of the innate immune system. These receptors are homologous to the Toll family of receptors, which were first discovered in the fruit fly to provide host defense against fungal infection (Lemaitre *et al.*, 1996). Toll-like receptors are type I transmembrane proteins that recognize pathogen-associated molecular patterns (PAMPs) and are expressed differentially in cells involved in the innate immune system.

*Reprinted, in part, from *Animal Biotechnology*. Jones, B.C. & Womack, J.E. 2012. Polymorphism and haplotype structure in river buffalo (*Bubalus bubalis*) toll-like receptor 5 (TLR5) coding sequence. *Anim Biotechnol* 23(2):132-40. doi: 10.1080/10495398.2012.658466. Copyright 2012 by *Animal Biotechnology*.

Ten Toll-like receptors have been identified in most mammals. Toll-like receptors are predominately expressed in macrophages, neutrophils, and dendritic cells, but they are not exclusive to these cell types. TLRs are also differentially expressed across a variety of tissues (Zarembek & Godowski, 2002; Vahanan *et al.*, 2008; Tirumurugaan *et al.*, 2010). Sequence variability in TLR genes has been explored extensively in cattle, with emphasis on finding genetic components of animal health and productivity (Seabury *et al.*, 2007; Fisher *et al.*, 2011).

In much of the world, however, water buffalo have more value and are produced with less expense than cattle. Water buffalo number approximately 194 million, with the majority located in Asian countries (FAO, 2012). They are able to utilize less digestible feeds better than cattle, are less susceptible to a variety of parasites and illnesses (often attributed to their wallowing behavior which coats them in a layer of mud), are better draught animals and have a higher percentage of total milk solids than cattle (Tripaldi *et al.*, 1997; FAO, 2000; Tripaldi *et al.*, 2003; Fagioli *et al.*, 2005; Michelizzi *et al.*, 2010). In this study, the sequence variability of TLR5 in river buffalo (*Bubalus bubalis bubalis*) was examined with the purpose of enhancing available genetic tools for the improvement of health and production in an animal of increasing worldwide economic importance.

This chapter will explore TLR5 single-nucleotide polymorphisms (SNPs), haplotypes, the theoretical impact of the SNPs detected, regulatory elements, and insertion/deletions in river buffalo (*Bubalus bubalis*). A comparative analysis of the protein domain architecture between river buffalo and other species and shared SNPs

within the three domains (extracellular leucine-rich repeat, transmembrane, and intracellular Toll-like/Interleukin-1 receptor) of TLR5 will also be examined. Ancestral characters, ancient alleles and evolutionary concerns will be discussed in Chapter IV.

Materials and Methods

DNA Samples

The origins and identifications of the samples used in this study are shown in Table 3.1. The majority of the samples were from clinically normal river buffalo at Bufala di Vermont located in Woodstock, Vermont (<http://www.bufaladivermont.com/>).

Buffalo DNA was extracted from whole blood using standard methodology (Sambrook *et al.*, 1989; Sambrook & Russell, 2006). Fifty ml of whole blood was added to 10 ml of 4% sodium-EDTA anticoagulant. The sample was kept cool (but not frozen) until processing. Fifteen ml of the sample was collected into a 50 ml conical tube and 15 ml of 2X sucrose- Triton X-100 was added and left on ice for 20 min to lyse the red and white blood cells. The sample was then centrifuged at 500 x g for 20 min at 4°C and the supernatant was decanted. The resultant pellet was gently resuspended in 10 ml of 2X sucrose-Triton X-100 and left on ice for 5 min. The sample was centrifuged at 500 x g for 20 min and the supernatant decanted. The pellet was gently resuspended in 5 ml 4% saline-EDTA (0.075M NaCl, 0.024M Na₂EDTA), 250 µl 20% sodium dodecyl sulfate (SDS), and 625 µl 20 mg/ml proteinase K and incubated overnight on a rotator at 8 rpm at 55°C. Five ml of phenol-chloroform-isoamyl alcohol (PCI) was then added; the test tubes were repeatedly inverted for at least 4 min and then centrifuged for 10 min at

approximately 500 x g at room temperature. The supernatant (top layer aqueous phase) was removed and placed into a new 15 ml test tube. The supernatant was then extracted twice with chloroform-isoamyl alcohol (CI), with each cycle requiring at least 4 min of inverting the tube, centrifugation for 10 min at 500 x g, and the supernatant placed into a new 15 ml test tube. After the second CI extraction, 450 µl of 3M, pH 5.5 sodium acetate (NaOAc) and 14 ml of 95% ethanol (EtOH) were added and mixed by swirling the tube. The mixture was allowed to incubate at room temperature for 1 hr. The tubes were then centrifuged at 500 x g for 7-10 min and the alcohol removed by pouring it off or pipetting. Ten ml of ice cold 70% EtOH was added and the tube swirled to dislodge the DNA pellet. The tube was centrifuged at 500 x g for 7-10 min and the alcohol was removed (via pipetting and/or pouring off). The DNA pellet was removed to a clean 1.5 ml microtube, briefly centrifuged in a table top microcentrifuge; and, if any alcohol remained, it was removed. The DNA was dried completely and 0.3 ml – 1 ml of 1X Tris-EDTA (TE, 0.01M Tris, 0.001M EDTA) was added. The DNA was incubated overnight in a 37°C water bath to allow it to resuspend. The tube containing the DNA was then rotated for 1 hr and then the concentration of DNA was determined using the NanoDrop ND 1000 spectrophotometer (ThermoScientific).

Bison DNA was graciously provided by the CVM DNA Technologies Laboratory at Texas A&M University (Halbert & Derr, 2008). The DNA concentration was determined as above.

Table 3.1

Study population for genetic variation in TLR5. Identification (ID) numbers, species, origin, and GenBank accession numbers for the TLR5 coding region are included.

Sample ID	Species	Common Name	Origin	Accession
684	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615215
729	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615216
736	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615217
737	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615218
739	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615219
748	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615220
755	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615221
765	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615222
772	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615223
ET562	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615224
ET567	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615225
ET604	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615226
ET611	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615227
ET613	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615228
ET616	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615229

Table 3.1 continued

Sample ID	Species	Common Name	Origin	Accession
ET629	<i>Bubabulus bubalis bubalis</i>	River Buffalo	Bufala di Vermont	JN615230
JEW41	<i>Bubabulus bubalis bubalis</i>	River Buffalo	American Water Buffalo Association	JN615231
JEW43	<i>Bubabulus bubalis bubalis</i>	River Buffalo	American Water Buffalo Association	JN615232
JEW42	<i>Bubabulus bubalis carabanesis</i>	Swamp Buffalo	American Water Buffalo Association	JN615235
SCNM-1-777	<i>Syncerus caffer nanus</i>	African Forest Buffalo	San Diego Zoo	JN615233
SCNM-2-875	<i>Syncerus caffer nanus</i>	African Forest Buffalo	San Diego Zoo	JN615234
BB08-1	<i>Bison bison</i>	American Bison	Yellowstone National Park	JN615236

Primers and Polymerase Chain Reaction (PCR) Amplification

Previously described cattle TLR5 primers (Seabury et al., 2007) (Table 3.2) were used to obtain the initial river buffalo and bison TLR5 gene sequences. Two series of species-specific primers were designed from the river buffalo (JN615231) and bison (JN615236) TLR5 sequences (BBU5_1 through BBU5_9 and BBI5_01 through BBU5_09 respectively; Table 3.2). Annealing temperatures of 58°C using Primer3 online (Rozen & Skaletsky, 2000; Rozen, 2009) were used to amplify and sequence the TLR5 gene of the two species. River buffalo TLR5 primers (BBU5_1 through BBU5_9; Table 3.2) were used to amplify swamp buffalo and African forest buffalo TLR5. River buffalo primers shown in Table 3.2 facilitated the sequencing of the entire length of the swamp and African forest buffalo TLR5 amplicons. Species-specific bison primers (BBI5_01 through BBI5_09, Table 3.2) were used to amplify and sequence TLR5 in bison.

Table 3.2

Primers used for PCR amplification and sequencing. River buffalo, bison, and cattle primers for TLR5 are shown. River buffalo primers were used to generate sequence data for swamp buffalo and African forest buffalo.

	Forward (5' to 3')	Reverse (5' to 3')
River Buffalo TLR5*		
BBU5_1 (715bp)‡	CGGAGGATAAGACTGGAATG	TGAAGAGGCTTTGTTGTATTGG
BBU5_2 (749bp)‡	CCACTGGACCACTAGGGAAG	TCCATCCTCACTCCTACACAG
BBU5_3 (707bp)‡	CAAATGCTCAACACAGACAGAC	AGAAGGTCAAGGCAGTCTCC
BBU5_4 (715bp)‡	GGACCCAGAGGAACACAGG	GGGTTTGAACTCCTGCTCAC
BBU5_5 (736bp)‡	CTGTGGTCTCTCCGATGC	CCCAATGTGATTCTTCTGC
BBU5_6 (745bp)‡	CCTCGCTACAACAAGATAAAC	ATCAGGATCAGGAGAGAGGAG
BBU5_7 (718bp)‡	AATTTCTTCCACCAGGAG	TCTTTCTGCTGCTCCACAC
BBU5_8 (716bp)‡	ACTTTGAATGGGTGCAGAATG	CACAGGAGACTTGGGTTTCG
BBU5_9 (716bp)‡	AGTTTCCACTTATCGCAAGC	TGACCTGTACTGAGCAATGG
Bison TLR5†		
BBI5_01 (733bp)§	TGGAAGGTAAAACACTGACTTGC	TGAAAACATCCCTGGTTCAG
BBI5_02 (740bp)§	GCCTGCTTTTGATACTTGG	ACTGTCTGTCTGGGTTGAGC
BBI5_03 (703bp)§	CCCCAAGCACCCAGTATC	CTCGGCATTCATTCATAAGG
BBI5_04 (720bp)§	TGCCTTGGGAAAGGAATG	ATCTGACTTCCACCCAGGTC
BBI5_05 (759bp)§	ACAGTCACAACCCGATCC	CTGGAGTGTCTCAAAGATTTCG
BBI5_06 (728bp)§	GGGTTCTTCATTTGGCTTC	AGAGGAGTTGGAGATGAGAAAAG
BBI5_07 (705bp)§	AAAACCATGCCCTTCAG	TGAAGCACAAATAGGCATCG
BBI5_08 (765bp)§	AAGTTTTCCCTTTTCATCTTGG	ATGACCGAGCAACTGAACAC
BBI5_09 (849bp)§	CCAGGATGTTGACTGGTTTC	ATCCCTGAGACTGGGTATGAC
Cattle TLR5¶		
TLR5_01 (642 bp)	TTTGGGAAACGGAGGATAAG	GCACCTTTGAGGCTGTGA
TLR5_02 (661 bp)	GCCTGCTTTTGATACTTGG	AGGTGTCCGCTATGTTCTCA
TLR5_03 (563 bp)	TCCCTTACCTTCCAGCAGA	AAGTTGGGGAAAACATTAGG
TLR5_04 (541 bp)	GGCAGATTAGAGGGGAAAGA	CCATCAAAGAAGCAGGAAGA
TLR5_05 (687 bp)	TCACTCTCCCTTCTTCTCCA	CAGACACTTGTTCCAGTCCA
TLR5_06 (700 bp)	CCTCCAAGGGAAAACACTCT	ATTGGCTGTAAGTGGGATGT
TLR5_07 (652 bp)	TTTTCTTCCAAGCATTCCTA	AGCCAGAGAGTTTGGGTACA
TLR5_08 (592 bp)	GAAACCAGCTCCTCTCTCCT	ATCTTTCTGCTGCTCCACAC
TLR5_09 (541 bp)	AGACTTTGAATGGGTGCAGA	TGGTAACTGGCGGAAATAAA
TLR5_10 (764 bp)	GGAGCAGTTTCCACTTATCG	ATTCTCATGCCGTTTCTTT

* GenBank accession number of sequence used for primer design: JN615231. Used to sequence TLR5 coding region in river buffalo (*Bubalus bubalis bubalis*), swamp buffalo (*Bubalus bubalis carabensis*), and African forest buffalo (*Syncerus caffer nanus*).

† GenBank accession number of sequence used for primer design: JN615236. Used to sequence TLR5 coding region in American bison (*Bison bison*).

‡ Expected amplicon size based on JN615236 (JEW41)

§ Expected amplicon size based on JN615236 (BB08-1)

¶ Seabury *et al.* 2007

Each 25 µl PCR contained the following: 50-100 ng DNA, 0.2 mM each dNTP, 0.4 µM forward and reverse primer, 1.5 mM MgCl₂, 1X Gene Amp PCR Gold Buffer (Applied Biosystems, Foster City, Ca, USA), 0.2X MasterAmp PCR Enhancer (Epicentre, Madison, WI, USA), 1.66 units of AmpliTaq Gold DNA polymerase (Applied Biosystems), and enough DNase/RNase-free distilled water (Invitrogen, Grand Island, NY, USA) to reach the correct reaction volume. PCR amplicons were generated via the following step-down thermocycling program on the ABI GeneAmp PCR 9700 (Applied Biosystems): initial denaturation of 5 min at 95°C; 30 s at 95°C, 20 s ranging from 58°C to 62°C, and extension of 1 min at 72°C for 5 cycles; then 30 s at 95°C, 20 s ranging from 57°C to 60°C, and extension of 1 min at 72°C for 45 cycles; with a final extension of 10 min at 72°C, and a hold at 4°C. PCR amplicons were then visualized by agarose gel electrophoresis. The PCR product was then purified using the QIAquick PCR Purification Kit (Qiagen, Inc., Valencia, CA, USA) according to manufacturer provided instructions. The DNA concentration was determined as described above.

Sequencing

The procedure for direct sequencing of all PCR products for river buffalo, swamp buffalo, African Forest buffalo, and bison was followed (Seabury *et al.*, 2007). After amplicons were amplified, visualized, and the PCR product was purified, a sequencing reaction protocol was followed. The sequencing reaction contained the following: 1-3 µl PCR product was used, depending on the concentration, to yield 6 ng/µl per 100 bp; 2.0 µl each of Big Dye (Applied Biosystems) and halfBig Dye (Genetix USA, Inc., Boston,

MA, USA); 1.0 µl of forward or reverse primer (10 µM); 0.5X MasterAmp PCR Enhancer (Epicentre, Madison, WI, USA); and distilled water (Invitrogen, Grand Island, NY, USA) to a final total reaction volume of 10 µl. Thermocycling parameters were as follows: 5 min at 95°C; 30 s at 95°C, 20 s at 50°C, and 4 min at 60°C for 50 cycles; final extension of 5 min at 60°C and hold at 4°C.

The reaction product was then purified using G-50 Sephadex columns (Biomax, Odenton, MD, USA) as follows: The Sephadex columns were centrifuged using a table top microcentrifuge at 1000 x g for 4 min. To each sequencing reaction, 15 µl of distilled water (Invitrogen, Grand Island, NY, USA) was added, the 25 µl mixture was applied to the Sephadex columns, and centrifuged at 1000 x g for 3 min. Sequencing was performed by the DNA Technologies Core Laboratory at Texas A&M University using the ABI 3130 automated sequencer (Applied Biosystems). After the series of TLR5 amplicons was sequenced, Sequencher 5.0 (Gene Codes Corp., Ann Arbor, MI, USA) was used to assemble one contiguous (contig) strand for each isolate. Each single-nucleotide polymorphism (SNP) on the assembled contig was visually flagged. DNA was sequenced bi-directionally twice. Another round of PCR and sequencing was performed if the sequence data was ambiguous or of poor quality.

The cattle and goat TLR5 sequences were retrieved from GenBank and have the accession numbers EU006639 and FJ659852, respectively.

Cloning

Three river buffalo samples (ET567, ET616, and ET748) were cloned to independently verify the presence of heterozygous haplotypes. Primers BBU5_4F and BBU5_9R (Table 3.2) were used to amplify the coding region of TLR5. MasterAmp™ Extra-Long PCR kit is a high-fidelity PCR amplification kit that can sequence up to approximately 40 kb (Epicentre, Madison, WI, USA). Reactions were conducted according to manufacturer's instructions. The kit includes 9 pre-mixes that contain dNTPs, buffer, and varying concentrations of MgCl₂. The primer was tested across all pre-mixes to determine the optimal salt (MgCl₂) concentration, and pre-mix 2 was selected. Amplification conditions were the same as described in the above section. The purified PCR product was mixed together with pCR-XLTOPO® vector and then transformed into One Shot® TOP10 *E.coli* chemically competent cells using the TOPO XL PCR Cloning Kit, which is a 5 min cloning of long PCR products (3-10 kb), according to manufacturer's instructions (Invitrogen, Grand Island, NY, USA).

After cloning, the resultant product was plated onto medium containing the antibiotic kanamycin (50 µg/ml). The colonies were allowed to grow overnight in a 37°C incubator. The following morning, 10 colonies were picked and labeled and a PCR was performed using the same parameters and electrophoresed as described in the above section. This is to confirm that the colony contained the inserted the target sequence. Based on the results of the PCR, the corresponding colony was picked and grown in 5 ml of Luria broth medium with kanamycin for 12-16 hours while vigorously shaking on a shaking incubator at 37°C.

The culture was processed to extract plasmid DNA using QIAprep Spin Miniprep Kit, which purifies up to 20 µg of molecular biology grade plasmid DNA, according to manufacturer's instructions (Qiagen, Inc., Valencia, CA, USA).

The resultant DNA was sequenced and analyzed as described in preceding sections.

Statistical Analysis

Fisher's Two-tailed Exact test was performed to compare the ratio of synonymous single-nucleotide polymorphisms (sSNPs) to non-synonymous single-nucleotide polymorphisms (nsSNPs) within the coding region using GraphPad Software, where $p < 0.05$ was accepted as statistically significant (GraphPad Software, 2002).

Simple Modular Architecture Research Tool Analysis

A comparative analysis of protein domain structure of TLR5 of various bovids was performed utilizing the Simple Modular Architecture Research Tool (SMART) (Letunic *et al.*, 2009). Analyses used the normal mode and with the following parameters for SMART to find: PFAM (protein family) domains, signal peptides, and internal repeats.

Polymorphism Phenotyping Analysis

PolyPhen-2 (Polymorphism Phenotyping v2) software predicts the possible impact on the structure and functionality of a protein due to amino acid substitutions (Adzhubei *et al.*, 2010; European Molecular Biology Laboratory, 2011). The default settings were utilized to analyze the TLR5 sequences obtained in this study. The

program makes a determination on the impact of phenotype and makes no comment on the genotype, i.e. there is no comment on whether the substitution is conservative, radical, or neutral and only comments if the predicted change, based on a human database, is benign, possibly damaging, or damaging.

PHASE v2.1.1

PHASE v2.1.1 was used to predict haplotypes for the nsSNPs (n=6) within the coding region of TLR 5 for this population of river buffalo (n=18) with the -X10 option (Stephens *et al.*, 2001; Stephens & Scheet, 2005; Adzhubei *et al.*, 2010; European Molecular Biology Laboratory, 2011). The input consisted of unphased diploid data. The best pairs for each sample were determined as well as frequencies of each determined haplotype within the population.

Regulatory Elements Prediction and Indel Scanning

Three non-long terminal repeats (LTR) retrotransposons were found using the CENSOR web server, which aligns sequences against a reference collection of repeats. Known repeats identified by CENSOR are classified and given in a report (Jurka *et al.*, 1996). CpGProD (CpG Island Promoter Detection) (Ponger & Mouchiroud, 2002) and PROSCAN (Prestridge, 1995) did not find any CpG islands or promoters, respectively.

The TLR5 sequences in river buffalo (*Bubalus bubalis*, JN615215) were manually scanned for insertions and deletions (indels).

Results and Discussion

Single Nucleotide Polymorphisms (SNPs) Detected

In this study, DNA sequence from 1760 bp upstream of the start codon to 711 bp downstream of the stop codon was generated for TLR5 (Figure 3.1). GenBank accession numbers for the coding regions of TLR5 obtained in this study are shown in Table 3.1. Analysis of all sequenced river buffalo TLR5 regions in this study yielded 16 novel SNPs, with 10 being transitions and 6 being transversions (Table 3.3). Of those observed SNPs, 6 were identified as non-synonymous, with 2 being transitions and 4 transversions. Overall, approximately 59% SNPs were identified as transitions (Table 3.3). The 2 SNPs located at genomic positions 947 and 948 were the second and third nucleotide of the same codon (Table 3.3). Fisher's Two-tailed Exact test revealed a mutational bias between transitions and transversions towards transitions within nsSNPs and sSNPs ($p=0.0345$).

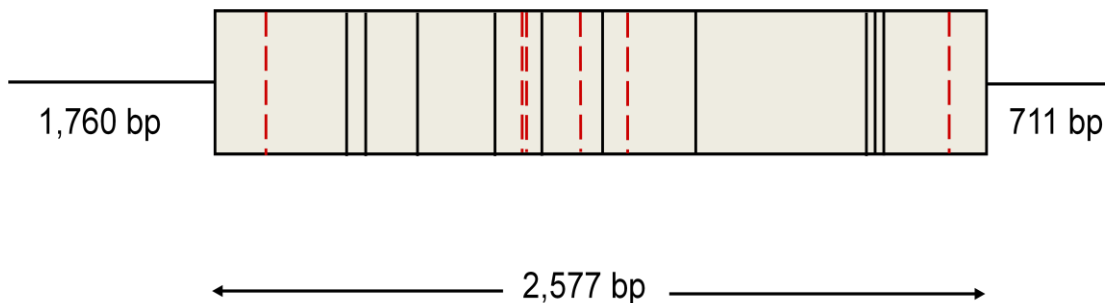


Figure 3.1 River buffalo TLR5 gene diagram. Dashed lines indicate non-synonymous single-nucleotide polymorphisms. Solid lines indicate synonymous single-nucleotide polymorphisms.

Table 3.3

Single-nucleotide polymorphisms. SNPs located in river buffalo TLR5 coding region. Allele, predicted SNP genomic position, predicted amino acid substitution, and SNP frequency are listed.

Alleles [*]	Genomic Position [†]	Predicted Amino Acid [‡]	Allele Frequency (%)
C/G (S)	140	Thr/Ser	86.0 / 14.0
C/T (Y)	396	Ser/Ser	94.0 / 6.0
A/G (R)	474	Gln/Gln	81.0 / 19.0
C/T (Y)	681	Val/Val	97.0 / 3.0
C/T (Y)	907	Leu/Leu	81.0 / 19.0
A/T (W)	947	Glu/Val	81.0 / 19.0
A/C (M)	948	Glu/Asp	81.0 / 19.0
T/C (W/M)	947/948	Glu/Val	-
G/A (R)	984	Ser/Ser	81.0 / 19.0
A/C (M)	1133	Lys/Thr	86.0 / 14.0
A/G (R)	1158	Leu/Leu	78.0 / 22.0
A/G (R)	1286	Gln/Arg	89.0 / 11.0
G/T (K)	1500	Gly/Gly	78.0 / 22.0
C/T (Y)	1944	Val/Val	78.0 / 22.0
G/A (R)	1977	Thr/Thr	86.0 / 14.0
G/A (R)	1992	Arg/Arg	86.0 / 14.0
C/G (S)	2571	Ile/Met	83.0 / 17.0

^{*} Alleles in bold type indicate non-synonymous single-nucleotide polymorphisms

[†] Begins at the start codon of the exon. Accession # JN615231 (river buffalo JEW41)

[‡] Amino acid/Amino acid substitution

This is the first study to examine SNPs within the coding region of buffalo TLR5. The presence of nsSNPs and the fact that the animals used in this study from Bufala di Vermont were clinically normal suggests that there may be some flexibility within TLR5 despite the fact that it is a member of a gene family that is generally known to be well-conserved amongst species. This also implies that there is a measure of response to pathogens, i.e. organisms and pathogens adapt to each other. To the best of the author's knowledge, there haven't been studies that have linked specific TLR5 SNPs or haplotypes to an exacerbation or mitigation of a disease condition in river buffalo.

Haplotype Prediction

Twelve haplotypes were predicted for TLR5 in this population and four were observed in the initial PCR direct sequencing (Table 3.4). The most frequent haplotype within this population was CAAAAC. The majority of river buffalo (approximately 80%) had the potential to transmit the CAAAAC haplotype. The samples acquired from the American Water Buffalo Association, JEW43 and JEW41, exhibited different haplotypes. JEW43 showed the predominant haplotype, CAAAAC; while JEW41 had the potential to transmit the CAAAAC haplotype and also the GTCCGG haplotype, which was the second most common haplotype present in the population at approximately 13%. Putative heterozygotes were determined to be true heterozygotes as the alternative allele was found after cloning and sequencing those clones (Table 3.5).

Table 3.4

Haplotypes of river buffalo TLR5 estimated by PHASE v2.1.1.

Haplotype	Frequency
CAAAAC	0.796879
GTCCGG	0.13367
CTCAAC	0.025147
GTCAAG	0.019849
GTCAAC	0.006575
CTCAAG	0.003983
CAAAG	0.003805
CTCCGG	0.002867
GAAAG	0.00249
GAAAC	0.00238
GTCCGC	0.0017
CTCCGC	0.000651

Table 3.5

River buffalo TLR5 sample clones. GenBank accession numbers and haplotypes are also shown.

Sample Identification	Accession Number	Haplotype
ET567A	JX456064	CAAAAC
ET567H	JX456065	GTCCGG
ET567I	JX456066	CAAAAC
ET567J	JX456067	CAAAAC
ET567X	JX456068	GTCCGG
ET616A	JX456069	CAAAAC
ET616B	JX456070	CTTAAC
ET616H	JX456071	CAAAG
ET616I	JX456072	CAAAAC
ET616J	JX456073	CTCAAC
ET616X	JX456074	CTCAAG
748X	JX456075	GTCCAC
748K	JX456076	CTCAAC
748L	JX456077	CTCAAC
748M	JX456078	GTCCAG

It is necessary to broaden the scope of haplotype scanning in river buffalo. The study population was a transplanted herd that was recently established in Vermont and then relocated to Canada. Older herds that have developed and progressed in the tropical and sub-tropical environments they are best suited for would be more informative as the haplotype structure would reflect their environment. Specifically, the sample herd was created from individuals from Italian sources and through the American Water Buffalo Association. Therefore, it is reasonable to assume that the sample herd might possibly have achieved its own Hardy-Weinberg equilibrium that is not indicative of any other region where buffalo are adapted to the environments where they are bred for food, fiber or draught. Sub-tropical and tropical regions share many features; the environment in southern Iraq might encourage a different haplotype structure than the herd established in Italy or herds that are in Thailand or China. A study of TLR5 haplotypes in different herds from around the world could reveal allele or haplotype associations with different environments and classes of pathogens.

Polymorphism Phenotyping Analysis

The majority of amino acid substitutions observed was determined to be benign. Only one of the nsSNPs that were observed within the coding region of TLR5 in river buffalo was found to be possibly damaging, that being AA⁸⁵⁷ (Figure 3.2), which is located two positions upstream of the stop codon. The AA⁸⁵⁷ converted an isoleucine to a methionine. Both amino acids are non-polar and have hydrophobic side chains. This substitution could possibly be damaging due to its proximity to the Toll-like/ Interleukin-1 (TIR) domain, which interacts with the TIR domain of MyD88. However, the substitution might not be damaging because the SNP is not actually within the domain may not interrupt its functionality. While PolyPhen 2 has predicted that there may or may not be an impact on the functionality of the TLR5 gene in river buffalo due to a particular variation, it is still possible that the variation at that position does negatively impact health.

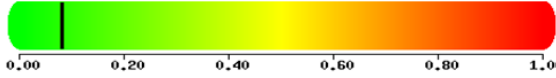
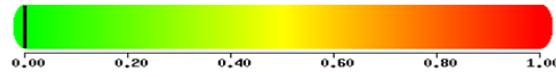

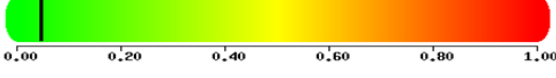


AA Position	AA Substitution	Results
47	Thr/Ser	This mutation is predicted to be BENIGN with a score of 0.081 (sensitivity: 0.92 ; specificity: 0.81) 
316	Glu/Val	This mutation is predicted to be BENIGN with a score of 0.000 (sensitivity: 1.00 ; specificity: 0.00) 
316	Glu/Asp	This mutation is predicted to be BENIGN with a score of 0.000 (sensitivity: 1.00 ; specificity: 0.00) 
378	Lys/Thr	This mutation is predicted to be BENIGN with a score of 0.046 (sensitivity: 0.94 ; specificity: 0.79) 
429	Gln/Arg	This mutation is predicted to be BENIGN with a score of 0.021 (sensitivity: 0.95 ; specificity: 0.76) 
857	Ile/Met	This mutation is predicted to be POSSIBLY DAMAGING with a score of 0.208 (sensitivity: 0.90 ; specificity: 0.83) 

Figure 3.2 PolyPhen-2 analysis of amino acid substitution effects. River buffalo TLR5 coding region was analyzed.

As discussed in Chapter I, there are studies that have linked SNPs (such as a premature stop codon in certain humans that confers resistance to lupus (Hawn *et al.*, 2005)) and expression levels of TLR5 production (regulation of TLR5 during various phases of bacterial growth (West *et al.*, 2009)), but not in water buffalo. While those studies can be informative, comparable studies in domesticated or wild ruminants have not been performed so direct conclusions cannot be inferred. Comparisons between the two species or multiple species or populations of river buffalo should be made to put the results into context. Cross species comparisons are important in an evolutionary sense, but they are also a way to indirectly measure the impact of environment on both the host organism and the pathogen.

Pathogens and their preferred host adapt to each other, but the environmental conditions can also serve to impact how they adapt together. For instance, a multi-year drought causes the host organism population to migrate and not return to its place of origin, but leaves a population behind that establishes a new equilibrium with the pathogen. Or, alternatively, the host organism still migrates but carries the pathogen with it and the new environment proves to be even better for the pathogen and/or the host organism than the environment of origin. In both scenarios, a new equilibrium must be established so the environment plays a role in how the two establish that equilibrium over time; but while that is happening, new alleles or haplotypes become more or less prevalent.

A basic violation of Hardy-Weinberg equilibrium would lead to different evolutionary hallmarks of both the host organism and pathogen due to environment as much as to basic evasion and adaptation tactics of the host and pathogen.

This makes case studies important. By case study, I mean to specifically use pedigrees and backcrossing to track the haplotypes or SNPs described here and possibly link them to susceptibility or resistance disease conditions, which should be made across river buffalo populations.

Comparative Analysis of Protein Domain Architecture

Leucine-rich repeats (LRRs) vary in length and the number of repeats (2-45). Three regions of leucine-rich repeats (Fig. 3.3) were observed in TLR5. River buffalo (*Bubalus bubalis bubalis*), swamp buffalo (*Bubalus bubalis carabanesis*), and African forest buffalo (*Syncerus caffer nanus*) all exhibited the same LRR patterns across all three regions of LRRs.

American bison (*Bison bison*) and cattle (*Bos taurus indicus*) also exhibited the same LRR patterns across all three LRR regions (Fig. 3.3), but shared an additional LRR next to the third LRR region. Goat (*Capra hircus*) was utilized as the outgroup and shared the same LRR patterning with the addition of an extra LRR region that was further upstream than the extra LRR region shared by American bison and cattle. Species that appear to be undergoing positive selection in the LRR region of TLR5 relative to river buffalo (pig, dog, chicken, ring-necked pheasant, human, and Philippine tarsier) have similar LRR regions, but there are variations within that group that depend on their divergence time from each other.

It is the same for species that appear to be undergoing neutral selection (chamois, white-tailed deer, goat, and greater kudu) and negative selection (African forest buffalo, cattle, and American bison). African-clawed frog was not analyzed for selective forces because its sequence was too divergent from river buffalo. Evolution and selective pressure are discussed in more depth in Chapter IV.

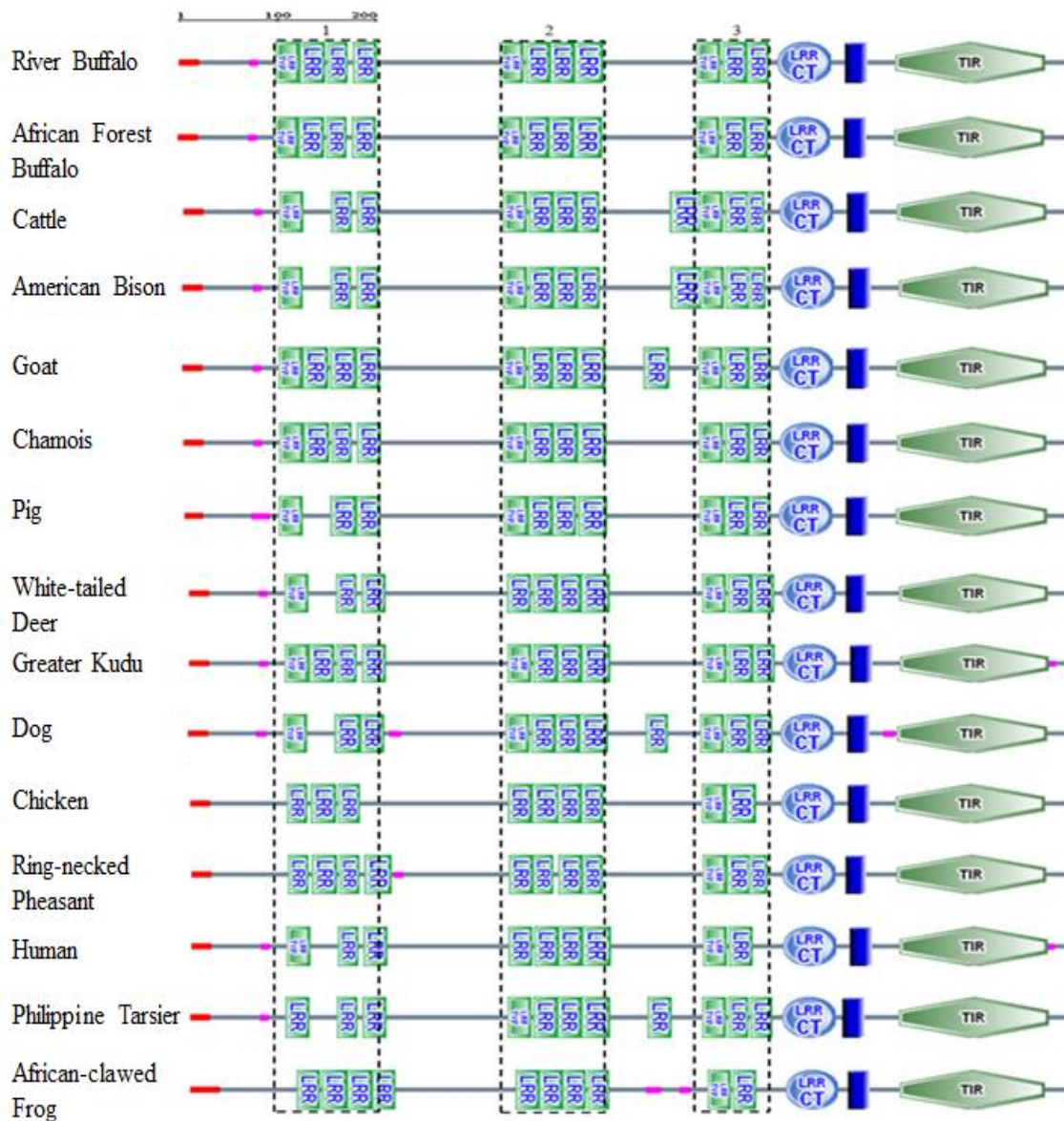


Figure 3.3 Comparative SMART analysis. The figure was generated using SMART. TLR5 predicted amino acid sequences for river buffalo (*Bubalus bubalis bubalis*; JN615218), African forest buffalo (*Syncerus caffer nanus*, JN615234), cattle (*Bos taurus taurus*, JQ805125), American bison (*Bison bison*, JN615236), goat (*Capra hircus*, HQ188378), chamois (*Rupicapra rupicapra*, JQ811845), pig (*Sus scrofa*, AB208697.2), white-tailed deer (*Odocoileus virginianus*, JQ811843), greater kudu (*Tragelaphus strepsiceros*, JQ811848), dog (*Canis lupus familiaris*, NM_001197176), chicken (*Gallus gallus*, HQ896214), ring-necked pheasant (*Phasianus colchicus*, JF767220), human (*Homo sapiens*, NM_003268), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1), African clawed frog (*Xenopus laevis*, NM_001094980). Predicted domains and proteins are as follows: signal peptides are represented by the longer, horizontal boxes at the beginning on the right, segments of low complexity are represented by small, horizontal boxes immediately following the signal peptide; conserved leucine-rich repeats (LRRs) are enclosed by dashed boxes; transmembrane segments are vertical lines; and the Toll - interleukin 1 - resistance is represented by TIR.

In addition to analyzing the protein domain structure and comparing it across multiple species, SNPs in these domains were analyzed across the coding region of TLR5 to determine which clades share SNP positions. River buffalo (*B. b. bubalis*) was used as the reference; therefore, the domain boundaries, as determined by SMART, for river buffalo were the reference to which all other species were compared (Table 3.6). From the tables (3.7-3.21), it can be seen that Clade 1 and 2 share a substantial number of SNP positions in all domains. The TIR domain had the largest number of clades that shared common SNP positions. Clade 1 shares the most SNP positions with all other clades. It is possible that the common ancestor between Clade 1 and other clades passed on those SNPs. LRRs vary and seem to have some flexibility; however, only 5 river buffalo SNPs were found to be non-synonymous, which still suggests a level of constraint that makes this family less likely to undergo rapid evolutionary changes. Primates (Clade 1) and avians (Clade 2) appear to be undergoing positive selection. Since these clades are undergoing various forms of selective pressure, it can be inferred that these pressures have encouraged changes in the LRR domain and thus these SNPs reflect those changes.

Table 3.6

River buffalo (*Bubalus bubalis*) TLR5 domain boundaries. Boundaries determined by SMART.

	Domain	Residue Range	Amino Acid Range
1 st Region	LRR TYP	94-117	280-351
	LRR	118-143	352-429
	LRR	144-163	430-489
	LRR	169-192	505-576
2 nd Region	LRR TYP	311-334	931-1002
	LRR	335-358	1003-1074
	LRR	359-382	1075-1146
	LRR	383-411	1147-1233
3 rd Region	LRR	501-524	1501-1572
	LRR	525-548	1573-1644
	LRR	549-570	1645-1710
	C-Terminal LRR	579-630	1735-1890
	Transmembrane	644-666	1930-1998
	Toll-like/ Interleukin-1 Receptor	692-837	2074-2511

Table 3.7

Common divergent sites across all clades summation. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*	Clade 4*	Clade 5*	Clade 6*	Clade 7*	Clade 8*	Clade 9*
Clade 1*		155	16	6	1	8	17	16	4
Clade 2*	155		12	4	1	5	12	10	7
Clade 3*	16	12		0	0	2	6	8	4
Clade 4*	6	4	0		0	1	0	2	0
Clade 5*	1	1	0	0		0	0	0	0
Clade 6*	8	5	2	1	0		1	2	0
Clade 7*	17	12	6	0	0	1		6	1
Clade 8*	16	10	8	2	0	2	6		0
Clade 9*	4	7	4	0	0	0	1	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229); **Clade 5**- African forest buffalo (*Syncerus caffer nanus*, JN615234 and JN615233); **Clade 6**- lesser kudu (*Tragelaphus imberbis*, JQ811849), greater kudu (*Tragelaphus strepsiceros*, JQ811848); **Clade 7**- goat (*Capra hircus*, HQ188378), sheep (*Ovis aries*, NM_001135926), chamois (*Rupicapra rupicapra*, JQ811845); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847); **Clade 9**- mule deer (*Odocoileus hemionus*, JQ811842), white-tailed deer (*Odocoileus virginianus*, JQ811843).

Table 3.8

Common divergent sites across multiple clades, residues 94-117. LRR TYP domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*
Clade 1*		5	1
Clade 2*	5		0
Clade 3*	1	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guinea fowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641).

Table 3.9

Common divergent sites across multiple clades, residues 118-143. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*	Clade 4*	Clade 8*
Clade 1*		4	1	1	1
Clade 2*	4		0	1	1
Clade 3*	1	0		0	0
Clade 4*	1	1	0		1
Clade 8*	1	1	0	1	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guinea fowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847).

Table 3.10

Common divergent sites across multiple clades, residues 144-163. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1 [*]	Clade 2 [*]	Clade 3 [*]	Clade 4 [*]
Clade 1 [*]		2	0	1
Clade 2 [*]	2		1	0
Clade 3 [*]	0	1		0
Clade 4 [*]	1	0	0	

^{*}Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229).

Table 3.11

Common divergent sites across multiple clades, residues 169-192. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1 [*]	Clade 2 [*]	Clade 3 [*]
Clade 1 [*]		5	1
Clade 2 [*]	5		0
Clade 3 [*]	1	0	

^{*}Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641).

Table 3.12

Common divergent sites across multiple clades, residues 311-334. LRR TYP domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1 [*]	Clade 2 [*]	Clade 4 [*]	Clade 6 [*]	Clade 8 [*]
Clade 1 [*]		4	1	1	1
Clade 2 [*]	4		2	0	1
Clade 4 [*]	1	2		1	0
Clade 6 [*]	1	0	1		0
Clade 8 [*]	1	1	0	0	

^{*}Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229); **6**- lesser kudu (*Tragelaphus imberbis*, JQ811849), greater kudu (*Tragelaphus strepsiceros*, JQ811848); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847).

Table 3.13

Common divergent sites across multiple clades, residues 359-382. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1 [*]	Clade 2 [*]	Clade 3 [*]	Clade 9 [*]
Clade 1 [*]		3	0	0
Clade 2 [*]	3		1	0
Clade 3 [*]	0	1		1
Clade 9 [*]	0	0	1	

^{*}Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 9**- mule deer (*Odocoileus hemionus*, JQ811842), white-tailed deer (*Odocoileus virginianus*, JQ811843).

Table 3.14

Common divergent sites across multiple clades, residues 383-411. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 6*	Clade 7*
Clade 1*		1	1	1
Clade 2*	1		0	0
Clade 6*	1	0		0
Clade 7*	1	0	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 6**- lesser kudu (*Tragelaphus imberbis*, JQ811849), greater kudu (*Tragelaphus strepsiceros*, JQ811848); **Clade 7**- goat (*Capra hircus*, HQ188378), sheep (*Ovis aries*, NM_001135926), chamois (*Rupicapra rupicapra*, JQ811845).

Table 3.15

Common divergent sites across multiple clades, residues 501-524. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*	Clade 4*	Clade 6*	Clade 7*
Clade 1*		5	1	0	1	1
Clade 2*	5		1	1	0	0
Clade 3*	1	1		0	0	0
Clade 4*	0	1	0		0	0
Clade 6*	1	0	0	0		0
Clade 7*	1	0	0	0	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229); **Clade 6**- lesser kudu (*Tragelaphus imberbis*, JQ811849), greater kudu (*Tragelaphus strepsiceros*, JQ811848); **Clade 7**- goat (*Capra hircus*, HQ188378), sheep (*Ovis aries*, NM_001135926), chamois (*Rupicapra rupicapra*, JQ811845).

Table 3.16

Common divergent sites across multiple clades, residues 549-570. LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 8*
Clade 1*		2	1
Clade 2*	2		0
Clade 8*	1	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847).

Table 3.17

Common divergent sites across multiple clades, residues 579-630. C-terminal LRR domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*	Clade 6*	Clade 8*
Clade 1*		14	1	1	4
Clade 2*	14		1	1	2
Clade 3*	1	1		0	2
Clade 6*	1	1	0		0
Clade 8*	4	2	2	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 6**- lesser kudu (*Tragelaphus imberbis*, JQ811849), greater kudu (*Tragelaphus strepsiceros*, JQ811848); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847).

Table 3.18

Common divergent sites across multiple clades, residues 644-666. Transmembrane Domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*	Clade 4*	Clade 7*	Clade 8*
Clade 1*		10	5	2	2	2
Clade 2*	10		3	0	2	1
Clade 3*	5	3		0	2	2
Clade 4*	2	0	0		0	1
Clade 7*	2	2	2	0		1
Clade 8*	2	1	2	1	1	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229); **Clade 7**- goat (*Capra hircus*, HQ188378), sheep (*Ovis aries*, NM_001135926), chamois (*Rupicapra rupicapra*, JQ811845); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847).

Table 3.19

Common divergent sites across multiple clades, residues 692-837. Toll-like/Interleukin-1 Receptor Domain with river buffalo (*Bubalus bubalis*) used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*	Clade 5*	Clade 6*	Clade 7*	Clade 8*	Clade 9*
Clade 1*		16	4	1	2	4	3	1
Clade 2*	16		2	1	1	1	1	0
Clade 3*	4	2		0	2	3	3	0
Clade 5*	1	1	0		0	0	0	0
Clade 6*	2	1	2	0		1	2	0
Clade 7*	4	1	3	0	1		1	0
Clade 8*	3	1	3	0	2	1		0
Clade 9*	1	0	0	0	0	0	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229); **Clade 5**- African forest buffalo (*Syncerus caffer nanus*, JN615234 and JN615233); **Clade 6**- lesser kudu (*Tragelaphus imberbis*, JQ811849), greater kudu (*Tragelaphus strepsiceros*, JQ811848); **Clade 7**- goat (*Capra hircus*, HQ188378), sheep (*Ovis aries*, NM_001135926), chamois (*Rupicapra rupicapra*, JQ811845); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847); **Clade 9**- mule deer (*Odocoileus hemionus*, JQ811842), white-tailed deer (*Odocoileus virginianus*, JQ811843).

Table 3.20

Common divergent sites across all clades and domains summation. River buffalo (*Bubalus bubalis*) is used as the reference to determine domain boundaries.

	Clade 1*	Clade 2*	Clade 3*	Clade 4*	Clade 5*	Clade 6*	Clade 7*	Clade 8*	Clade 9*
Clade 1*		80	14	5	1	6	8	12	1
Clade 2*	80		9	4	1	2	3	6	0
Clade 3*	14	9		0	0	2	5	7	1
Clade 4*	5	4	0		0	1	0	2	0
Clade 5*	1	1	0	0		0	0	0	0
Clade 6*	6	2	2	1	0		1	2	0
Clade 7*	8	3	5	0	0	1		2	0
Clade 8*	12	6	7	2	0	2	2		0
Clade 9*	1	0	1	0	0	0	0	0	

*Clade composition with scientific name and GenBank accession number in parenthesis: **Clade 1**-marmoset (*Callithrix jacchus*, ACFV01163303.1), sooty mangabey (*Cercocebus torquatus atys*, EU204938), crab-eating macaque (*Macaca fascicularis*, AB445650), Rhesus macaque (*Macaca mulatta*, NM_001130429.1), gorilla (*Gorilla gorilla*, AB445648), human (*Homo sapiens*, NM_003268), pygmy chimpanzee (*Pan paniscus*, AB445647), chimpanzee (*Pan troglodytes*, NM_001130462), Bornean orangutan (*Pongo pygmaeus*, AB445649), Philippine tarsier (*Tarsius syrichta*, ABRT010212218.1); **Clade 2**- chicken (*Gallus gallus*, HQ896214), Ceylon junglefowl (*Gallus lafayetii*, FJ915547), turkey (*Meleagris gallopavo*, HQ436463), ring-necked pheasant (*Phasianus colchicus*, JF767220), helmeted guineafowl (*Numida meleagris*, JF767221), zebra finch (*Taeniopygia guttata*, XM_002188726); **Clade 3**- banteng (*Bos javanicus*, JQ811841), domestic yak (*Bos grunniens*, JQ811841), American bison (*Bison bison*, JN615236), cattle (*Bos taurus taurus*: JQ805125, JQ805128, JQ805129, JQ805134, JQ805135, JQ805136, JQ805137; *Bos taurus indicus*: EU006636, EU006641); **Clade 4**- swamp buffalo (*Bubalus bubalis carabanesis*, JN615235), river buffalo (*Bubalus bubalis bubalis*; JN615218, JN615220, JN615224, JN615225, JN615229); **Clade 5**- African forest buffalo (*Syncerus caffer nanus*, JN615234 and JN615233); **Clade 6**- lesser kudu (*Tragelaphus imberbis*, JQ811849), greater kudu (*Tragelaphus strepsiceros*, JQ811848); **Clade 7**- goat (*Capra hircus*, HQ188378), sheep (*Ovis aries*, NM_001135926), chamois (*Rupicapra rupicapra*, JQ811845); **Clade 8**- Gemsbok oryx (*Oryx gazelle*, JQ811846), scimitar-horned oryx (*Oryx dammah*, JQ811850), Arabian oryx (*Oryx leucoryx*, JQ811847); **Clade 9**- mule deer (*Odocoileus hemionus*, JQ811842), white-tailed deer (*Odocoileus virginianus*, JQ811843).

Regulatory Elements and Indel Scanning

As previously discussed, 1760 bp upstream of the start codon and 711 bp downstream of stop codon which form the 5'- and 3'- untranslated regions (UTR) were sequenced (Figure 3.1). There are numerous insertion/deletions (indels) in comparison to cattle sequences throughout both the 5'- and 3'-UTRs (Figure 3.4). These indels, particularly in the 5'-UTR, would make it difficult for human- or cattle-based regulatory element databases to correctly align and find regulatory elements as candidate sequences might be disrupted by indels.

Interspersed elements are repetitive elements with the ability to move and copy themselves into other parts of the genome and comprise 40-50% of a mammalian genome (Adelson *et al.*, 2009). There are two classes of mobile elements: class I (retrotransposons) and class II (DNA transposons). Retrotransposons copy and paste themselves in the genome by transcribing their mRNA, which is then reverse transcribed and the resultant DNA is inserted into the new location. This results in an increased copy number of that element and can increase the size of a genome (Ray, 2007). Transposons cut themselves from their original location and paste into a new location (Grabundzija *et al.*, 2010). Despite the possible alignment issues stated above, CENSOR (Jurka *et al.*, 1996) was able to find two transposable elements, which are classed as non-long terminal repeat retrotransposon short-interspersed nuclear elements (SINEs) by CENSOR (Figure 3.5, Figure 3.6, Table 3.21). Artiodactyla was chosen as the DNA source and all defaults were maintained for CENSOR.

5'-UTR

Cattle	AACAGAGTAGACTTGAAGGTA AA ACTGAC ---- TTGCTAACAT-GGGGGTGACATTTC	54
River Buffalo	AACAGAGTAGACTTGGGAGGTA AA ACTGAC ATGAC TTGCTAACAT T GGGGGTGACATTTC	60

Cattle	TTCAAATGTGAAACGGCAATGGTTGTTTTTCATCTGATGGTGTACACGAGT-TACCATGC	293
River Buffalo	TTCAAATGTGAAATGGCAATGGTTATTTTTTCATCTCATGGTATA CA TGAGT AT AACCATGC	300

Cattle	CCCC CC AACTCTTTTCTTTTAATTTAATG --- TATTGATTTTGGCTGCCTTGGATCT	349
River Buffalo	CCCC --- AACTCTTTTCTTTTAATTTAAT GAAT TATTATTTTGGCTGCCTTGGATCT	358

Cattle	TTGGGTCAACTCAGGAGTTGATGT ----- GTGT CACAGCC	564
River Buffalo	TTGGGTCAACTCAGGAGTTGATGT CTCCTTCTGATCAGCTGTAAAT TGTGTGT CACAGCC	598

Cattle	TTCTTT CTTTC TTTTTTTTTATTTTAAACTTTACATAATTTGATTTAGTT TTG CC	804
River Buffalo	TTCTTT -----	784

Cattle	AAATATCAAAATGAATCCGCCACAGGTATACAGTGCTCCCCATCCTGA ACCC T CC TCC	864
River Buffalo	----- ACTCTCC CC ---	794

Cattle	TCCTCCTCCCCCACCACATCCCTCTGGTCGTCCCAGTGCCACCAGCCCAAGCACCCAGT	924
River Buffalo	----- TC ACT CTG --- CC ---	805

Cattle	ATCGTGCATCGAACCTGGACTGGCATCTCGTTTCATACGTGATATTTTACATGTT TCTGA	984
River Buffalo	----- TCTGA	810

Cattle	T G AGGGGCCCGTGTGCACCCCTCTGTACCCTCACAGCTCCCAGCACAGCACTGAGAACATA	1164
River Buffalo	T-AGGGGCCCTCGTGCACCCCTCTGTACCCTCACAGCTCCYAGCACAGCACTGAGAACATA	989

Cattle	-GCGGACACCTTCATTTCGGCGCCTTTTGCCGCTCTGTACAAGCAAATGCTCAACCCAGAC	1223
River Buffalo	AGCGGACACCTTCATTTCGGCGCCTTTTGCCGCTCTGTACAAGCAAATGCTCAACACAGAC	1049

Cattle	CACATGGT CAC CAAGTGCAGGCATGCAGTTGGTGCTTAGTGCATCCTTATTAAACTG	1343
River Buffalo	CACATGGT CAC -ACAAGTGCAGGCATGCAGTTGGTGCTTAGTGCATCCTTATTAAACTG	1168

Cattle	GAATTCACAACCTTATGAATGAATGCTGAGTTATCACAAAGATTAAATAT ---- TTTCTG	1639
River Buffalo	GAATTCACAACCTTATGAATGAATGCTGAGTTATCACAAAGATTAAATA AGTAT TTTCTG	1468

Cattle	ACACAGGGTCTAAGAAGCAACCACATCACAAAGGGTCCCCAGGCC TAA -CAC CT CA	1818
River Buffalo	ACACAGGGTCTAAGAAGCAACTACATCACAAAGGGTCCCCAGGCC TAA GCAT CT CA	1648

3'-UTR		
Cattle	AGA --- GGGGCTGGT CAGT GGTTCTGAGG-CTCTGTGCCTAGCACAA CA --- CTAAATAGA	5112
River Buffalo	AGA AG GGGGCTGGT CAGT GATTCTGAGG GCT CTGTGCCTAGCACAA CA CA CA CTAAATAGA	4948

Figure 3.4 Indels located within the 5'- and 3'-UTR. River buffalo (*Bubalus bubalis*, GenBank Accession No. JN615215) was used as the reference to cattle (*Bos taurus*, GenBank Accession No. JQ805125). Red bolded sequence is a deletion, while blue bolded is insertion.

CHR-2B, region 419-575

```

419 GGTTCAGTAGTTGTGGCACAKGGGCTTAGTTGCCCCACGGCATGTGGGATCTTCCCAGACCAGGGATGAA 488
  ||:||||||||||||||:| | ||||||||||||:||||||||||||||||||:||||||| | :|
129 GGCTCAGTAGTTGTGGCGCACGGGCTTAGTTGCTCCACGGCATGTGGGATCTTCCCGACCAGGGATTGA 60

489 ACCCATGTCTCCTGCCCTGGCAGGCAGATTCTTAACCACTGGACCACTAGGGAAGTC 545
  |||:||||:|||| | :|||||||||||||||||||||||||||||||:|||||||
59 ACCCGTGTCCCCTGCATTGGCAGGCAGATTCTTAACCACTGGACCACTAGGGAAGTC 3

```

Bov-tA1

```

4421 TGTTCAAGTTGCTT-GGTCATGTCCTACTCTTTGCGACCCATGGACTGTAGCCCACCAGGCGCCTCTGTT 4489
  ||:|+|:|:-:||||||| | ||||||||||||:||||||||||||||:||||+ |||||:
216 TGCTCARTTACTTCAGTCATGTCCGACTCTTTGCGACCCATGGACTGTAGCCCGCCAGGTCCTCTGTC 147

4490 CATGGGATTTCTTAGGCAAGAATACTGGAGTGGTTGCCATTTCTCTCCTCCAGGGGATCTTCGTGACCCA 4559
  |||||||||:|:|||||||||||||||||| | ||||| +||||||||||||||||| :|||||
146 CATGGGATTTCTCAGGCAAGAATACTGGAGTGGTTGCCATGYCCTCCTCCAGGGGATCTTCCCGACCCA 77

4560 GGGATCGAACCCAAGTCTCTGTGTCTCTTGTATTAGCAGGCAGAGTCTTTACCACT-GAGTCACCTAGG 4628
  |||||||||: | |||:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|:|
76 GGGATCGAACCCGCGTCTTACGTCTCCTGCATTGGCAGGCGGGTCTTTACCACTAGCGCCACCTGGG 7

4629 AAGCCC 4634
  |||||
6 AAGCCC 1

```

Figure 3.5 Retrotransposons found by CENSOR. Cetartiodactyl was the DNA source that was chosen as the reference for repeat elements. River buffalo (*Bubalus bubalis*, GenBank Accession No. JN615215) was the sequence used to generate the CENSOR repeat report.

River Buffalo: 419-545

```

GACTTCCTAGTGTTCCAGTGGTTAAGAATCTGCCTGCCAGGGCAGGAGACATGGGTTTCATCCCTGGTC
TGGAAGATCCCACATGCCGTGGGGCAACTAAGCCMTGTGCCACAACCTACTGAACC

```

River Buffalo: 4421-4634

```

GGGCTTCTAGGTGACTCAGTGGTAAAGACTCTGCCTGCTAATACAAGAGACACAGGAGACTTGGGTTCG
ATCCCTGGGTCACGAAGATCCCCTGGAGGAGGAAATGGCAAACCACTCCAGTATTCTTGCCTAGGAAATC
CCATGAACAGAGGCGCCTGGTGGGCTACAGTCCATGGGTCGAAAGAGTAGGACATGACCAAGCAACTG
AACA

```

Figure 3.6 Masked regions sequence. Cetartiodactyl was the DNA source that was chosen as the reference for repeat elements. River buffalo (*Bubalus bubalis*, GenBank Accession No. JN615215) was the sequence used to generate the CENSOR repeat report.

Table 3.21

Repeat element summary generated by CENSOR.

Repeat Class	Fragments	Length
Transposable Element	2	341
Non-LTR Retrotransposon	2	341
SINE	2	341
SINE2/tRNA	1	214
Total	2	341

* Cetartiodactyl was the DNA source that was chosen as the reference for repeat elements. River buffalo (*Bubalus bubalis*, GenBank Accession No. JN615215) was the sequence used to generate the CENSOR repeat report.

A previous study with Iranian river buffalo has looked at repeat elements by sequencing random amplified polymorphic DNA (RAPD) fragments (Shokrollahi *et al.*, 2010). CHR-2B was previously discovered in Iranian river buffalo and is generally found in the genome of ruminants. CHR-2B is a member of the CHR-2 SINE family, which has been associated with a common ancestor of cetaceans, hippopotamuses, and ruminants, forming the basis for the acronym CHR (Shimamura *et al.*, 1999). The other SINE discovered by CENSOR is a member of the Bov-tA family, which has been shown to have developed from recombination between CHR-2 and Bov-A (Shimamura *et al.*, 1999). Unlike the results for Iranian river buffalo (Shokrollahi *et al.* 2010), CENSOR found Bov-tA1 for the river buffalo in this study, and not Bov-tA2. Bov-tA is composed of a Bov-A that is 115 bp and a tRNA pseudogene that is 73 bp (Nijman *et al.*, 2002).

Impact of these regulatory elements and indels on gene expression between species cannot be resolved without determining gene expression of each individual species and comparing the data with the sequence, in essence, an association study between levels of gene expression and the indel to link the observed phenotype with the genotype. Sequencing the region containing TLR5 would be necessary to capture the full UTR regions of river buffalo and would yield the full sequence for bioinformatic scanning or regulatory elements and the full exploration of the sequence for gene expression studies.

It is becoming increasingly important to predict the possible impact of variability in genes of interest on both the functionality of the gene and the organism's ability to detect and overcome illness. Despite the results from SMART analysis that suggest

differences in the number and position of LRR regions between members of family bovidae in TLR5, specifically between *Bos taurus*, *Bison bison*, and *Bubalus bubalis*, the impact to animal health is not necessarily solely due to structural differences in this particular region of the gene, but also to differences in gene expression. These observed differences in gene structure could be impacted by regulatory components upstream of the start codon, and might also play a role in how these animals have adapted to their varying environments; however, it is necessary to generate both UTRs and actually conduct gene expression analysis to link the presence of indels to expression. The regulatory elements that have been predicted are consistent with ruminant SINE families. In addition, the immune system, as a whole, is complex. Because of this complexity and interactions between different parts of the immune system, the potential exists for compensatory changes in other families in the immune system. Therefore, investigating single components and elucidating what the roles they might play within the system can serve to reduce this complexity.

River buffalo are important to global agriculture, and the exploration of their genome for variation is only beginning. Case studies can examine the impact of regional differences and biota diversity on the haplotypes described here and even potentially reveal more with a larger and more varied population.

Therefore, it is not a leap to focus on the ruminant gastro-intestinal tract to develop tools that can potentially be exploited to assess diversity in breeding populations or in selection for enhanced health and productivity.

Previous studies in mice have investigated the impact of TLR5 on commensal bacterial loads (Vijay-Kumar *et al.*, 2007). True ruminants have four compartments of their digestive tract that allows them to acquire nutrients from plant substances. As such, to varying degrees, these compartments will be exposed to bacteria so an investigation that looks at native commensal bacterial loads, specifically flagellated bacteria, and how TLR5 regulates the load and if it is differentially expressed in the four compartments would serve to add to the profile of TLR5 in context of disease and maintenance. Furthermore, linking commensal load maintenance and TLR5 gene expression to a haplotype or SNP has the potential to impact animal breeding.

CHAPTER IV

A PHYLOGENETIC EXAMINATION OF TOLL-LIKE RECEPTOR 5 (TLR5) IN A VARIETY OF SPECIES

Introduction

The ability of the vertebrate immune system to recognize broad motifs which are not shared by the host organism enables them to successfully respond to invasions by pathogens without prior exposure. The innate immune system depends on pattern recognition receptors (PRRs) for its ability to recognize broad motifs of pathogens (Akira *et al.*, 2001). These broad motifs or pathogen-associated molecular patterns (PAMPs) are functionally important and are evolutionarily conserved within pathogens, thus making it difficult for organisms to mutate these features and still be able to successfully invade and colonize the preferred host organism (Medzhitov, 2001).

An important PRR family within the innate immune system of vertebrates is the Toll-like receptor (TLR) family. The TLR family, first discovered in *Drosophila melanogaster* for its contribution to dorsoventral polarity, provides fruit flies defense against fungal infection (Steward & Nusslein-Volhard, 1986; Lemaitre *et al.*, 1996). Toll-like receptors are type I transmembrane proteins, which differentially expressed across tissues and cells within the innate immune system in mammals and localize on the surface of cells or within the cell on specialized organelles (Kawai & Akira, 2006; Vahanan *et al.*, 2008). Toll-like receptors form either hetero- or homodimers and signal through MyD88 to begin a cytokine storm (Takeuchi *et al.*, 2000). To date, there have

been ten TLRs discovered in most vertebrates, including water buffalo (Akira *et al.*, 2001).

There are two competing hypotheses on the evolution of TLR genes. This family recognizes PAMPs, which are difficult for pathogens to mutate and still maintain the ability to invade and colonize the host (Medzhitov, 2001). Therefore, the first hypothesis is that this system should be evolutionarily conserved and should not change as robustly over time as other genes. Thus, Toll-like receptors are generally referred to as an example of an evolutionarily conserved gene family (Wlasiuk *et al.*, 2009). Despite the inability of pathogens to easily mutate PAMPs to evade TLR stimulation, there are classes of pathogens that can successfully invade and colonize their preferred host (Andersen-Nissen *et al.*, 2005). The ability of certain pathogens to successfully mutate their flagellin recognition site to evade TLR5 detection or to downgrade their flagellin implies a co-evolutionary response of host and pathogen and forms the basis of the second hypothesis that TLRs do evolve and change over time in response to unique evasion tactics of pathogens. Studies in *Drosophila* indicate that PRRs evolve quickly between species, though it has not been demonstrated that vertebrate and invertebrate responses are similar (Sackton *et al.*, 2007). Previous studies in primates (including humans) and avians have identified changes in Toll-like receptor 5 (TLR5) that are generally associated with the leucine-rich repeat (LRR) domains, which are extracellular and are involved with recognizing bacterial flagellin (Hawn *et al.*, 2005; Wlasiuk *et al.*, 2009; Ruan *et al.*, 2012).

This study focuses on the evolutionary relationship of the TLR5 gene within the

artiodactyl order. Phylogenetic trees were drafted for the coding region of TLR5 across multiple orders and also specifically for the order artiodactyl. In addition, the McDonald-Kreitman Poisson Random Field test was applied across representatives from select orders to examine the selective pressures that have occurred over time between species separated at the order level.

Materials and Methods

DNA Samples

Samples used in this study are shown in Table 4.1. Cattle DNA samples BTA1 through BTA13 were provided by the J.E. Womack Laboratory (Texas A&M University) (Seabury *et al.*, 2007). The remaining DNA samples from *Giraffa*, *Oryx*, *Odocoileus*, *Rupicapra*, and *Tragelaphus* were provided by the J.E. Womack Laboratory cell collection.

Primers and Polymerase Chain Reaction (PCR) Amplification

Previously described *Bos taurus* TLR5 primers (Seabury *et al.*, 2007) (Table 3.2) were used to amplify the TLR5 gene from the DNA samples. PCR amplicons were generated via the following step-down thermocycling program: 5 min at 95°C; 30 s at 95°C, 20 s ranging from 58°C to 62°C, 1 min at 72°C for 5 cycles; then 30 s at 95°C, 20 s ranging from 57°C to 60°C for 45 cycles. Each 25 µl PCR contained the following: 50-100 ng DNA, 0.2 mM each dNTP, 0.4 µM forward and reverse primer, 1.5 mM MgCl₂, 1X Gene Amp PCR Gold Buffer (Applied Biosystems, Foster City, Ca, USA), 0.2X MasterAmp PCR Enhancer (Epicentre, Madison, WI, USA), and 1.66 units of AmpliTaq

Gold DNA polymerase (Applied Biosystems). PCR amplicons were then visualized by agarose gel electrophoresis. The PCR product was then purified using the QIAquick PCR Purification Kit (Qiagen, Inc., Valencia, CA, USA) according to manufacturer provided instructions.

Sequencing

Toll-like receptor 5 sequence data for river buffalo, swamp buffalo, African forest buffalo, and bison were previously determined (Chapter III). Cattle (*Bos taurus*), banteng (*Bos javanicus*), Masai giraffe (*Giraffa camelopardalis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), scimitar-horned oryx (*Oryx dammah*), Gemsbok oryx (*Oryx gazella*), Arabian oryx (*Oryx leucoryx*), chamois (*Rupicapra rupicapra*), lesser kudu (*Tragelaphus imberbis*), and greater kudu (*Tragelaphus strepsiceros*) TLR5 sequences were obtained using the previously described *Bos taurus* primers (Seabury *et al.*, 2007) (Table 3.2). Sequencing reactions were performed by the DNA Core Laboratory at Texas A&M University.

Toll-like receptor 5 DNA sequence data were assembled individually for each isolate as described in Chapter III. Thirty-eight additional TLR5 sequences were retrieved from GenBank (Table 4.1).

Table 4.1

Evolutionary study species. Identification (ID) numbers, species, and GenBank accession numbers for TLR5 are included.

Sample IDs	Species	Common Name	Accession Number
BBU1*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615215
BBU2*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615216
BBU3*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615217
BBU4*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615218
BBU5*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615219
BBU6*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615220
BBU7*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615221
BBU8*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615222
BBU9*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615223
BBU10*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615224
BBU11*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615225
BBU12*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615226
BBU13*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615227
BBU14*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615228
BBU15*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615229
BBU16*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615230
BBU17*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615231
BBU18*	<i>Bubalus bubalis bubalis</i>	River Buffalo	JN615232
BCA*	<i>Bubalus bubalis carabanesis</i>	Swamp Buffalo	JN615235
SCA1*	<i>Syncerus caffer</i>	African Forest Buffalo	JN615234
SCA2*	<i>Syncerus caffer</i>	African Forest Buffalo	JN615233
BBI*	<i>Bison bison</i>	American Bison	JN615236
BTA1†	<i>Bos taurus</i>	Cattle	JQ805125
BTA2†	<i>Bos taurus</i>	Cattle	JQ805126
BTA3†	<i>Bos taurus</i>	Cattle	JQ805127
BTA4†	<i>Bos taurus</i>	Cattle	JQ805128
BTA5†	<i>Bos taurus</i>	Cattle	JQ805129
BTA6†	<i>Bos taurus</i>	Cattle	JQ805130
BTA7†	<i>Bos taurus</i>	Cattle	JQ805131
BTA8†	<i>Bos taurus</i>	Cattle	JQ805135
BTA9†	<i>Bos taurus</i>	Cattle	JQ805132
BTA10†	<i>Bos taurus</i>	Cattle	JQ805133
BTA11†	<i>Bos taurus</i>	Cattle	JQ805134
BTA12†	<i>Bos taurus</i>	Cattle	JQ805136
BTA13†	<i>Bos taurus</i>	Cattle	JQ805137
BTA14	<i>Bos indicus</i>	Cattle	GQ248711
BTA15	<i>Bos taurus</i>	Cattle	EU006639
BTA16	<i>Bos taurus</i>	Cattle	EU006640
BTA17	<i>Bos indicus</i>	Cattle	EU006636
BTA18	<i>Bos indicus</i>	Cattle	EU006641
BGR	<i>Bos grunniens</i>	Yak	GU647093
AME	<i>Ailuropoda Melanoleuca</i>	Giant Panda	XM_002922391
CHI	<i>Capra hircus</i>	Goat	HQ188378
CJA	<i>Callithrix jacchus</i>	Common Marmoset	ACFV01163303.1
CLU	<i>Canis lupus familiaris</i>	Dog	NM_001197176
CTO	<i>Cercocebus torquatus atys</i>	Sooty Mangabey	EU204938
DRE	<i>Danio rerio</i>	Zebrafish	NM_001130595

Table 4.1 continued

Sample IDs	Species	Common Name	Accession Number
ETE	<i>Echinops telfairi</i>	Lesser Hedgehog Tenrec	AAIY01425931.1
GCA [†]	<i>Giraffa camelopardalis</i>	Masai Giraffe	JQ811844
GGA	<i>Gallus gallus</i>	Chicken	HQ896214
GGO	<i>Gorilla gorilla</i>	Gorilla	AB445648
GLA	<i>Gallus lafayetii</i>	Sri Lankan junglefowl	FJ915547
HSA	<i>Homo sapiens</i>	Human	NM_003268
MDO	<i>Monodelphis domestica</i>	Gray Short-tailed Opossum	XM_001376152
MFA	<i>Macaca fascicularis</i>	Crab-eating Macaque	AB445650
MGA	<i>Meleagris gallopavo</i>	Turkey	HQ436463
MMU	<i>Mus musculus</i>	House mouse	NM_016928
MMUL	<i>Macaca mulatta</i>	Rhesus Monkey	NM_001130429.1
MPU	<i>Mustela putorius</i>	Ferret	AEYP01103745.1
NME	<i>Numida meleagris</i>	Helmeted Guineafowl	JF767221
OAN	<i>Ornithorhynchus anatinus</i>	Platypus	XM_001512183
OAR	<i>Ovis aries</i>	Sheep	NM_001135926
ODA [†]	<i>Oryx dammah</i>	Scimitar-horned Oryx	JQ811850
OGA [†]	<i>Oryx gazella</i>	Gemsbok Oryx	JQ811846
OHE [†]	<i>Odocoileus hemionus</i>	White-tailed Deer	JQ811842
OLE [†]	<i>Oryx leucoryx</i>	Arabian Oryx	JQ811847
OMY	<i>Oncorhynchus mykiss</i>	Rainbow Trout	AB062504
OPR	<i>Ochotona princeps</i>	American Pika	AAYZ01013936.1
OVI [†]	<i>Odocoileus virginianus</i>	Mule Deer	JQ811843
PAL	<i>Pteropus alecto</i>	Black Flying Fox	GU045604
PCO	<i>Phasianus colchicus</i>	Ring-necked Pheasant	JF767220
PPA	<i>Pan paniscus</i>	Pygmy Chimpanzee	AB445647
PPY	<i>Pongo pygmaeus</i>	Bornean Orangutan	AB445649
PTR	<i>Pan troglodytes</i>	Chimpanzee	NM_001130462
RRU [†]	<i>Rupicapra rupicapra</i>	Chamois	JQ811845
SSC	<i>Sus scrofa</i>	Pig	AB208697.2
SHA	<i>Sarcophilus harrisii</i>	Tasmanian Devil	AFEY01269194.1
TGU	<i>Taeniopygia guttata</i>	Zebra Finch	XM_002188726
TIM [†]	<i>Tragelaphus imberbis</i>	Lesser Kudu	JQ811849
TST [†]	<i>Tragelaphus strepsiceros</i>	Greater Kudu	JQ811848
TSY	<i>Tarsius syrichta</i>	Philippine Tarsier	ABRT010212218.1
XLA	<i>Xenopus laevis</i>	African Clawed Frog	NM_001094980

^{*}TLR5 sequence data obtained in Chapter III.

[†]TLR5 sequence data obtained in this study.

Phylogenetic Analysis

Sequences used in the phylogenetic analyses were edited with BioEdit (ver. 7.0.5.3) (Hall, 1999; Hall, 2005) and aligned with ClustalX (ver. 2.0.12) (Larkin *et al.*, 2007). The protein-coding genes were aligned based on translated amino acid sequences. The nucleotide substitution model, GTR+ Γ +I, was selected by MrModeltest (ver. 2.3) (Nylander, 2004) based on the corrected Akaike Information Criterion (AICc). The phylogenetic tree that shows multiple orders was inferred by MrBayes (ver. 3.1.2) (Ronquist & Huelsenbeck, 2003) utilizing Bayesian phylogenetic analysis under Metropolis-coupled Markov Chain Monte Carlo (MCMC) algorithm (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Every 1,000th tree was sampled after two analyses were performed for 12 million generations. Each analysis consisted of four incrementally heated chains. After the posterior distribution of tree was summarized by removing 2,001 sample trees as burn-in, 10,000 sample trees remained.

Nodal support was estimated under a Neighbor-Joining method by PAUP* 4.0b10 (Swofford, 1993). The previously outlined procedure (Huelsenbeck & Crandall, 1997) was followed for substitution model selection. All model parameters were estimated by the likelihood procedure as implemented in PAUP* through an iterative process. The likelihood scores were compared by using likelihood ratio test as implemented in Modeltest 3.7 (Huelsenbeck & Crandall, 1997). The model of GTR+ Γ +I was selected as the best-fit model for the data sets. The frequencies of each nucleotide base were 0.2669 for A, 0.2626 for C, 0.2167 for G, and 0.2538 for T. When assumed GT substitution rate [R(GT)] was 1, then the relative substitution rate of R(AC) was

1.3605, R(AG) was 4.8247, R(AT) was 0.6122, R(CG) was 1.2353, and R(CT) was 3.8617. The proportion of invariable sites was 0.1324, and the gamma shape was 1.7364. Support values were based on the full heuristic search on 10,000 bootstrap replications. Starting trees were obtained by stepwise addition with one tree held at each step.

For the phylogenetic tree that emphasized the artiodactyl order, nodal support was estimated under a Maximum Parsimony method by PAUP* 4.0b10 (Swofford, 1993). The likelihood scores were compared by using likelihood ratio test as implemented in Model test 3.7 (Posada & Buckley, 2004). The model of GTR+ Γ +I was selected as the best-fit model for the data sets. The frequencies of each nucleotide base were 0.2606 for A, 0.2518 for C, 0.2067 for G. When assumed GT substitution rate [R(GT)] was 1, then the relative substitution rate of R(AC) was 1.4604, R(AG) was 7.0795, R(AT) was 0.7200, R(CG) was 1.5526, and R(CT) was 4.8039. The proportion of invariable sites was 0.8246, and the gamma shape was 0.3437. Support values were based on the full heuristic search on 1,000 bootstrap replications. Starting trees were obtained by stepwise addition with one tree held at each step. Phylogenetic trees were visualized and formatted with TreeGraph 2 software package (Stover & Muller, 2010).

Selective Constraint of Evolution

The program MKPRF (Swofford, 1993) was used to estimate the selection coefficient γ ($=2N_e s$) of TLR5 coding region gene that diverged in different clades. The program samples from the posterior distribution of parameters in the MKPRF models using a Markov Chain Monte Carlo algorithm (Bustamante et al., 2002; Barrier et al., 2003; for Poisson random field theory, see Sawyer & Hartl, 1992).

Results and Discussion

The McDonald-Kreitman Poisson Random Field (MKPRF) test was utilized to examine the divergence over time between multiple orders. River buffalo (*B. b. bubalis*) was the reference species in this study. The MKPRF test is normally performed in one species to examine the fixed changes between closely related species. This study essentially compared divergent sites between species. Therefore, it is a more appropriate analysis is to say that the overall divergent sites between closely and distantly related species appears to conform to the appearance of positive, neutral, or negative selection in relation to river buffalo. That is, species that appear to be undergoing positive selection are retaining certain alleles while negatively selected species appear to be removing certain alleles. In this study, humans were determined to be undergoing positive selection in relation to river buffalo, but a more accurate statement would be that humans are retaining certain alleles that may or may not be beneficial or sweeping the population.

The direction of selection in comparison with the divergence time from river buffalo is shown in Figure 4.1. Unlike other methodologies, notably PAML, utilizing the MKPRF in this way allowed for the determination of the direction of the selection of the entire coding region of TLR5. Previous studies used the software PAML to examine site specific selection. In other words, each site was compared independently of other sites. Therefore, it is possible for sites in the LRR region to be positively selected and the entire coding region to be undergoing negative selection.

Phylogenetic trees were inferred for the coding sequence of TLR5 to show the evolutionary relationships between representative species across multiple orders (Figure 4.2). Primates (including humans) and avians have previously been determined to be undergoing strong positive selection. Another tree that focused exclusively on the artiodactyls order was also constructed to show the evolutionary relationship between members of the order that are more closely related (Figure 4.3).

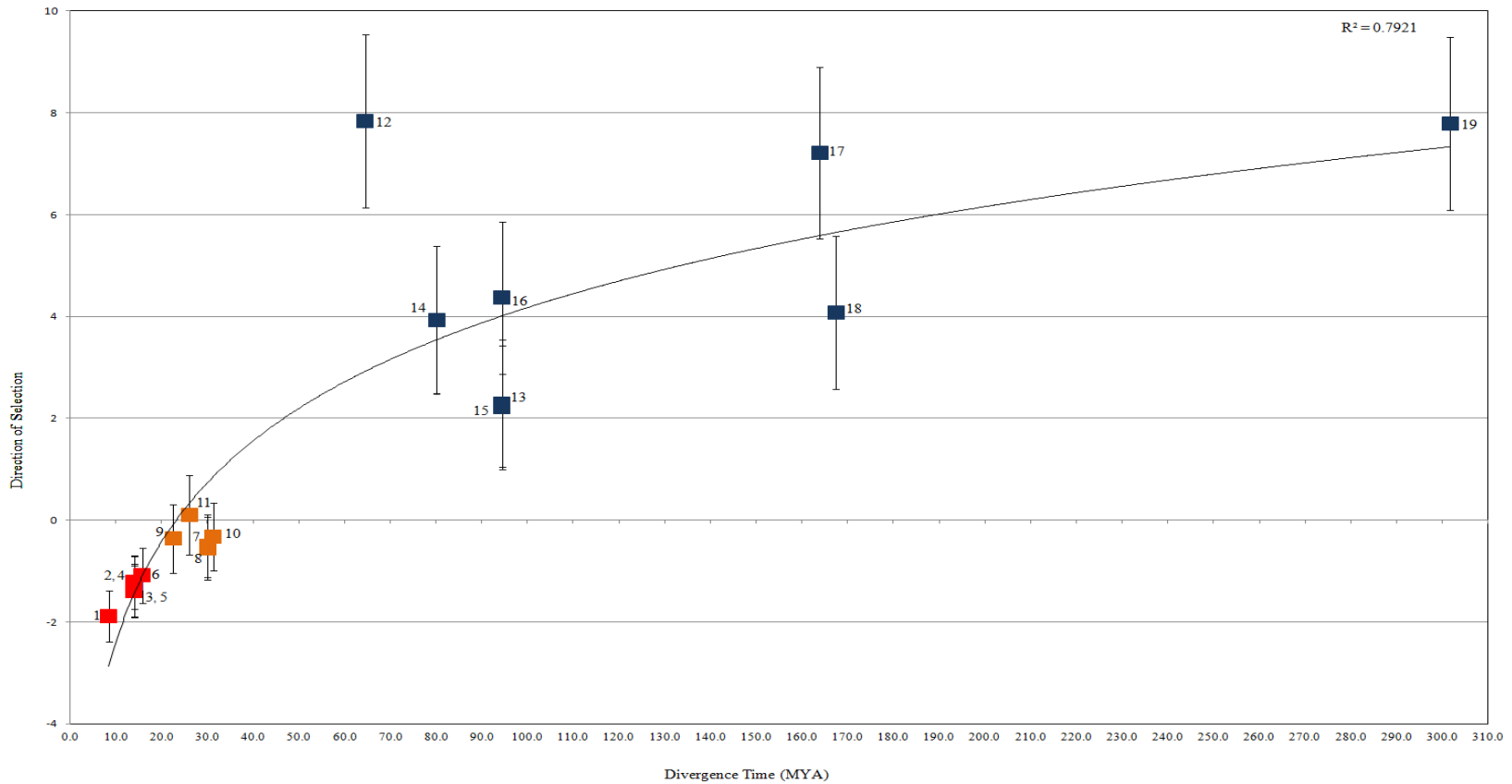


Figure 4.1 The McDonald-Kreitman Poisson Random Field (MKPRF) test. MKPRF was plotted with the divergence time for the TLR5 coding sequence. Error bars represent the standard deviation unique to each species. For clarity, species included have been assigned the following numbers on the figure with the Latin name, selection value, and divergence time in parenthesis: 1-African forest buffalo (*Syncerus caffer*, -1.89, 8.5 MYA), 2-American bison (*Bison bison*, -1.40, 14 MYA), 3-domestic yak (*Bos grunniens*, -1.23, 14 MYA), 4-cattle (*Bos taurus*, -1.38, 14 MYA), 5-banteng (*Bos javanicus*, -1.22, 14 MYA), 6-greater kudu (*Tragelaphus strepsiceros*, -1.09, 15.8 MYA), 7-sheep (*Ovis aries*, -0.51, 30.1 MYA), 8- chamois (*Rupicapra rupicapra*, -0.55, 30.1 MYA), 9-Arabian oryx (*Oryx leucoryx*, -0.37, 22.6 MYA), 10-Masai giraffe (*Giraffa camelopardalis*, -0.33, 31.3 MYA), 11-white-tailed deer (*Odocoileus virginianus*, 0.10, 26.1 MYA), 12-domestic pig (*Sus scrofa*, 7.83, 64.5 MYA), 13-human (*Homo sapiens*, 2.29, 94.4 MYA), 14-dog (*Canis lupus familiaris*, 3.93, 80.2 MYA), 15-mouse (*Mus Musculus*, 2.21, 94.4 MYA), 16-common marmoset (*Callithrix jacchus*, 4.37, 94.4 MYA), 17-Tasmanian devil (*Sarcophilus harrisii*, 7.21, 163.9 MYA), 18-platypus (*Ornithorhynchus anatinus*, 4.08, 167.4 MYA), 19-chicken (*Gallus gallus*, 7.79, 301.7 MYA). The trendline exhibits Poisson distribution. $R^2=0.7921$.

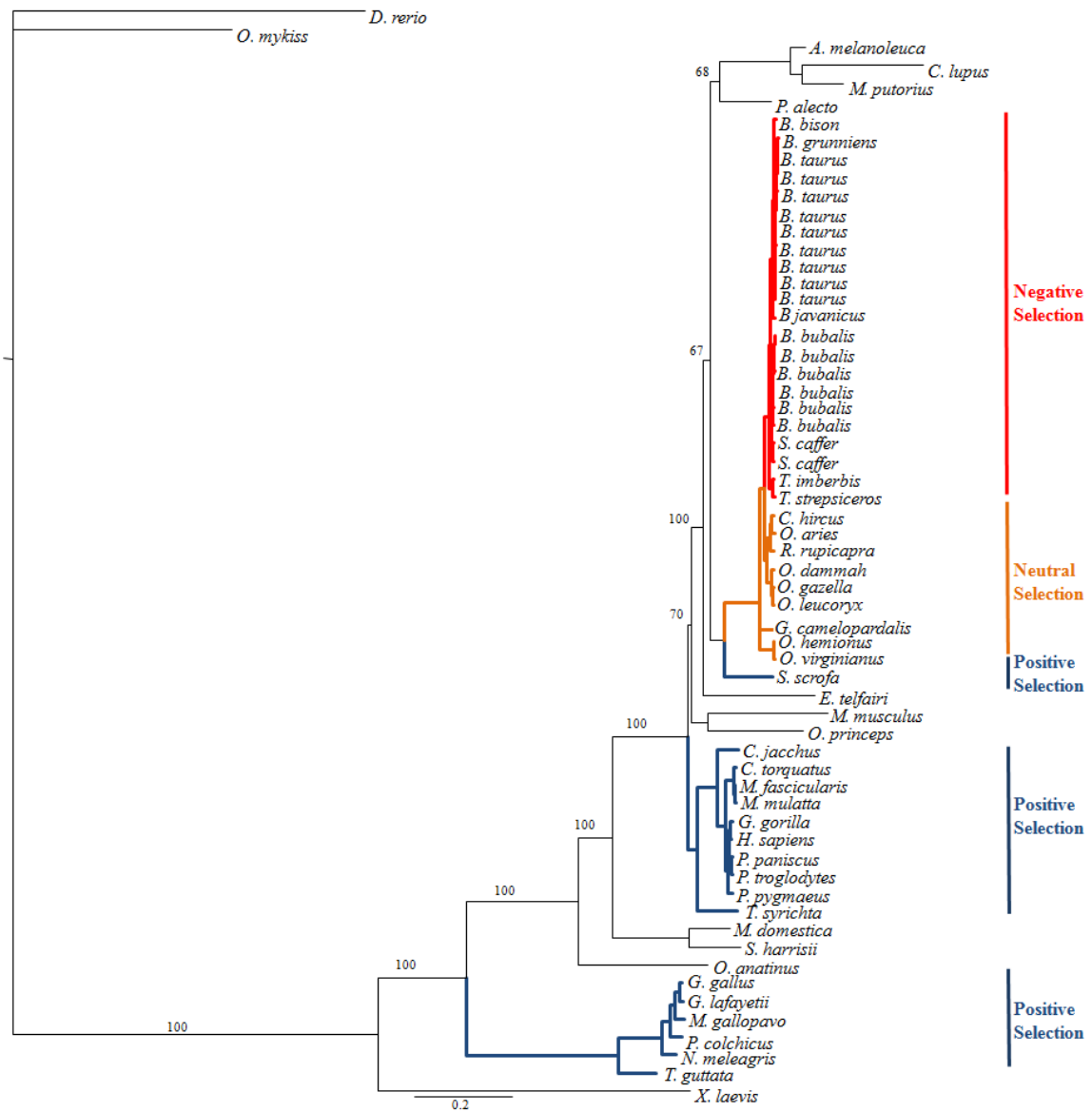


Figure 4.2 Phylogenetic tree inferred across multiple orders. The tree is based on TLR5. Bootstrap values for the coding region of TLR5 with a scale bar to indicate branch distance (in units of nucleotide substitution per site) and an outgroup are included. The tree was inferred using Mr Bayes and nodal support was estimated under a Neighbor-Joining method by PAUP*. The bootstrap value was determined on 10,000 replications. Negative, neutral, and positive selection are noted at the side.

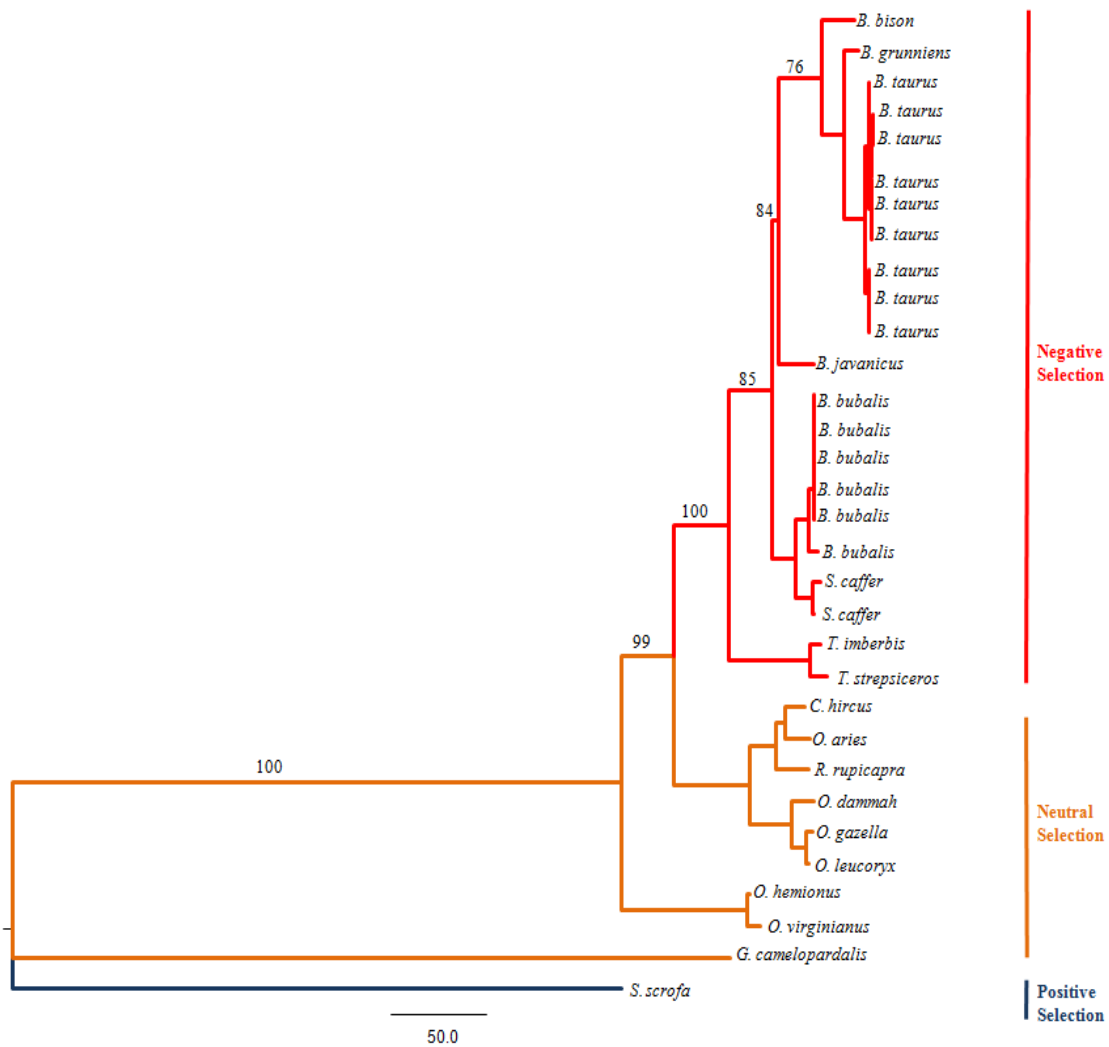


Figure 4.3 Phylogenetic tree inferred for artiodactyls. The tree is based on the TLR5 coding region. Bootstrap values for the coding region of TLR5 with a scale bar to indicate distance branch distance (in units of nucleotide substitution per site) and an outgroup are included. The tree is inferred under Maximum Parsimony by PAUP*. Every 1,000th tree was sampled for the bootstrap value. Negative, neutral, and positive selection are noted at the side.

Figure 4.4 is a modified phylogenetic tree (Figure 4.2) that shortens the branch length to the fish species (zebra fish and rainbow trout) and shows six characters that were previously determined to be river buffalo TLR5 haplotypes (Chapter III). Specifically, Figure 4.4 is Figure 4.2 but with the specific characters examined listed alongside the species. Ancestral characters that were found to be SNPs in the river buffalo are not necessarily SNPs in other species; however, by comparing these sites in other species, allele origin can be possibly assessed to examine where the allele might have originated. Characters that are the same color represent identical characters (Figure 4.4). Characters in black are not observed in other species. These seem to be orphan characters that may or may not have originated in that species. Most of the shared characters will be derived through a common ancestor and not through interspecies breeding. *Bos taurus* is fully capable of producing hybrids with other *Bos* species and the American bison. This represents the species that would most likely perpetuate these characters at these specific sites through species interbreeding.

American bison, domestic yak, cattle, banteng, goat, sheep, chamois, scimitar-horned oryx, Gemsbok oryx, Arabian oryx, Masai giraffe, mule deer, and white-tailed deer share the same 6 characters, CTCAAC, however, these characters appear to have originated with cervid species (Figure 4.4). One river buffalo was found to share the same characters of one of their haplotypes with the aforementioned group as did one of the African forest buffaloes. No viable hybrids have been found between river buffalo and cattle, although it is possible to create them in vitro (Kochhar *et al.*, 2002), or between river buffalo and African forest buffalo. This would be unlikely to occur since

these species do not share any bi-armed chromosomes.

The characters CAAAAC are represented in the majority of river buffalo, an African forest buffalo, lesser kudu, and the greater kudu. The characters GTCCGG are not represented outside of river buffalo in this study. One river buffalo was previously determined to be heterozygous at these sites (Chapter III). The aforementioned river buffalo sequence was phase resolved and revealed that the river buffalo had the potential to transmit CAAAAC or CTCAAC. CTCAAC are characters that are represented in *Bos* and *Bison*. This suggests that these characters are present in the study river buffalo population.

The characters CTT--- seem to have originated with monotremes and are well represented in primates. The characters ---AAC seem to have originated in avians. All of the primates, the lesser hedgehog Tenrec, and the black flying fox have CTTAAC, which is a combination of the two oldest characters. The most common characters that have survived are ---AAC, which are well represented in primates, avians, and artiodactyls as well as the black flying fox (*Pteropus alecto*), the domestic ferret (*Mustela putorius*), and the dog (*Canis lupus*) in this study.

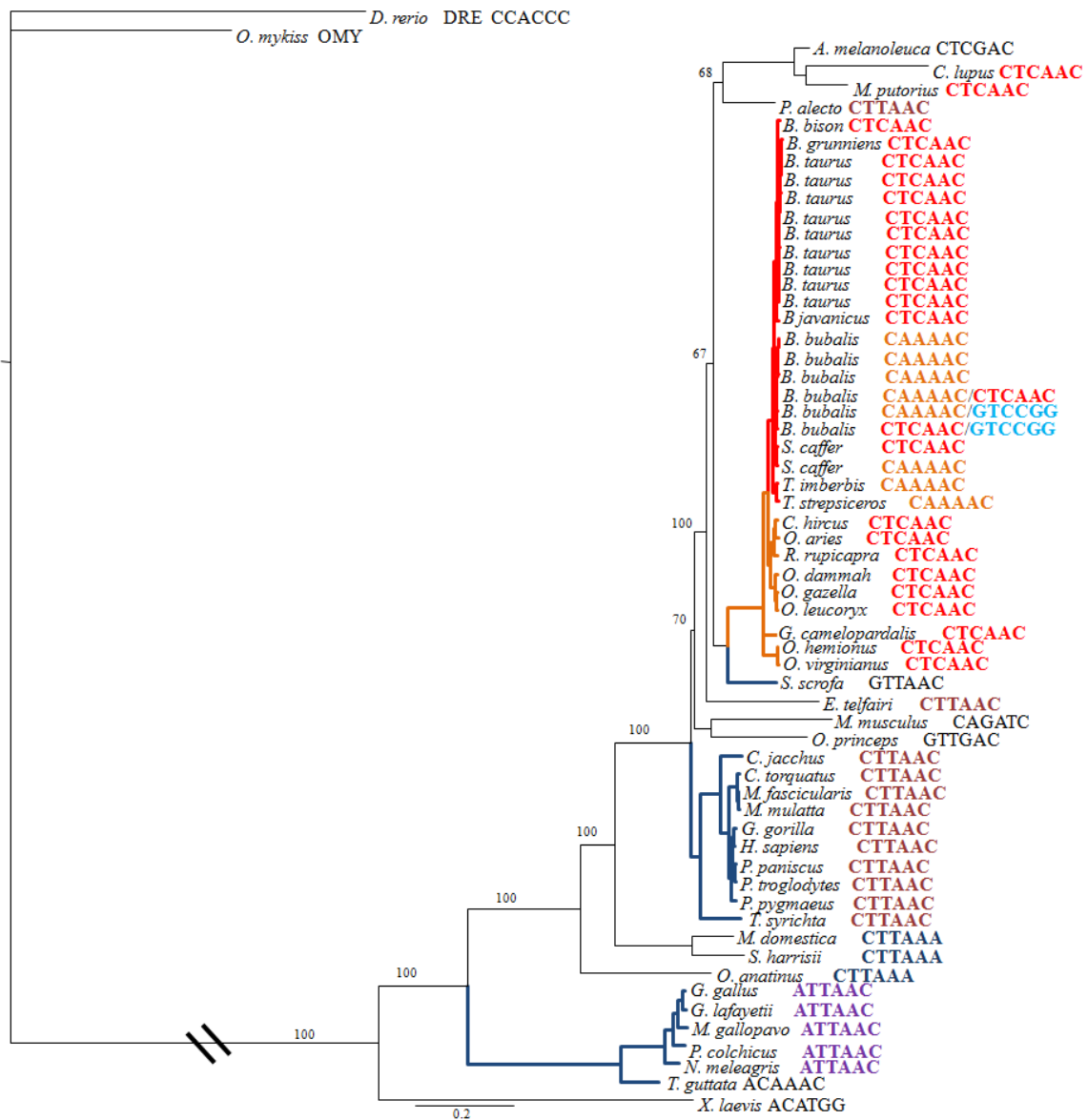


Figure 4.4 Modified Figure 4.2 to show TLR5 site characters. Bootstrap value for the coding region of TLR5 with a scale bar to indicate distance and an outgroup are included. The tree was inferred using Mr. Bayes and nodal support was estimated under a Neighbor-Joining method by PAUP. Every 10,000th tree was sampled for the bootstrap value. Haplotypes that are the same are represented by the same font color. Black, non-bolded haplotypes do not have another haplotype in common with other species. The double hash mark represents the break point in the phylogenetic tree.

African forest buffalo (*Syncerus caffer*), American bison (*Bison bison*), domestic yak (*Bos grunniens*), cattle (*Bos taurus*), banteng (*Bos javanicus*), and greater kudu (*Tragelaphus strepsiceros*) appear to exhibit weak negative selection relative to river buffalo. Sheep (*Ovis aries*), chamois (*Rupicapra rupicapra*), Arabian oryx (*Oryx leucoryx*), Masai giraffe (*Giraffa camelopardalis*), and white-tailed deer (*Odocoileus virginianus*) fit the neutral model of selection. Pig (*Sus scrofa*), human (*Homo sapiens*), dog (*Canis lupus familiaris*), mouse (*Mus musculus*), the common marmoset (*Callithrix jacchus*), Tasmanian devil (*Sarcophilus harrisii*), platypus (*Ornithorhynchus anatinus*), and chicken (*Gallus gallus*) appear to be undergoing strong positive selection.

It is useful to examine the natural history of the species studied when considering these results. The American bison suffered a severe population contraction during the early history of the United States due to the combination of hunting and foreign diseases that came with the expansion of cattle (Halbert *et al.*, 2012). This contraction caused a bottleneck and reduced genetic variability. In addition, certain populations of American bison in the United States exhibit cattle introgression (Halbert & Derr, 2007). The bison sample utilized in this study originated from Yellowstone National Park, which has not exhibited cattle introgression (Halbert & Derr, 2007; Halbert *et al.*, 2012).

This contraction of the population would have removed alleles, many of which might have been beneficial to overall robustness of the herd, and could produce results that reflect negative selection when alleles become fixed, prove to be deleterious, and are subsequently not passed on to offspring. Introgression of cattle genes into bison herds would increase variability, but it may introduce traits that have been specifically selected for by producers, which would limit the nature of the variability and could also produce results that would be similar to the strength and direction of cattle selection.

Cattle, domestic yak, and banteng are heavily influenced by human breeding programs that have selected for specific economically important traits. This specific selection of other traits may effectively reduce the population size and the pool of available alleles. In general, when breeding programs are used to select for a trait, other traits may be selected against. This kind of selective pressure exerted onto domesticated livestock by humans may have the same effect as the population contraction of the American bison. Selection for specific traits necessarily implies the reduction in population variability. For example, the effective population size of dairy cattle is low since the same sires are used extensively to maintain high milk production, thus the genetic variability of this breed is reduced (Flori *et al.*, 2009).

The exceptions to the possible link between domestication and the direction and strength of selection presented here is that both African forest buffalo and the greater kudu are not livestock species that have been heavily bred to achieve specific outcomes but they also exhibit weak negative selection. Sheep are domesticated but exhibit neutral selection within the margin of error. Pig, dog, and chicken have also been heavily influenced by human intervention but they exhibit strong positive selection. This possible positive selection could represent the populations recovering variability as the aforementioned species diverged from river buffalo long ago and humans have influenced these species over a longer period of time.

The divergence time is relatively close to the selection value for all species used as an outgroup for MKPRF analysis, except for the domestic pig (Figure 4.1). A phylogenetic tree was constructed for multiple orders (Figure 4.2) and another for artiodactyls (Figure 4.3). Study designations can be found in Table 4.1. Comparing the MKPRF test results with the phylogenetic tree that spans multiple orders and the phylogenetic tree that emphasizes artiodactyls reveals that negative, neutral, and positive selection are consistent within clades. Pig, which had the largest gap between its selection value (Figure 4.1) and divergence time, was used as the outgroup (Figure 4.3).

The species that diverged later from river buffalo, less than 20 million years ago (MYA), and are more closely related to river buffalo, were found to undergo weak negative selection. Species with a slightly later divergence time, 20-31 MYA, were found to undergo neutral selection. Species that diverged from river buffalo more than 64 MYA show strong positive selection.

Pig appears to be an outlier in that it diverged later, but exhibits a much stronger positive selection in relation to its divergence time from river buffalo.

Studies have shown that both avians and primates (including humans) exhibit positive selection in the LRR domain (Wlasiuk *et al.*, 2009; Ruan *et al.*, 2012). Data presented here for representative species of both avians and primates also show positive selection when utilized as outgroups for the MKPRF test in relation to river buffalo.

It is reasonable to infer a continuum for other orders in relation to their divergence time from river buffalo, which is to say that the relationship between the strength and direction of selection and divergence time will maintain a Poisson distribution, i.e. there is a relatively rapid substitution rate at the beginning and the time required, or rate, to reinstate the original nucleotide becomes slower with a wider distribution.

CHAPTER V

CONCLUSION

Results presented here were derived from three studies, comparative mapping, SNP analysis, and an evolutionary study, all focused on the TLR5 gene in river buffalo.

River buffalo chromosome 5 is the smallest of the bi-armed chromosomes. Cytogenetic studies have determined that BBU5 is a fusion of BTA 16 and BTA 29 (El Nahas *et al.*, 2001; Iannuzzi *et al.*, 2003). The radiation hybrid map was generated using methods described in Chapter II. Forty-six markers were used to generate the RH map, which is estimated to be 932.1 cR in total length. Retention frequencies (RF) of individual markers ranged from 17.8% (IDVGA26) to 54.4% (BZ919809). Even though IDVGA26 has a relatively low RF, it was incorporated into the single linkage group for the BBU5 chromosome map. The average RF for the markers used in this study was 36.6%, which compares favorably to the RF across the whole-genome radiation hybrid map (Amaral *et al.*, 2008).

Comparative mapping revealed two possible rearrangements relative to the cattle genome. These two regions have been previously shown to contain cattle QTLs which are related to milk protein and muscle fat (Casas *et al.*, 2000; MacNeil & Grosz, 2002; Casas *et al.*, 2003; Kim *et al.*, 2003; Viitala *et al.*, 2003; Casas *et al.*, 2004). River buffalo differ from cattle in both milk protein content and in reduced muscle fat, making further comparative study of this chromosome a potentially worthwhile endeavor. While it can be argued that the presence of QTLs in one species does not predict QTLs in

another species, comparative analysis serves to narrow the focus. Regardless of whether buffalo QTLs exist in this region or whether the inversions observed between river buffalo and cattle on the RH map proves to be real, this region should be a prime target of investigation for important QTLs in buffalo. Next-generation sequencing (non-Sanger methods) will provide sequence of large regions of targeted chromosomes. It seems that the next steps might be the study of a BAC library or high resolution *in situ* hybridization to resolve the issue of the inversion observed on the RH map between river buffalo and cattle and inclusion of markers from this region in association studies for QTLs.

Variation in the TLR5 coding region was examined in a population of 18 river buffalo. Those results were then compared to other closely related species. The analysis revealed 16 total SNPs within the TLR5 coding region. Ten SNPs were determined to be sSNPs and 6 were nsSNPs. Fisher's Two-tailed Exact test determined that there was a mutational bias between transitions and transversions within nsSNPs and sSNPs. In addition, 4 total haplotypes were determined for this population. The most prevalent haplotype discovered was CAAAAC, which was present on about 80% of the genotyped haplotypes present in the population. The second most common haplotype was GTCCGG, which was present at a frequency of about 13%.

Utilizing the SMART software, the predicted TLR5 protein domain structure in river buffalo was compared to other species, both closely related and not. River buffalo, swamp buffalo, and African forest buffalo exhibited common LRR patterning. American bison and cattle exhibited LRR patterning common to each other but different from the

buffalo group. The LLR domain is directly responsible for recognizing bacteria. This comparison of the protein domain architecture is useful in determining whether functional differences in TLR5 between species could be due in part to sequence variation within the TLR5 coding region. It can be reasonably inferred that differences in the predicted protein domain structure implies the possibility of differential immunity between species.

An analysis of the possible impact of the SNPs discovered in river buffalo was also performed. Polyphen-2 Analysis predicted that only one SNP, which was located near the TIR domain, might have an impact on the function of the protein. This observation is important because the TIR domain is responsible for signaling through MyD88 to begin the cytokine storm so this polymorphism could impact how well TLR5 functions. Case studies would help to properly understand and place these discovered haplotypes into context of the variation found within the coding region of TLR5. Linking the SNP to a haplotype could help determine if that SNP is beneficial or harmful in river buffalo. It is possible that the predicted amino acid substitution near the TIR domain could result in either more efficient or less efficient signaling through MyD88.

It is apparent that the scope of SNP characterization in river buffalo should be widened. Data here were generated with a few individuals in a population that was a new transplant and did not have time to adapt to the new environment. Populations in different environs that mirror its natural habitat would be a better measure of evolutionary adaptation and variation in TLR5. That is, these animals have not had the long evolutionary history of their current environment, but their microbiota has changed

to reflect their new environment. Despite this, it doesn't represent the evolutionary history of the current environment's pathogens in relation to TLR5, but gut pathology has changed to allow these animals to survive. So they no longer reflect the microbiota of their native environment, nor does TLR5 adaptation reflect the current environment.

In addition, human studies have characterized the microbiota within the gut (Gupta *et al.*, 2011) and the same can be done with river buffalo. Their four compartments provide four different environments in the same animal for commensal bacteria to develop with the purpose of extracting nutrients from food sources. An association of the expression level of TLR5 within these tissues with SNPs and environment could provide a good profile and genetic tool for breeding and management purposes. Being able to link the haplotype or SNP profile with the microbiota profile of the gut in river buffalo (and other species) has the potential to allow managers to select for specific haplotypes within the animal population to increase herd health.

SNP characterization and evolution across all TLRs have been reported (Fisher *et al.*, 2011). A key finding from the study is the flexibility that surface TLRs, such as TLR5, have in terms of variation in their sequence. Surface TLRs recognize bacterial PAMPs. Most bacteria will express more than one PAMP. Therefore, if one TLR has weak engagement or the bacterial agent in question has adapted evasion tactics to evade that particular TLR, another can also engage and recognize the bacterial pathogen. In addition to that, how a TLR engages a bacterial agent can be tissue dependent. A good example of this phenomenon is pneumonic *Burkholderia thailandensis*. *B. thailandensis* is avirulent in humans and a close relative of *Burkholderia pseudomallei*, which causes

meliodosis (West *et al.*, 2009). TLRs 4, 2, and 5, and MyD88 (an adaptor molecule) are involved in disease clearance. The key finding of the study is that TLR4 and MyD88 are required for tumor necrosis factor α induction. However, TLR4 was found to not be needed for bacterial containment in late infection, while MyD88 controls infection and host survival (West *et al.*, 2009). TLR5 and 2 are not needed for low-dose infection, but TLR2 does offer a slight survival advantage. Since TLR5 recognizes bacterial flagellin, it does engage *B. thailandensis*, but it is time dependent. TLR5 is more stimulated when the pathogen is in log-phase (West *et al.*, 2009). This system suggests that redundancy is necessary. TLR5 and 2 may not be required at key points but they function in containment and clearance nonetheless.

The last part of this study focused on TLR5 and river buffalo in the context of evolution. Toll-like receptors are generally believed to be evolutionarily conserved and would not change robustly over time. Toll-like receptors recognize PAMPs, which are not subject to change since any changes might negatively impact the ability of pathogens to successfully infect and colonize the preferred host organism (Andersen-Nissen *et al.*, 2005). However, there are flagellated bacteria that have successfully found ways to evade detection by TLR5, which implies a degree of co-evolution (Andersen-Nissen *et al.*, 2005). Studies in primates have shown the presence of positive selection in the LRR domain and that certain populations of humans possess a premature stop codon and suggest that there might be redundant functionality elsewhere that allows for the detection of flagellated bacteria (Hawn *et al.*, 2005; Wlasiuk *et al.*, 2009; Ruan *et al.*, 2012).

In this study, two phylogenetic trees were constructed of the TLR5 coding region, one across multiple orders and the other including only artiodactyls. The strength and direction of selection was plotted in conjunction with the divergence of each species from river buffalo. Generally the MKPRF test is employed to detect fixed differences within species, however, in this study it was deployed to detect fixed differences with multiple outgroups in relation to river buffalo. Results of positive selection within avians and primates was also seen when the MKPRF was deployed in this way. The species that diverged from river buffalo less than 20 MYA showed weak negative selection, the 20-31 MYA divergence range showed neutral selection, and those species that diverged from river buffalo over 65 MYA showed strong positive selection. Analysis appears to support the idea that TLR5 might not be so evolutionarily constrained and can tolerate a fair amount of sequence variation.

The research presented here is only a beginning. It represents a foundation that can be built upon to potentially enhance animal health in both river buffalo and cattle, to add more understanding of how variation in the TLR5 gene coding region might change its functionality and to enhance the economic and social profile of river buffalo.

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APPENDIX B

SPECIES ALIGNMENT

The aligned sequences as generated by Clustal W (Larkin *et al.*, 2007). Refer to Chapter IV, Table 4.1 for study species IDs and designations.

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PPA          ATGGGAGACCACC---TGGACCTTCTCCTAGGAGTGGTGCTCATGGCCGGTCCCTGTGTTT 57
PTR          ATGGGAGACCACC---TGGACCTTCTCCTAGGAGTGGTGCTCATGGCCGGTCCCTGTGTTT 57
HSA          ATGGGAGACCACC---TGGACCTTCTCCTAGGAGTGGTGCTCATGGCCGGTCCCTGTGTTT 57
GGO          ATGGGAGACCACC---TGGACCTTCTCCTAGGAGTGGTACTCATGGCCGGTCCCTGTGTTT 57
PPY          ATGGGAGACCACC---TAGACCTTCTCCTAGGAGTGGTGCTCATGGCCAGTCCCTGTGTTT 57
MFA          ATGGGAGACCACC---TGGACCTTCTCCTAGGAGTGGTGCTTGTGGCCAGTCCCTGTGTTT 57
MMUL         ATGGGAGACCACC---TGGACCTTCTCCTAGGAGTGGTACTTGTGGCCAGTCCCTGTGTTT 57
CTO          ATGGGAGACCACC---TGGACCTTCTCCTAGGAGTGGTGCTTGTGGCCAGTCCCTGTGTTT 57
CJA          ATGGGAGACCACC---TGGACCTTCTCCTAAGAGTGGTGCTTGTGGCCAGTCCCTGTGTTT 57
TSY          ATGGGAGGCCGCC---TTGACCTTCTCCTAGGAGTGGTGCTCATGGTCAGTCCCTGTGTTT 57
CHI          ATGGGAGACTGCC---TTGACCTTCTCCTAGGAGTCGTACTCCTGACCAGTCCCTGCACTT 57
OAR          ATGGGAGACTGCC---TTGACCTTCTCCTAGGAGTCGTACTCCTGACCAGTCCCTGCACTT 57
RRU          ATGGGAGATTGCC---TTGACCTTCTCCTAGGAGTCRTACTCCTGACCAATCCTGCACTT 57
OGA          ATGGGAGACTGCC---TTGACCTTCTCCTTGGAGTCGTACTCCTGACCAGTCCCTGCACTT 57
OLE          ATGGGAGACTGCC---TTGACCTTCTCCTTGGAGTCGTACTCCTGACCAGTCCCTGCACTT 57
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 BTA14 CAAGTGCCCCAGGTCCCCAACAC---CACCAAGAGCCTCCTGCTCAGCTTCAACTATATC 174
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 BBI CAAGTGCCCCAGGTCCCCAACAC---CACCAAGAGCCTCCTGCTCAGCTTCAACTATATC 174
 BJA CAAGTGCCCCAGGTCCCCAACAC---CACCAAGAGCCTCCTGCTCAGCTTCAACTATATC 174
 TIM CAAGTGCCCCAGGTCCCCAGCAC---CACCAAGAGCCTCCTGCTCAGCTTCAACTATATC 174
 TST CAAGTGCCYCAAGTCCCCAGCAC---CACCAAGAGCCTYCTGCTCAGCTTCAACTATATC 174
 GCA CAAGTGCCCCAGGTCCCCAACAC---CACCAAGAGCCTCCTGCTCAGCTTCAACTATATC 174
 OHE CAAGTGCCCCAGGTCCCCAACAC---CACCAAGAGCCTCCTGCTCAGCTTCAACTATATC 174
 OVI CAAGTGCCCCAGGTCCCCAACAC---CACCAAGAGCCTCCTGCTCAGTTTCAACTATATC 174
 SSC CAGGTTCCCCAGGTCCCCAGTGG---CACCAAGAGCCTCCTGCTCAGCTTCAACTACATC 171
 PAL CAGATACCCCGGGTCTCAACAC---CACTGAGAGCCTCCTGCTAAGCTTCAACTATATC 174
 AME CAGGTGCCCCCGGTCCCCAGCAC---CACCCAGGTCTCCTGCTCAGCTTCAACTATATC 174
 MPU CAGGTGCCGCCAGTCCCCAGCAC---CACCCAGATCTCCTGCTTAGCTTCAACTATATC 174
 CLU CAGGTGCCCCCGGTCCCCAGCAC---CACCGAGATCTCCTGCTGAGCTTCAACTACATC 174
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 OPR CAGGTCCCGCAGGTCTCAACAG---CACAGAGAGTCTTCTGCTAAACTTCAACTATATC 174
 MMU CAGATTCCTGGATCTCAATACTACCAGTACTGAGAGGCTCCTGCTCAGCTTCAACTATATC 177
 MDO CAAGTCCCCAAGTGCCAAATAC---TACAACAAAGCTGTGTAAAGTTTCAACTACATC 174
 SHA GAAGTCCCCCAGTACCAAAACAC---CATTATTAAGCTATCTTAAAGTTATAACTATATC 171
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 GGA GGTGTTCCACCTGTGCCAAAGGA---CACTGCAAAGCTTTTTTCTAACTTCAACTATATC 174
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 HSA AGGACAGTCACTGCTTCATCC--TTCCCCTTCTGGAACAGCTGCAGCTGCTGGAGCTCG 232
 GGO AGGACAGTCACTGCTTCATCC--TTCCCCTTCTGGAACAGCTGCAGCTGCTAGAGCTCG 232
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MMUL CGGACAGTCACTGTTTCATCC--TTCCCCTTCTGGAACAGCTGCAGCTGCTGGAGCTCG 232
CTO CGGACAGTCACTGTTTCATCC--TTCCCCTTCTGGAACAGCTGCAGCTGCTGGAGCTCG 232
CJA AGGACAGTCACTGCTTCATCC--TTCCCCTTCTGGAGCAGCTGCAGCTGCTGGAGCTCG 232
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OAR AGGACAGTCAAGACCACATCC--TTCCCCTTCTGGAGCAGTTGCAGCTGCTGGAGCTGG 232
RRU AGGACAGTCAAGACTACATCC--TTCCCCTTCTGGAGCAGTTGCAGCTGCTGGAGCTGG 232
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PAL AAGACAGTCAAGCCGCTCT--TTCCCCTTCTGGAGCGCTGCAGCTGCTGGAGCTCG 232
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CLU CGGGCCGTAC--CCGCGCTTCTCCCCTTCTGGAGCGCTGCAGCTGCTGGAGCTGG 232
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SHA AGGATGATTAATGCTACTTCA--TTCCCTCTATTGGAGATGCTCCAATTGCTACAGCTAG 229
 OAN AGGACAGTGAACGCCACCTCC--TTCCCTCTGCTGGAGAAGCTGGAGCTGCTGGAGCTCG 232
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 MPU TCAGGGTGTGGACCTGGGCAAGAGTCAGGTGGATTCTTGCATCCCGATGCTTTTCAGG 349
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HSA AAGATGGTTATTTTCAGAAATTTAAAGGCTTTAACTCGCTTGGATCTATCCAAAAATCAGA 469
GOO AAGATGGTTATTTTCAGAAATTTAAAGGCTTTAACTCGCTTGGATCTATCCAAAAATCAGA 469
PPY AAGATGGTTATTTTCAGAAATTTAAAGGCTTTAACTCGCTTGGATCTATCCAAAAATCAGA 469
MFA AAAATGGTTATTTTCAGAAATTTAAAGTCTTTAACTCGCTTGGATCTATCCAAAAATCAGA 469
MMUL AAAATGGTTATTTTCAGAAATTTAAAGTCTTTAACTCGCTTGGATCTATCCAAAAATCAGA 469
CTO AAGATGGTTATTTTCAGAAATTTAAAGTCTTTAACTCGCTTGGATCTATCCAAAAATCAGA 469
CJA AAGATGGTTATTTTCAGAAATTTAAAGTCTTTAACTCGCTTGGATCTATCCAAAAATCAGA 469
TSY GAGATGGTTATTTTCAGAAATTTAAACTCTTTAATTCGCTTGGATCTGTCAAAAAATCAGA 469
CHI AAGATGGTTATTTTCAGAAATTTGGCATCTTTGACTCGCTTGGACCTATCCAAAAATCAA 469
OAR AAGATGGTTATTTTCAGAAATTTGGCATCTTTGACTCGCTTGGACCTATCCAAAAATCAA 469

PAL	TTCGCAGCCTTCCCCCATCCTTCGTTTCAGGGAATTGAATTCCTTGAAGTCCATCGATT	529
AME	TTCGTAGCCTTAAGCTTCATCCTTCATTCTGGGAATTGAATTCCTTGAAGTCCATTGATT	529
MPU	TTCAAAGCCTTAACCTTCACCTTCATTCTGGGAATTAAATTCCTTGAAGTCCATTGATT	529
CLU	TTGGGAGCCTCGAGCTTCACGCCTCCTTCCGGGAGCTGGGTTCCTTGAAGTCCCTGGACT	529
ETE	TTGGCAGCCTTACCCTCCATCCTTCCTTCCGAGAGTTGAATGCCTTGAAGTCCATAGACT	529
OPR	TTCAAAGTCTTCCCTTCATGCTTCATTTGAGACTTGAATTCCTTAAAGTCCGTAGACA	529
MMU	TTACAGCCTCGGCCTCCATTCCTTCATTCCGGGAATGAATTCCTTAAAGCAGCTAAATT	532
MDO	TAGAAAATCTCCAGCTTCATCCTTCTTTTGAAAATCTGGAATCCTTGAATCCATAGATT	529
SHA	TCCAGAATATCCACCTTCATCCTTCTTTTGAAGATCTGAAATCCTTGAATCTATAGACT	526
OAN	TCCAAAGTCTTCCCTTTCACGCCTCGTTTCGGGAGTTGAGATCTCTGGAGACCTTGACC	529
GGA	TCACAAAACCTTCATCCACACCCTTATTTTATAATCTAACCATCTTGAAGCTGTGAACC	532
GLA	TCACAAAACCTTCATCCACACCCTTATTTTATAATCTAACCATCTTGAAGCTGTGGACC	532
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PCO	TCACAAAACCTTCATCCACACCCTTATTTTATAATCTAACCATCTTAAAGTTGTGAACC	532
NME	TCACAAAACCTTCATCCACACCCTTATTTTATAATCTAACCATCTTGAAGCTGTGGACC	532
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 HSA CGCTCTCCTTTTTTTAGCCTCGCAGCTAA-TAGCTTGTATAGCAGAGTCTCAGTGGACTGG 648
 GGO CGCTCTCCTTTTTTTAGCCTCGCAGCTAA-TAGCTTGTATAGCAGAGTCTCAGTGGACTGG 648
 PPY CACTCTCCTTTTTTTAGCCTCGCAGCTAA-TAACTTGTACAGCAGAGTCTCAGTGGACTGG 648
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 OAR CACTCTCCTTTCTTAAGCCTTGCTGATAA-CCACTTGTACAGCAGGGTGTCTCAGTGGACTGG 648
 RRU CACTCTCCTTTCTTAAGCCTTGCTGATAA-CCACTTGTACAGCAGGGTGTCTCAGTGGACTGG 648
 OGA CACTCTCCTTTCTTAAGCCTTGCTGATAA-CCACTTGTACAGCAGGGTGTCTCAGTGGACTGG 648
 OLE CACTCTCCTTTCTTAAGCCTTGCTGATAA-CCACTTGTACAGCAGGGTGTCTCAGTGGACTGG 648
 ODA CACTCTCCTTTCTTAAGCCTTGCTGATAA-CCACTTGTACAGCAGGGTGTCTCAGTGGACTGG 648
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 SHA TTATCCCATAACTCCTACTATCCCTGACCCATCCATATTTGCATCACTGAGCCACTTA 1719
 OAN TTATCCAGAAACCAGTTGTTTTTCCCTGATCCTAACCCTCTCATGTCCTGCAAGTCTG 1722
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 PCO TTGTCTGGAAACCAGCTTTTTTCCCTAAGCCTGAAGTCTTTATGACTTTGAGTATTCTG 1725
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 TGU TTATCTGGAAACCAGCTATTTTTCCCTGAGCCTGAAGTCTTTATGACTTTGAGTATTCTG 1719
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 CHI GACATAACTCATAACAAATTCATCTGTGATTGTGAACCTTAGTGCTTTTATCCATTGGGTC 1782
 OAR GACATAACTCATAACAAATTCATCTGTGATTGTGAACCTTAGTGCTTTTATCCATTGGGTC 1782
 RRU GACATAACTCATAACAAATTCATCTGTGATTGTGAACCTTAGTGCTTTTATCCATTGGGTC 1782
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BBU4	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
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BBU16	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
BBU18	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
BCA	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
BBU7	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
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BBU6	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
BBU10	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
SCA1	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
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BJA	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
T1M	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
TST	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
GCA	GACATAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
OHE	GACCTAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
OVI	GACCTAACTCATAACAATTTTCATCTGTGAGTGTGAAGCTTAGTGCTTTTATCCATTGGCTC	1782
SSC	GACCTGAGTCATAACAAGTTTGTGTTGTGACTGTGAAGCTTAGCAGCTTTTATCAATTGGCTC	1779
PAL	GACATAACTCATAACAAGTTTCATCTGTGAGTGTGAAGCTTAGCGCTTTCATCAGGTGGCTC	1782
AME	GACATAACGCACAACAGGTTTCATCTGTGAGTGTGACCTCCGTCCTCTCATCACTTGGCTC	1782
MPU	GACATAACACACAACAATTTTCATCTGTGAGTGTGACCTCCGTTCTCTCGTTGTTGGCTC	1782
CLU	GACCTAACGCACAACAAGTTTCATCTGCGGCTGCGAGCTCCGTTCCCTTGGTGGGTGGCTC	1782
ETE	GACCTCGGCATAACAGTTTCATCTGTGCGTGTGAAGCTGAGCGCTTTATCAGCTGGCTC	1782
OPR	GACATACCCATAACAAGTTTCATCTGTGTTGTGTGAAGCTTAGCAAGTTTATCAGTTGGCTT	1782
MMU	GACATAACTCATAACAGTTTCGTCGTGCAACTGTGAAGCTTAGCAGCTTTTATCCTCGGCTC	1785
MDO	GATATAACCCATAACAATATATCTGTGAGTGTGAAGCCAGAAATTTTATACTTTGGTTG	1785
SHA	GATATAAGCCACAATCAATATATTTGTGATTGTGAAGTCAAAAATTTTATCCTTTGGCTG	1779
OAN	GATATAACCCATAACAGTTACATCTGTGAGTGTGAGCTCAGAGACTTCTAGGCTGGCTA	1782
GGA	GATATAACACATAACAAGTATGTCTGTGACTGTGCTTTAAAAAGCCTATTAGTGTGGCTA	1785
GLA	GATATAACACATAACAAGTATGTCTGTGATTGTGCTTTAAAAAGCCTACTAGTGTGGCTA	1785
MGA	GATATAACACATAACAAGTATGTCTGTGACTGTGCTTTAAAAAGCCTACTAGTGTGGCTA	1788
PCO	GATATAACACATAACAATATGTCTGTGATTGTGCTTTAAAAAGCCTACTAGTGTGGCTA	1785
NME	GATATAACACATAACAATATGTCTGTGACTGTGCTTTAAAAAGCCTGCTAGTGTGGCTA	1785
TGU	GATATAACACATAAATAATTATGTCTGTGATTGTGCTTTAAAGAGCCTGCTAGTGTGGTTG	1779
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PTR	AATCACACCAATGTCACTATAGCTGGGCCTCCTGCAGACATATATTGTGTGTACCCCTGAC	1842

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MDO AACCAAACCAAAGTCAACATGCTTGGGTCCCCTGAGGATGTCTACTGCACATACCCTGAC 1845
SHA AATCAAACCAATGTTACCATGCTTGGGTCCCCTGAGGATGTTTACTGCACATACCCTGGC 1839
OAN AACCGTCAAATGTCACTTTTTGGGGTCACCCAAGGACATGTACTGTGTATCCAGAC 1842
GGA AATGAAACCAATGTAACCCTAGCTGGCTCGGAGTCTGACAGGTACTGTGTGTACCCACCT 1845
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MGA AATGAAACCAATGTAACCCTAGCTGGCTCAGAGTCTGACAGGTACTGTGTGTACCCACCT 1848
PCO AATGAAACCAATGTAACCCTAGCTGGCTCAGAGTCTGACAGGTACTGTGTATACCACCT 1845
NME AATGAAACCAATGTAACCCTAGTTGGCTCAGAGTCTGACAGGTACTGTGTATACCACCT 1845
TGU AATGAAACCAATGTAACCCTGGCTGGCTCCCAGTCTGACAGGTACTGTGTGTACCCCCCT 1839

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PPA TCACTCTCTGGGGTTTCCCTCTTCTCTCTTTCCACGGAAGGTTGTGATGAAGAGGAAGTC 1902
PTR TCACTCTCTGGGGTTTCCCTCTTCTCTCTTTCCACGGAAGGTTGTGATGAAGAGGAAGTC 1902
HSA TCGTTCTCTGGGGTTTCCCTCTTCTCTCTTTCCACGGAAGGTTGTGATGAAGAGGAAGTC 1902
GGO TCGCTTCTGGGGTTTCCCTCTTCTCTCTTTCCACAGAAGGTTGTGATGAAGAGGAAGTC 1902
PPY TCGCTCTCTGGGGTTTCCCTCTTCTCTCTTTCCACAGAAGGTTGTGATGAAGAGGAAGTC 1902
MFA TCGCTCTCCGGGGTTTCCCTCTTCTCTCTTTCCACGGAAGGTTGTGATGAAGAGGAAGTC 1902
MMUL TCGCTCTCCGGGGTTTCCCTCTTCTCTCTTTCCACGGAAGGTTGTGATGAAGAGGAAGTC 1902
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CJA TCGTTCTCTGGGGTTTCCCTCTTCTCTCTTTCCACAGAAGACTGTGATGAAGAGGAAGTC 1902
TSY TCGCTCTTGGGGTTTCCCTTACTCTGTGTCCACGGAAGATTGTGATGAAGAGGAAGTC 1902
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OAR TCTCTGGCTGGGGTTTCCATTTACAGTCTTTCCACAGAAGGTTGTGAAGAAGAAGATTT 1902
RRU TCTCTGGCTGGGGTTTCCATTTACAGTCTTTCCACAGAAGGTTGTGAAGAAGAAGATTT 1902
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 ETE GCATTTGCTGGGGTCCCCCTGGACTCTATTTCCACGGATGGGTGTGACGAAGAGAAAGCC 1902
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PPA TTAAAGTCCCTAAAGTTCTCCCTTTTCATTGTATGCACTGTCACCTGACTCTATTCCCTC 1962
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TSY	AGTGTGCAACTATCTC---CTAA	2580
CHI	AGTGTAACCACCATCTC---CTAG	2577
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SHA	ACCGTAGCAACTGTATC---CTAG	2577
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GLA	ACTATAGCGACAGTCTCACACTGA	2583
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PCO	ACTATAGCGACAGTCTCACACTGA	2583
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