INBREEDING AND INBREEDING DEPRESSION IN LINEBRED BEEF CATTLE

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Animal Science

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2020

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DEDICATION

To my family and close friends for their continuous support and countless words of encouragement. To my great papa, great grandma, and grandpa who I know are watching over me and cheering me on from above.

ACKNOWLEDGEMENTS

First and foremost, I must thank Drs. Jennifer Thomson, Jane Ann Boles, and Rachel Endecott for their constant support and friendship since I moved to Montana, and Dr. Elhamidi Hay for his expertise and being a member of my committee. This project also would not have been possible without the funding provided by the Montana State University Montana Agricultural Experiment Station, the United States Department of Agriculture – Agriculture Research Service, and the Montana State University Graduate School.

I would like to thank those at the Northern Agricultural Research Center who helped collect data and work cows for my project, especially Dr. Darrin Boss, Julia Dafoe, and Cory Parsons. To my academic "siblings" and fellow graduate students, thank you for all the laughs, support, and shoulders to lean on. I also cannot forget all the amazing faculty and staff within ABB that have provided guidance and given countless words of encouragement.

I owe the largest thank you to my support system over the last four years, my family and friends. Thank you for providing an endless amount of support and reassurance throughout this adventure, I love you all! To my boyfriend, thank you for all of your support! You may be a recent addition to my life, but you have provided limitless encouragement. Staying up with me during the late nights means more to me than you'll know. I love you more!

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NOMENCLATURE

AFC ..... age at first calving

AI ..... artificial insemination

ARS ..... Agricultural Research Service

ASA ..... American Simmental Association

BF ..... 12^{th} rib fat

bp ..... base pair

BRD ..... bovine respiratory disease

BW ..... birth weight

CE ..... calving ease

CED ..... calving ease direct

CEM ..... calving ease maternal

CMP ..... Carcass Merit Program

EPD ..... expected progeny differences

ET ..... embryo transfer

F ..... inbreeding coefficient

F_G ..... genomic inbreeding

F_{GPED} ..... genomic pedigree inbreeding

F_{PED} ..... pedigree inbreeding

F_{ROH} ..... inbreeding calculated by runs of homozygosity

GBLUP ..... genomic best linear unbiased prediction

GWAS ..... genome-wide association studies

NOMENCLATURE CONTINUED

HCW ..... hot carcass weight

IBD ..... identity by descent

IBS ..... identity by state

JSNP ..... Japanese Single-Nuceleotide Polymorphisms

KPH ..... internal fat

LARRL ..... Livestock and Range Research Laboratory

LD ..... linkage disequilibrium

MAF ..... minor allele frequency

MARB ..... marbling

MAS ..... marker-assisted selection

Mb ..... megabase

MSU ..... Montana State University

NARC ..... Northern Agricultural Research Center

PCA ..... principle component analysis

QTL ..... quantitative trait loci

REA ..... ribeye area

ROH ..... runs of homozygosity

SNP ..... single nucleotide polymorphism

USDA ..... United States Department of Agriculture

USMARC ..... U. S. Meat Animal Research Center

WW ..... weaning weight

NOMENCLATURE CONTINUED

YW ..... yearling weight

ABSTRACT

This research applied genomics and phenotypic information in three different beef cattle populations. The methods applied were association analyses, runs of homozygosity, and genetic correlations. This incorporated both genomic and phenotypic approaches to identify the results of linebreeding in two closed Hereford populations. Further work evaluated carcass and maternal traits from the American Simmental Association Carcass Merit Program using genomic and phenotypic information to identify how carcass-based selection decisions impact maternal performance of Simmental-based cattle. Line 4 pedigree inbreeding, genomic inbreeding, and genomic pedigree inbreeding ranges were 0 – 36%, 0 – 49%, and 0 – 29%, respectively, and average inbreeding was 12.6%, 12.3%, and 17.7%, respectively. Line 1 pedigree inbreeding, genomic inbreeding, and genomic pedigree inbreeding ranges were 0 – 71%, 0 – 46%, and 0 – 63%, respectively, and average inbreeding was 42.1%, 14.4%, and 31.0%, respectively. Average rate of change in inbreeding per year was 0.03% over 55 years for Line 4 and -0.03% over 83 years for Line 1. Identified for Line 4 were 45 ROH regions, 35 strongly significant single nucleotide polymorphisms, three strongly significant SNP within ROH, and some significant SNP within 12 previously identified genes. Identified for Line 1 were 50 ROH regions, 93 strongly significant SNP, three strongly significant SNP within ROH, and some significant SNP within 11 previously identified genes. Within the Simmental dataset, nine chromosomes had genome-wide significance, explaining 0.2142 percent of total phenotypic information. The single-locus model identified 365 novel regions and 251 novel positional candidate genes. The multi-locus model identified 393 novel regions and 283 novel positional candidate genes. Also, detrimental genetic correlations between carcass characteristics and maternal traits were less than previously reported. Analyses utilized in this study indicate ROH and significant SNP can be used to identify regions of the genome affected by inbreeding. Also, simultaneous selection for carcass and maternal traits reduced the negative impact seen with single-trait selection for carcass traits.

CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

Introduction

Inbreeding and Inbreeding Depression in Linebred Beef Cattle

The effects of inbreeding depression have been well documented in livestock and has been reported to reduce performance and reproduction, with a resulting reduction in profitability. Advances in genotyping have allowed researchers to move beyond pedigree analysis and study the effects of inbreeding at the molecular level. Previous research (Sumreddee et al., 2019) has looked at identifying regions of the genome which allows us to use a combination of techniques to place more emphasis on functionality of those regions.

Chapters 2 and 3 will investigate the Line 1 Hereford population at the United States Department of Agriculture (USDA) – Agriculture Research Service (ARS) Fort Keogh Livestock and Range Research Laboratory (LARRL) in Miles City, MT, and the Line 4 Hereford population at the Montana State University (MSU) Northern Agricultural Research Center (NARC) near Havre, MT. Surplus Line 1 females were purchased by NARC after the line had closed and these females were used as the foundation females for the Line 4. Most recently, the Line 1 selection decisions have been based on growth to one year of age and the Line 4 selection decisions have been based on increased yearling weight (YW) while keeping inbreeding levels low. Both populations will be described in more detail later. These populations provide a unique

opportunity to increase the understanding of the molecular mechanisms involved in inbreeding depression because while they share the same origin, they have been managed differently, as has the degree of phenotypic inbreeding depression they demonstrate. The objectives of chapters 2 and 3 include:

- to understand the effect of individual and maternal inbreeding on reproductive, growth, and carcass traits in the Line 1 and Line 4 Hereford cattle populations;
- to assess the potential for non-linear associations between pedigree and genomic inbreeding and performance traits;
- to evaluate if there are differences between lines in the effect of maternal and individual inbreeding on performance traits; and
- to utilize high density genotyping data to identify candidate markers and genes associated with performance decline due to inbreeding.

Genetic Improvement with the Carcass Merit Program

While the USDA Quality grade is the driving force of how consumers purchase and consume beef, quality is subjective to each consumer (Henchion et al., 2014). Ultimately consumers are after a good eating experience that costs the least, therefore genetic improvement in the quality of beef products can benefit both producers and consumers. Chapter 4 will utilize data from the American Simmental Association's (ASA) Carcass Merit Program (CMP) as well as some of the methodology that was used in Chapters 2 and 3. The goal of ASA CMP is to build the accuracy for economically important expected progeny differences (EPD) and assist in early screening for bulls that

possess unique levels of traits differential and therefore provide maximum selection leverage. The objectives of chapter 4 include:

- to identify genetic markers and quantitative trait loci (QTL) for carcass traits and
- to evaluate correlations between carcass merit traits and maternal performance.

Linebreeding and Heterosis

Robert Bakewell revolutionized sheep and cattle breeding in the 1700s, which laid the foundation for animal breeding concepts that are still being used today (Encyclopaedia Britannica, 2020). Bakewell founded his reputation on the theory of "in-and-in breeding", or the persistent inbreeding of closely related animals (Wykes, 2004). Linebreeding, a milder form of inbreeding, can be defined as continually mating descendants of particular animals, while avoiding relationships through other animals as much as possible (Wright, 1939). Linebreeding is a form of inbreeding practiced to preserve desirable traits of a superior ancestor by increasing the number of descendants from that ancestor and minimizing inbreeding of other traits while maintaining desired traits (Lush, 2017).

Between 1934 and 1955, 14 lines of Hereford cattle were developed at the USDA Range Station in Miles City, MT, in an effort to fulfill the goal of developing true-breeding lines of Hereford cattle. Once each line was established, the populations were closed and purposefully inbred to produce true-bred lines (MacNeil, 2009). These lines of Herefords were initially developed as foundation animals in hopes of using them for evaluating heterosis by crossing selected inbred lines (MacNeil, 2009) that were adapted

to western range areas while possessing high fertility and superior quality (Black, 1936), however that hope was never fulfilled as it was replaced by crossbreeding.

Bakewell successfully created new breeds by crossbreeding, or the mating of two different breeds or lines of livestock, in his effort of improving the old Lincolnshire sheep breed. This project resulted in the establishment of the New Leicester or what is known as the Border Leicester today (Wykes, 2004). Heterosis, or hybrid vigor, is an increase in the performance of hybrids of breeds or lines over that of purebreds (Bourdon, 2000). Heterosis takes advantage of breed complementarity, or rather an improvement in the overall performance of offspring as the result of mating individuals with different yet complementary breeding values (Bourdon, 2000). Heterosis is often seen when purebred parents are mated to produce crossbred offspring, with the expectation that the offspring will out-perform their parents based on the average of the parent breeds. Increased performance resulting from heterosis can be seen in inbred lines (Falconer and Mackay, 1996). It has been found that heterosis is the recovery of accumulated inbreeding depression that has occurred when forming inbred lines due to heterosis appearing to be the primary result from dominance effects of genes (Gregory et al., 1994; Pariacote et al., 1998).

Heterosis has been studied in both inbred and non-inbred lines of cattle for several traits. Anderson et al. (1986) looked at five closed lines of Herefords but did not find any significant heterosis estimates for carcass traits, which was supported by the results of Kincaid (1962), Gaines et al. (1967), and Long and Gregory (1975) who all reported that carcass traits, not directly related to growth, have little evidence of heterosis in Angus,

Hereford, Shorthorn, and reciprocal crosses. The results of crossing closed lines within a breed agreed with many reports that post-weaning growth traits have a tendency to exhibit some heterosis (Flower et al., 1963; Brinks et al., 1967; Urick et al., 1968; Burfening and Kress, 1973), but there have been limited cases of heterosis having been important for carcass traits that were not associated with growth.

Inbreeding and Inbreeding Depression

Inbreeding can be defined as the mating of related individuals (Northcutt et al., 2004), yet essentially all individuals in a breed are related. Therefore, the term inbreeding is generally defined as the mating of animals that are more closely related than the average of the breed (Brinks and Knapp, 1975; Northcutt et al., 2004). It is known that inbreeding can have negative effects on all species of livestock (Burrow, 1993; Kristensen and Sorensen, 2005; Leroy, 2014), resulting in individuals receiving identical alleles from each of their parents. If the parents are related, they are more likely to have alleles that are identical and there is a higher chance that their offspring will receive these alleles. This would be ideal if alleles received led to superior performance, however most livestock carry undesirable alleles that are usually hidden unless the animal is homozygous for the alleles at a specific gene. An inbred individual is more likely to have a homozygous genotype; therefore, they are more likely to express undesirable alleles, resulting in undesirable phenotypic traits (Northcutt et al., 2004).

The most common measure of inbreeding is based on pedigree and is measured by the inbreeding coefficient (F_x; Bourdon, 2000), developed by Wright (1922), which is defined as the probability that at any locus, two alleles in an individual are identical by

descent (IBD; Falconer and Mackay, 1996). Falconer and Mackay (1996) define IBD as two alleles originating from the replication of a single gene in a previous generation. A related concept is identity by state (IBS), which can be defined as genes that are physically identical but don't stem from the same ancestral chromosome (Elandt-Johnson, 1971). Identity by state is used in reference to molecular inbreeding and coancestry whereas IBD is used in reference to genealogical inbreeding and coancestry (Saura et al., 2013). When two alleles are IBD, it is implied that they are IBS, but two alleles being IBS does not imply that they are IBD (Falconer and Mackay, 1996; Lynch and Walsh, 1998).

Inbreeding alone does not create undesirable, recessive genes, but it does tend to enhance unfavorable genotypes. This leads to inbreeding depression, or the decline in average phenotypic performance, which is well documented in all major species of livestock (Ercanbrack et al. 1991; Rodrigañez et al., 1998; Huang et al., 2012; Martikainen et al., 2017). In terms of the magnitude of how production traits are affected, inbreeding depression has the greatest impact on reproductive traits, followed by growth traits, and little to no effect on carcass traits (Dickerson, 1973). This pattern is the reverse of the magnitude of heritability for these same traits, indicating that inbreeding depression is the opposite effect of heterosis.

Inbreeding depression can be explained by two main hypotheses (Kristensen and Sorensen, 2005; Howard et al., 2017). The partial dominance hypothesis assumes that inbreeding depression is caused by homozygous individuals expressing deleterious recessive alleles. As inbreeding increases, the frequency of deleterious recessive

homozygotes, which were hidden by heterozygotes, will be expressed at an increasing rate. The overdominance hypothesis assumes that heterozygotes are superior to homozygotes and as inbreeding increases, the opportunities for heterozygotes to be expressed is reduced and over dominated. There are similar underlying mechanisms related to the degree of dominance at loci with both hypotheses, but their long-term implications are different. For the partial dominance hypothesis, unfavorable alleles generated by mutations over time within a population would be eliminated with selection (Kristensen and Sorensen, 2005). Under the overdominance hypothesis, selection would favor heterozygotes at multiple loci and therefore mechanisms related to balancing selection would maintain mutations. For both hypotheses, intermediate frequencies in loci are expected to contribute to inbreeding depression more than loci with extreme frequencies (Kristensen and Sorensen, 2005).

A third hypothesis for inbreeding depression is epigenetics. Vergeer et al. (2012) found that changes in gene-expression regulation could possibly contribute to differences in fitness, an individual's phenotype, genotype, and ability to contribute offspring to the next generation, as well as the number of offspring it produces (Bourdon, 2000), between inbred and outcrossed progeny. As the environment impacts gene expression, those fitness differences are likely identified as part of the environmental contribution to the phenotype. Flower size work done by Kelly and Willis (2001) concluded loci that are responsible for inbreeding depression often occur at higher frequencies than can be predicted by just mutation-selection balance. The genetic foundation of inbreeding depression does not fit with unconditionally deleterious allele scenarios; rather, the

number of deleterious alleles may be dependent upon environmental conditions. A credible example of such is when methylation is used to regulate gene expression in plants. It should be noted that these epigenetic mechanisms might be relevant for both the evolution of inbreeding depression and for the maintenance of genetic variation in fitness traits in natural populations (Charlesworth and Willis, 2009).

Again, inbreeding depression is the opposite effect of heterosis or hybrid vigor (Northcutt et al., 2004) so while inbreeding impairs some traits, heterosis helps to make them better. Both heterosis and inbreeding depression depend on the occurrence of dominance (Falconer and Mackay, 1996; Zeng et al., 2013). Falconer and Mackay (1996) discussed that if there is no dominance at a loci, inbreeding depression and heterosis do not occur and the amount of heterosis after crossing lines or populations is dependent on the square of the difference of the gene frequencies between the two.

The reproductive capacity of individuals has greatly increased with the use of reproductive technologies such as artificial insemination (AI) and embryo transfer (ET). This increased use has allowed for superior germplasm to be utilized across multiple herds and/or countries (Brotherstone and Goddard, 2005), resulting in genetic improvements in populations. The use of AI and ET leads to these perceived superior livestock being used multiple times in a breeding season and reduces the number of animals being used as parents, resulting in inbreeding increasing as a whole (Weigel, 2001; Nicholas and Smith, 2010; Granleese et al., 2015)

Effects of Inbreeding on Production Traits

Burrow (1993) reviewed studies previously published that evaluated the effects of inbreeding on economically important traits. With an increase in inbreeding, it is expected to see a decrease in the average performance for traits associated with fitness and viability (Burrow, 1993). In 1989, Smith et al. studied data on 779 Hereford, Angus, and Red Angus heifers and found a 1% increase in inbreeding increased the age of puberty by 0.146 days, age at first calving (AFC) by 0.209 days, and age at second calving by 0.007 days. MacNeil et al. (1989) reported reduced conception rates of 0.072%, prenatal survival of 0.426%, post-natal survival of 0.751%, and a reduction in weaning weight (WW) of offspring per heifer successfully bred of 1.355 kg for every 1% increase in inbreeding. Furthermore, inbreeding has negative effects on male reproductive traits (Burrow, 1993). Overall, breeding soundness exams scores were reduced by 0.17 units, scrotum size by 0.03 mm, sperm motility by 0.04%, and percentage of live sperm by 0.14% for every 1% increase in inbreeding, while percentage of primary and secondary sperm abnormalities were increased by 0.06% and 0.08%, respectively (Burrow, 1993). All of the bulls used in the studies that Burrow (1993) reviewed were over 14 months of age at the time of testing, therefore it was impossible to conclude the reasoning for the reduced values for the estimates of reproductive capacity of the inbred bulls.

Burrow (1993) also found consistent negative effects on calf birth weight (BW) with increased inbreeding of an individual. Overall, for every 1% increase in inbreeding, there was a decrease of 0.06 kg in BW, with there being a larger depression in females

than in males (Burrow, 1993). These findings were consistent with the work of Willis and Wilson (1974), as they saw a reduction of 0.12 kg in BW for every 1% increase in inbreeding. Burrow (1993) also observed negative effects on WW, post-WW, and mature weights for inbred individuals. Again, for every 1% increase in inbreeding, there was a 0.44 kg decrease in WW, a 0.69 kg decrease in post-WW, and a 1.30 kg decrease in mature weights, on average (Burrow, 1993).

Line 1 and Line 4 Hereford Histories

Line 1

Line 1 was developed in 1934 when two sons of Advance Domino 13, Advance Domino 20 and Advance Domino 54, were purchased from Fred C. DeBegrard of Kremmling, CO (MacNeil, 2009; Durham, 2010). The two sons were then bred to 50 cows purchased from George M. Miles of Miles City, MT, followed by daughters of Advance Domino 20 being bred to Advance Domino 54 and vice versa (Durham, 2010). The line was closed in 1935 and all of the animals are descendants of those foundation animals (MacNeil, 2009). The increase in inbreeding per generation that is normally seen in line-bred animals has been reduced as the line's herd has increased and mating closely related individuals has been avoided. In the 1930s, the Line 1 Herefords were used for research focusing on methods of measuring performance of beef cattle, including progeny testing. The implied breeding objective of the line was economic return above feed costs that came from steer carcasses slaughtered at a live weight of 408 kg (MacNeil, 2009). In the 1940s, the advancement of feeding trial testing procedures became the focus of the

research, which drove the decision to base future Line 1 sire selection on growth to one year of age (MacNeil, 2009).

Line 1 Herefords have made major contributions to beef cattle breeding research since the line was started. Since 1924, the beef breeding that has happened at the USDA-ARS station in Miles City, MT changed the direction of the beef industry and led to developing a production record program in Montana by 1936 (Eller, 2007). The formation of the Beef Improvement Federation was majorly impacted by such research along with Montana cattlemen and the American Hereford Association (MacNeil, 2009). In the 1940s, Knapp and Nordskog (1946) and Knapp and Clark (1950) published the first papers about estimates of heritability and Knapp and Clark (1947) published about estimates of genetic correlations. Line 1 germplasm was also distributed during the 1940s through the sale of bulls to livestock producers through public sales. According to Dickenson (1984), 57% of the bulls listed in the 1984 American Hereford Association sire evaluation could be traced to Line 1 ancestry, while Leesburg et al. (2014) found that 79% of Herefords recorded from 2006 – 2008 were related to the Line 1 population. A greater understanding of the maternal genetic effects in beef cattle is due in part to work that was been done with Line 1 animals (Koch, 1951; Koch and Clark, 1955a; Koch and Clark, 1955b; Brinks et al., 1967; Brinks et al., 1972). Studies done by Woodward and Clark (1950), Burns et al. (1979), Butts et al. (1971), Koger et al. (1979), and Pahnish et al. (1983, 1985) supported the idea that genotype by environment interactions may have greater practical importance than what was previously thought. The long-term performance records kept from Line 1 animals has also been useful in developing

national cattle evaluation systems. Some of the greatest scientific contributions that have come from research using Line 1 animals was using the DNA from L1 Dominette 01449 to sequence the entire bovine genome (Bovine Genome Sequencing and Analysis Consortium, 2009), while DNA from her sire L1 Domino 99375 was used for the bovine Y chromosome sequence project, which was used as a calibrator (https://www.hgsc.bcm.edu/content/y-chromosome-genome-project).

Line 4

In 1962 and 1963, MSU NARC purchased surplus Line 1 cows from Fort Keogh, which served as the foundation females for the Line 4 Herefords that have been maintained by NARC since 1962 (Nevins, 1986). The Line 4 herd has been closed since 1976 and from 1976 to 1995, selection decisions for the line were made based on using an index for adjusted YW minus 3.2 times adjusted BW (Nevins, 1986; Rumph et al., 2004; D. Anderson, personal communication, 2018). Selection decision criteria changed to selecting for scrotal circumference from 1995 to 2006 (Rumph et al., 2004), and the most current selection is for increased YW while keeping increased inbreeding at a low level (D. Anderson, personal communication, 2018).

Methodology

Runs of Homozygosity

Runs of homozygosity (ROH) is one of the methods developed to estimate the genomic level of inbreeding and can be used to supplement pedigree-based estimates or when pedigree information is unavailable. As DNA is contained and passed down in

haplotypes, or groups of genes that are passed down from a single parent, rather than single markers inherited independently, ROH are continuous lengths of homozygous genotypes where the two inherited haplotypes are identical (Gibson et al., 2006). More recently, inbreeding estimated from ROH (F_{ROH}) is considered the most powerful method of estimating inbreeding as it makes it possible to distinguish between recent and ancient inbreeding (Keller et al., 2011) or rather chromosome segments that are IBD or IBS, which in-turn informs whether the inbreeding is due to a founder effect or selection effect. Long ROH segments have a low probability of randomly happening and are more likely to be segments of two similar chromosomes within the one individual descending from a recent common ancestor (Keller et al., 2011). Keller et al. (2011) found F_{ROH} is preferable to that estimated from other measures of genomic inbreeding or a pedigree due to containing additional information on the homozygous mutation load that is not captured by other methods of calculating inbreeding. Another advantage of F_{ROH} is its ability to be adjusted to determine inbreeding that is from a recent common ancestor (longer ROH) or more distant common ancestors (shorter ROH; Howard et al., 2015).

Szpiech et al. (2013) and Zhang et al. (2015) have shown that ROH in both humans and cattle are enriched with deleterious mutations, therefore there are a higher proportion of deleterious mutations found within ROH compared to outside of ROH. This greater occurrence of deleterious variants within long ROH comes from the fact that ROH contain rare IBD haplotypes that combine at a low frequency and those low frequency variants have a higher incidence of being deleterious than common variants (Howard, 2017). Runs of homozygosity could be used to identify homozygous regions

that are responsible for having negative effects on a phenotype (Pryce et al., 2014), but also distinguish associations between traits of economic interest and genes present in these regions (Szmatola et al., 2016). Certainly, given the nature of recombination, ROH occurrence is highly heterogeneous across the genome and ROH hotspots across a large number of samples may be suggestive of selection pressure (Zavarez et al., 2015), which can lead to the fixation of favorable alleles within the population. Identifying genomic regions that display a lower number of polymorphisms or no polymorphisms may indicate the occurrence of recent selection and may help to detect QTL and candidate genes. In the research presented in the following two chapters looking at two highly inbred beef cattle populations, ROH will allow us to identify specific regions of the genome that are being impacted by inbreeding, more specifically those that are IBD.

Genome-Wide Association Studies

Genome-wide association studies (GWAS) scan the genome and identify genetic variants that are in linkage disequilibrium (LD) that are associated with a specific trait of interest. Genome-wide association studies were first developed to study the human genome to better understand diseases (Ikegawa, 2012). Through international collaboration, the first draft sequence of the human genome was published in 2001 (International Human Genome Sequencing Consortium, 2001). Collaborative work of the Human Genome Center in the Institute of Medical Science at the University of Tokyo and the Japan Science and Technology Corporation developed the Japanese Single-Nucleotide Polymorphisms (JSNP), the first population-specific single nucleotide polymorphisms (SNP) database with the help of the draft sequence (Hirakawa et al.,

2002). Based on the information in the JSNP database, a research group at the SNP Research Center in Japan successfully identified a susceptible gene for myocardial infarction (Ozaki et al., 2002).

In livestock, GWAS have been used in mapping QTL to economically important traits such as growth traits, feed intake, meat quality, birth weight, etc. (Sharma et al., 2015). Sharma et al. (2015) also mentioned if GWAS were utilized properly, they can be an ideal way to identify genes associated with various phenotypes and clarify the mechanisms of complex traits. Some of the first successful GWAS studies done in beef cattle include Charlier et al. (2008), Hayes et al. (2009), and Snelling et al. (2010). Charlier er al. (2008) identified five recessive disorders in beef cattle, Hayes et al. (2009) reported a response in milk production of dairy cattle to heat stress and nutrition level, and Snelling et al. (2010) identified two candidate genes related to growth in crossbred beef cattle.

Most recently, GWAS has been used in more complex cases. Kramer et al. (2019) used GWAS to better understand the viral neutralization antibody level and response to vaccination against four different viruses associated with bovine respiratory disease (BRD) in Angus calves. In dairy cattle, GWAS have been used to identify QTL for displaced abomasums in Chinese Holsteins (Huang et al., 2019). Traits of economic importance were the first direction that GWAS were used for in livestock, and now they are being used for more specific traits like those previously mentioned.

The GWAS process of identifying markers with mutations that are affecting the trait of interest and are in LD is the first step in marker-assisted selection (MAS),

followed by the second step of incorporating the significant markers identified in step one into the prediction of breeding values leading to genomic selection. Genomic selection predicts the performance of an animal at birth based on genotype without recording a physical phenotype, which has a huge impact on cost of traditional progeny testing and the length of time needed to make selection decisions. Selection emphasis on milk and meat production traits in beef and dairy cattle has worked to improve such traits, however reproductive traits have suffered the consequences due to a negative correlation between production traits and functional traits (Kadarmideen et al., 2003).

Several studies done on dairy breeds and *Bos taurus* breeds have used GWAS to investigate genomic regions associated with fertility traits. Daetwyler et al (2008) found a SNP on chromosome 14 associated with age at first service in Holsteins. In various dairy breeds including Nordic Red, Jersey, Danish, Swedish, and Ayrshire, QTL have been reported for non-return rate, or the proportion of females that are not rebred within a specified period of time after insemination, on chromosomes 2, 3, 4, 6, 13, 15, 26, and 27 (Höglund et al., 2009, 2014, 2015; Schulman et al., 2011). Hawken et al. (2012) found three QTL on chromosome 1 associated with age at puberty in Brahman and tropical-adapted beef cattle. In Hanwoo cattle, Hyeong et al. (2014) found two SNP associated with age at first service on chromosome 2 and chromosome 7. In Brangus cattle, Peters et al. (2013) found two QTL on chromosome 8 and two on chromosome 26 to be associated with first service conception. The traits that have been previously investigated and mentioned are traits that are also negatively impacted by inbreeding. Meeting the

objectives of chapters 2 and 3 coupled with the use of GWAS, we expect to identify regions of the genome where inbreeding affects reproductive traits.

Carcass Characteristics and Maternal Performance

In an effort to develop uniformity in classification and grading terms for market reporting, the USDA began developing livestock grading standards in 1916. Beef quality grading standards have been changed extensively and frequently over the past 100 years, and historically, beef has been sold using the USDA Quality Grades of Prime, Choice, Select, and Standard, where Prime is expected to have the best palatability and Standard the worst (Smith, 2005). Since the early 1990s, the beef industry had been promoting the adoption of value-based marketing strategies through including the adoption of instrument grading, identification of genetic markers that influence carcass quality, and the adoption of a value-based pricing system (Fausti et al., 2010). Value-based pricing systems have rewarded producers for producing carcass with higher USDA quality grades, and the concept of value-based marketing was driven by the desire to improve beef's competitive position in the red meat industry and reverse the dramatic decline the industry saw from 1979 to 1998. Value-based beef has been marketed on quality factors that target perceived desires of the consumer.

Increased marbling (MARB) has a positive effect on beef tenderness, flavor, juiciness, and overall palatability (Emerson et al., 2013). Several studies have shown overall consumer acceptance to be more highly correlated with flavor instead of juiciness or tenderness, regardless of tenderness variation (Neely et al., 1998; O'Quinn et al., 2012; Thompson, 2004). With Guelker et al. (2013) finding over 94% of retail and foodservice

rib and loin steaks being considered tender or very tender, the importance of flavor to overall beef eating satisfaction is imperative (Corbin et al., 2015). The results of Corbin et al. (2015) were consistent with numerous reports demonstrating increased beef palatability and flavor scores with increased fat or MARB level (Smith et al., 1985; Lorenzen et al., 1999; Emerson et al., 2013), indicating that fat level was the primary driver of beef flavor acceptability. Producers have recognized that consumers have standards for meat and are willing to pay more for beef of higher quality (Lyford et al., 2010).

Due to consumer demand for a higher quality product, producers have placed an emphasis on improving carcass characteristics when making selection decisions. Therefore, research with purebred and commercial sectors has focused on increasing the genetic predisposition for desirable carcass characteristics in a cowherd, yet there are limited results on the presence or absence of the relationship between carcass traits and maternal traits. There is a concern in how making carcass-based selection decisions are impacting the maternal performance in these cowherds. If maternal characteristics such as calving ease (CE) and milk production are decreased, there could be detrimental impacts on overall calf performance, especially before calves reach harvest.

Research done by Gregory et al. (1993) and Cundiff et al. (1993) showed breed differences in cattle used in U.S. Meat Animal Research Center (USMARC) germplasm projects for scrotal circumference, puberty age, reproductive traits, maternal traits, and MARB scores, indicating that breed has more of an influence on reproductive traits than MARB potential. However, in crossbred cattle, MacNeil et al. (1984) reported that when

bulls were selected for reduced back fat in their male progeny, the female progeny were expected to be older and weigh more when reaching puberty and had reduced fertility. Furthermore, Splan et al. (1998) found negative correlations between CE and carcass traits, with correlations ranging from -0.29 to -0.04.

The average genetic correlation between MARB score and preweaning gain has been reported to be 0.21 (Splan et al., 1998) and 0.39 (Marshall, 1994), which is favorable if selection for WW and MARB are desired in the same direction. Due to the direct and positive relationship between WW and dam's milk production (Knapp and Black, 1941; Neville et al., 1960; Wyatt et al., 1977; Boggs et al., 1980; Marston et al., 1992), one would consider increased milk production would have a positive association with greater MARB potential.

Kuhlers and Jungst (1992) found that selecting for increased 70-day litter weight in breeding lines of swine resulted in market hogs with greater MARB scores. In an effort to increase 70-day litter weights, sows were selected for increased milk production, litter size, and pig survivability, suggesting that selecting for increased milk production is genetically linked to an increased ability to marble. Yet, Fiss and Wilton (1993) did not find a relationship between dam milk yield and their progeny's feedlot or carcass characteristics. A positive genetic relationship was found by Arnold et al. (1991) between post weaning rate of gain and MARB, indicating that environmental conditions during the finishing phase of the diet would limit MARB expression instead of improving it beyond an animal's genetic potential. This would demonstrate a genetic link between carcass characteristics and MARB, and producers should remain aware of these

relationships when making selection decisions and should practice multiple trait selection in a way to match progeny to available resources and management.

CHAPTER TWO

INBREEDING LEVELS OF THE LINE 4 HEREFORD CATTLE POPULATION

Introduction

Inbreeding is defined as the mating of animals that are more closely related than the average of the breed (Brinks and Knapp, 1975; Northcutt et al., 2004). Inbreeding often results in inbreeding depression, or the decline in average phenotypic performance, and its impacts have been well documented including reduced performance, reproduction, and profitability (MacNeil et al., 1989; Burrow, 1993).

Inbreeding is an increasing issue in the beef cattle industry due to increased use of artificial insemination (AI) and embryo transfer (ET; Granleese et al., 2015). However, there is a lack of understanding of the molecular mechanisms involved in inbreeding depression. Pearl (1913, 1915) was the first to develop an inbreeding coefficient, which is now of historical interest only; however, it was later refined by Wright in 1921 (Lush, 1948), but to date nothing has been determined about the molecular basis of inbreeding depression. Long-term linebred populations, such as the Line 4 Hereford population, offer a unique opportunity to better understand this (Rumph et al., 2005). The hypothesis of this work is to determine if a combination of runs of homozygosity (ROH) analysis and genome-wide association can be used to identify regions of the genome associated with inbreeding depression. The specific objectives of this chapter were to: 1) understand the effect of individual and maternal inbreeding on growth and maternal traits in the Line

4 Hereford cattle population and 2) utilize high density genotyping data to identify candidate markers and genes associated with performance decline due to inbreeding.

Materials and Methods

This study used data compiled from the Line 4 Hereford population maintained at the Montana State University (MSU) Northern Agricultural Research Center (NARC). These animals were maintained under an approved Agricultural Animal Care and Use standard operating procedure that was evaluated every three to five years.

Data used in this study were from the Line 4 Hereford population at MSU NARC near Havre, MT. In 1962 and 1963, MSU NARC purchased surplus Line 1 cows that were maintained at the United States Department of Agriculture (USDA) – Agriculture Research Service (ARS) Fort Keogh Livestock and Range Research Laboratory (LARRL) near Miles City, MT. The Line 1 was closed in 1935 and has continued to be maintained at USDA – LARRL. These cows served as the foundation females for Line 4 and they have been maintained by NARC since 1962 (Nevins, 1986). The Line 4 herd was closed in 1976, and from 1976 to 1995, selection decisions for the line were made based on an index for adjusted yearling weight (YW) minus 3.2 times adjusted birth weight (BW; Nevins, 1986; Rumph et al., 2004; D. Anderson, personal communication, 2018). Selection decision criteria changed to selecting for scrotal circumference from 1995 to 2006 (Rumph et al., 2004), and current selection is for increased YW while keeping increased inbreeding at a low level (D. Anderson, personal communication, 2018).

Pedigree and phenotypic information consisted of phenotype data collected from 1976 – 2018 at NARC, from the American Hereford Association Herdbook, and from breeding records dating back to the origins of the line. A pedigree containing 3,430 animals was constructed covering 1964 – 2018, and the following traits were used in this study: BW, weaning weight (WW), YW, calving ease (CE), and age at first calving (AFC). A subset of the population was selected for genotyping based on genetic contributions to the population and availability. Genetic contribution was determined with composition and number of offspring results from PedScope (version 2.5.01ms; Tenset Technologies Ltd). Two hundred and forty-four semen, tissue, and blood samples were collected. Blood and semen DNA were extracted using Promega Maxwell® 16 LEV Blood DNA Kits and tissue DNA was extracted using Qiagen DNeasy Blood and Tissue Kits. Samples were then genotyped with the Illumina Bovine GGP 50K BeadChip.

Inbreeding was estimated using a complete pedigree (F_{PED}; PedScope, version 2.5.01ms) and genomic information. Genomic inbreeding (F_G) and pedigree inbreeding (F_{GPED}) were evaluated for 241 genotyped animals. Three samples were removed due to failure to pass quality control at the single nucleotide polymorphism (SNP) chip level. Genomic inbreeding coefficients were calculated in Golden Helix SVS software (version 8.7.2-2017-08-11) using Wright's within-subpopulation fixation index and genomic pedigree inbreeding was calculated by taking the pedigree inbreeding values for the genotyped animals from F_{PED} analysis. After calculating F_G, five samples were removed due to extremely high and unrealistic genomic inbreeding coefficients. Average rate of change in inbreeding per year was also evaluated by using the F_{PED} results and averaging

inbreeding for each year of birth. Runs of homozygosity analysis was performed in Golden Helix SVS software (v8.8.3) and ROH were defined as a minimum run length of 2,500 kb with a minimum of 250 SNP appearing in 20 samples. This scans the genome with a sliding window of 2,500 kb looking for a minimum of 250 consecutive homozygous SNP. Regions of the genome with increased homozygosity potentially contributes to inbreeding depression as the size and density of blocks of homozygosity increase with inbreeding depression.

The parameters used identified ROH that can be classified as short ROH. Ferenčaković et al. (2011) indicated that ROH that are less than one megabase (Mb) are a result of ancient inbreeding. Furthermore, Zhang et al. (2015) found that short ROH regions were shared between all individuals in their cattle population, confirming that short ROH were selected and derived from ancient haplotypes that became fixed in their population. The significant correlation between shared ROH regions and regions consistently passed down from generation to generation with selection suggests that some of the short ROH are a result of both inbreeding and selection. Rather than ROH regions being scattered among the genome, there are regions with dense-ROH peaks that are consistent across individuals (Zhang et al. 2015). When more conventional ROH parameters were used, essentially the whole genome was identified as being homozygous. Due to the goal of identifying regions of the genome being impacted by inbreeding depression in the current study, the ROH parameters were adjusted to identify the most consistent and most dense regions of homozygosity. This allowed regions of the genome that could be impacting phenotype to be better pinpointed.

For each trait, expected phenotypes were calculated by adjusting each animal's individual phenotype with the published negative impact of inbreeding depression using the animal's own inbreeding coefficient. Regression values were based upon previous research (SMith et al., 1989; Burrow, 1993; Hinrichs and Thaller, 2011). For every 1% increase in inbreeding, the review done by Burrow (1993) found BW decreased by 0.06 kg, WW decreased by 0.44 kg, and YW decreased by 0.69 kg, while Hinrichs and Thaller (2011) found CE decreased by 0.1, and Smith et al. (1989) found AFC increased by 0.209 days. The difference between expected phenotype and reported phenotypes was used as a variable in the analysis.

Genotype data quality control was done through a series of filters (Golden Helix, 2019). First, samples were removed if they had a call rate ≤ 0.95 indicating reduced DNA quality. Data were then pruned to remove markers in linkage disequilibrium. Quality control of markers excluded SNP with spurious position, low call rates (<90%), a heterozygous deviation > 20% from Hardy-Weinberg equilibrium, or less than 5% minor allele frequency (MAF). This left 38,111 out of 47,887 markers in the downstream analysis.

Samples were then filtered to determine relatedness. An identity by descent (IBD) relationship matrix was created to correct the association analysis for genomic relationship amongst samples and a heatmap was produced. Principal component analysis (PCA) was used to account for cryptic relatedness and the first two eigen vectors represented greater than 80% of the stratification on the SNP data. Calculated relatedness between individuals was used as a covariate in the association analysis.

A regression association analysis in Golden Helix SVS software (Golden Helix, version 8.7.2-2017-08-11) was used on the genotype data while correcting for cryptic relatedness and pedigree structure, and then used to generate Manhattan plots. Bonferroni multiple comparison corrections and false discovery rate were used to minimize false-positive associations. Traditionally, a genome-wide significance level with -log10(*p*-value) is 5×10^{-8} (Ehret, 2010) and markers above the level of significance are used to identify regions of the genome being impacted by inbreeding. However, due to this being novel research, the level of significance is unknown and a significance level of 5×10^{-4} was used. Markers above the level of significance were considered strongly significant. Regions with clusters of significantly associated markers were then labeled as putative quantitative trait loci (QTL) and used to identify potential positional candidate genes within each trait.

Results and Discussion

The blue rectangles along the diagonal of the heatmap in Figure 1 are individuals plotted against themselves. The darkest blue rectangles above or below the diagonal line represent individual animals that are more related (higher IBD estimate). This was expected due to the inbreeding in the population. This was further supported by the results of the PCA analysis (Figure 2) where there was a tight cluster of points in the bottom right corner, which again was expected due to the inbreeding levels within the population.

Inbreeding ranges were 0 – 36%, 0 – 49%, and 0 – 29% and the average inbreeding was 12.6%, 12.3.0%, and 17.7% for F_{PED}, F_{G}, and F_{GPED}, respectively. The

average rate of change in inbreeding per year was 0.03% over 55 years (Figure 3). The reduction in the number of animal records between 1988 and 1992 is due to females from the line being used for outside research projects (i.e. Davis et al., 1998).

Forty-five regions were identified by ROH (Table 1), indicating that ROH analysis can be used to identify regions of the genome being impacted by inbreeding depression. Although the significance threshold from the regression analyses on the Manhattan plots is unknown due to the novelty of this research, there were 35 SNP across all 5 traits that were above 5×10^{-4}, and those were considered strongly significant SNP (Table 2). Birth weight had five strongly significant SNP (Figure 4), WW had four strongly significant SNP (Figure A1), YW had 11 strongly significant SNP (Figure A2), CE had three strongly significant SNP (Figure A3), and AFC had 12 strongly significant SNP (Figure A4). There was one strongly significant SNP that was strongly significant for BW, WW, CE, and AFC, two strongly significant SNP that were strongly significant for BW and CE, and one strongly significant SNP that was strongly significant for BW and YW. Areas of the chromosome with vertical clusters of markers were of interest as they suggested putative QTL in those regions.

For the significant SNP ($p < 0.005$) of each trait, previously identified genes and their functions were identified using Genome Build Bos taurus UMD 3.1.1 (Tables A1 – A5). Of the identified genes that could potentially be responsible for impaired traits seen with inbreeding depression, one gene was related to meat and growth traits, 10 were related to male and female fertility, and one was related to milk production.

Calcium channel, voltage-dependent, alpha-2/delta subunit 1 (*CACNA2D1*) has been previously identified to be related to meat and growth traits, such as backfat thickness (Yuan and Xu, 2011), average daily gain (Casas et al., 2001) and residual feed intake (Sherman et al., 2009). The current analysis highlighted *CACNA2D1* on chromosome 4 with five significant SNP (bp position 38,486,244 – 38,680,360) that were associated to changes seen in BW, CE, and AFC and for one significant SNP (bp position 38,435,198) associated to changes seen in WW. The five significant SNP for BW, CE, and AFC were located within a ROH (Figures 5, 8, and 9). This growth-related trait could be responsible for the depression in growth rate that has been associated with inbreeding depression (Burrow, 1993).

Five of the 10 traits related to impaired fertility associated with inbreeding depression were related to impaired male fertility. Wiebe et al. (2010) identified VRK serine/threonine kinase 1 (*VRKI*) in relation to loss of spermatogonia. The current analysis highlighted *VRKI* on chromosome 21 (bp position 63,286,443) and it was associated to changes seen in BW, YW, CE, and AFC. Yoshima et al. (1998) identified heat shock transcription factor 2 binding protein (*HSF2BP*) in relation to testis development, which the current analysis highlighted on chromosome 1 (bp position 146,433,117) in association to changes seen in WW and YW. Small ArfGAP2 (*SMAP2*) was identified by Funaki et al. (2013) in relation to spermiogenesis, which the current analysis highlighted in association to changes seen in WW on chromosome 3 (bp position 106,322,730); this was located within a ROH. Steroid 5 alpha-reductase 2 (*SRD5A2*) was identified by Zhao et al. (2012) in relation to semen quality. The current analysis

highlighted *SRD5A2* in association to changes seen in WW on chromosome 11 (bp position 14,362,410) and in AFC on chromosome 11 (bp position 14,391,315). Lastly, Miller et al. (2016) identified abhydrolase domain containing 2, acylglycerol lipase (*ABHD2*) in relation to sperm activation, which the current analysis highlighted on chromosome 21 (bp position 21,042,466) and associated it to changes seen in WW, YW, and AFC. Reduced male fertility is a result of inbreeding and inbred bulls have been found to have decreased fertility such as reduced sperm motility (Dorado et al., 2015) and semen concentration and number of spermatozoa (Maximini et al., 2011).

DEAD-box helicase 31 (*DDX31*) has been identified as being related to both spermatogenesis and embryogenesis (https://www.genecards.org/cgi-bin/carddisp.pl?gene=DDX31&keywords=ddx31). The current analysis highlighted *DDX31* in association to changes seen in WW on chromosome 11 (bp position 102,704,292). Santos-Biase et al. (2012) identified bone morphogenetic protein receptor type 2 (*BMPR2*) in relation to embryogenesis. In this analysis, *BMPR2* was highlighted in two significant SNP on chromosome 2 (bp positions 91,392,375 and 91,411,176) in association with changes seen in WW and YW. The two significant SNP were located within a ROH (Figures 6 and 7). Phosphoinositide kinase, FYVE-type zinc finger containing (*PIKFYVE*) was identified by Ikonomov et al. (2011) in relation to early embryonic development, which was highlighted in the current analysis for changes seen in WW and YW on chromosome 2 (bp position 97,003,581); this was located within a ROH (Figure 7). Araki et al. (2010) identified KIAA1324 like (*KIAA1324L*) in relation to embryonic development, which was highlighted in the current analysis for changes seen

in BW and CE on chromosome 4 (bp position 33,636,014). Ring finger protein 130 (*RNF130*) has been identified in relation to embryonic development (https://www.genecards.org/cgi-bin/carddisp.pl?gene=RNF130). The current analysis highlighted *RNF130* on chromosome 7 (bp position 1,140,600) in association to changes seen in WW. All of these genes are related to reduced fertility. Inbred cows produced a lower number of transferable embryos and higher rates of unfertilized oocytes (Bezdíček et al., 2014).

For milk production, leucine aminopeptidase 3 (*LAP3*) was previously identified by Zheng et al. (2011), which the current analysis highlighted in three significant SNP on chromosome 3 (bp position 38,599,667 – 38,599,993) for changes seen in WW. In dairy cows, McParland et al. (2007) found a decrease of 61.8 kg in milk yield for every 12.5% increase in inbreeding in Holsteins, while Pryce et al. (2014) found for every 1% increase in inbreeding in Holsteins there was a 0.73 kg and 0.63 kg decrease in fat and protein yield, respectively.

Using the National Center for Biotechnology Information Gene Search, the molecular functions of the previously identified genes that could potentially be responsible for impaired traits seen with inbreeding depression were identified. There are five genes that are transcription factors including *VRK1*, *HSF2BP*, *PIKFYVE*, *KIAA1324L*, and *RNF130*. These transcription factors regulate the expression of other genes related to immunity, fertility, and growth in this study. Many transcription factors have multiple targets that aren't typically tissue-specific (MacQuarrie et al., 2012). There are five genes associated with immune function including *CACNA2D1*, *SMAP2*, *ABHD2*,

BMPR2, and *RNF130*. These genes could be responsible for reduced viability that is seen with inbreeding depression. The following genes are related to either male or female fertility: *VRK1*, *HSF2BP*, *SMAP2*, *ABHD2*, *BMPR2*, *PIKFYVE*, *KIAA1324L*, and *RNF130.* The combination of all of these genes could be impacting the growth retardation, reduced breeding capacity, and reduced viability in these long-term linebred cattle.

Each trait had significant SNP located within ROH identified regions (Figure 5 – 9), further indicating there are regions of the genome being impacted by inbreeding. The highest number of significant SNP located within a ROH were for WW. Chromosome 2 had 41 significant SNP within a 102,569,771 bp ROH. Chromosome 5 had 30 significant SNP within a 49,322,821 bp ROH. Finally, chromosome 1 had 25 significant SNP within a 36,181,265 bp ROH (Table 2). Further research is warranted to expand the identified ROH regions to investigate the linkage blocks.

Conclusions

Forty-five regions across the genome are impacted by inbreeding resulting in inbreeding depression and thus reduced growth and fertility. Thirty-five strongly significant SNP were identified and five of those SNP were strongly significant across two to four traits. Three strongly significant SNP identified are located within ROH, suggesting increase in allele homozygosity contributing to inbreeding depression. Some of the significant SNP were located within 12 previously identified genes, some of which are transcription factors or associated with immune function. However, a large number of significant SNP have not previously been associated with a specific gene. This is the first

known research that has located regions of the genome that are potentially explaining phenotypic inbreeding depression. Work of this type has future applications to all species of livestock where inbreeding levels as a whole are rising in herds as a result of reproductive technology and poor breeding management. This research also has implications outside of agriculture in dealing with the impacts of inbreeding in wildlife conservation and captive breeding programs.

Table 1. Runs of homozygosity (ROH) locations and number of significant single nucleotide polymorphism (SNP) within a ROH for each trait in each location.

Chromosome	Base Pair Start Position	Base Pair End Position	BW[1]	WW[1]	YW[1]	CE[1]	AFC[1]
1	35,367,693	71,548,958	3	7	25	3	7
	76,522,594	117,403,970	0	3	5	0	0
2	6,889	102,576,660	0	21	21	0	1
	104,892,874	132,602,751	1	8	41	1	4
3	42,919,371	85,331,746	0	1	5	0	1
	68,968,701	109,858,507	1	6	1	1	13
4	37,986,985	74,266,771	8	9	0	8	16
5	3,012,267	52,335,088	2	2*	30	1	0
	58,067,406	74,602,216	0	2*	3	0	0
6	38,689,886	62,913,615	2	8	6	2	8
7	10,685,223	31,011,979	0	1	1	1	0
	36,127,497	78,120,462	2	5	0	0	2
8	20,855	19,917,570	0	0	8	0	0
	27,940,946	35,671,830	0	0	0	0	0
	25,423,164	29,962,998	0	0	0	0	0
9	36,960,364	37,708,677	0	0	0	0	0
	47,935,923	71,721,889	0	4	0	0	0
	89,877,827	99,366,446	0	0	0	0	0
	89,877,827	96,693,865	0	0	0	0	0
10	29,836,917	47,945,151	3	0	0	3	2
	44,481,175	44,859,207	0	0	0	0	0
	48,225,546	84,039,652	0	0	11	0	3
11	53,334,055	55,391,965	0	0	0	0	0
	53,334,055	97,186,523	0	3	1	0	2
12	9,574,292	53,009,331	12	7	1	10	11
13	21,849,615	77,022,083	0	8	3	0	0
14	25,003,338	78,245,176	0	11	4	2	2
15	49,076,839	84,130,311	3	0	4	2	17
	55,185,032	55,714,862	0	0	0	0	0
16	24,613,337	68,480,760	1	7	22	0	4
17	12,148,802	41,650,184	0	4	2	0	0
	51,692,889	72,038,421	0	0	0	2	0
18	27,769,678	48,719,962	18	8	3	11	11
19	28,804,007	34,864,734	0	5*	4*	0	0
	30,022,677	32,959,952	0	3*	1*	0	0

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

*SNP that fall within more than one ROH on the same chromosome

Table 1. Continued.

Chromosome	Base Pair Start Position	Base Pair End Position	BW[1]	WW[1]	YW[1]	CE[1]	AFC[1]
20	12,020,256	13,182,785	0	1	0	0	0
	34,904,622	71,992,748	4	0	0	4	0
22	32,693,879	34,734,049	1	0	0	1	0
	40,079,119	43,744,791	13	13	0	16	16
23	22,120,429	27,429,820	0	0	0	0	0
	19,778,282	21,380,914	0	0	0	0	0
27	25,972,753	43,378,976	1	0	3	1	0
28	6,376,480	17,758,273	0	0	0	0	0
	10,298,666	15,924,519	0	0	0	0	0
	24,280,257	42,928,473	0	0	0	0	0

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

[*]SNP that fall within more than one ROH on the same chromosome

Table 2. Strongly significant single nucleotide polymorphism (SNP; located above -log10(*p*-value) of 5 x 10^{-4}) on a Manhattan plot.

Trait[1]	Chromosome	Base Pair Position	ROH Overlap[2]
BW	4	35,183,415	
		35,558,998	
		36,533,621	
	12	49,123,661	X
	15	20,171,885	
WW	4	35,183,415	
		36,533,621	
	22	45,455,314	
		45,954,406	
YW	6	78,862,493	
		79,063,882	
	7	105,621,232	
		107,706,815	
		107,921,509	
	11	100,817,959	
	21	61,355,008	
		61,503,433	
		62,656,572	
		63,286,443	
		64,152,628	
CE	4	35,183,415	
		35,558,998	
	12	49,123,661	X
AFC	4	35,183,415	
		36,533,621	
	12	48,902,740	X
	15	3,061,918	
		3,078,493	
		3,369,565	
		3,462,006	
		6,938,962	
		6,962,261	
		7,728,537	
		7,944,599	
		9,125,948	

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

[2]ROH = runs of homozygosity

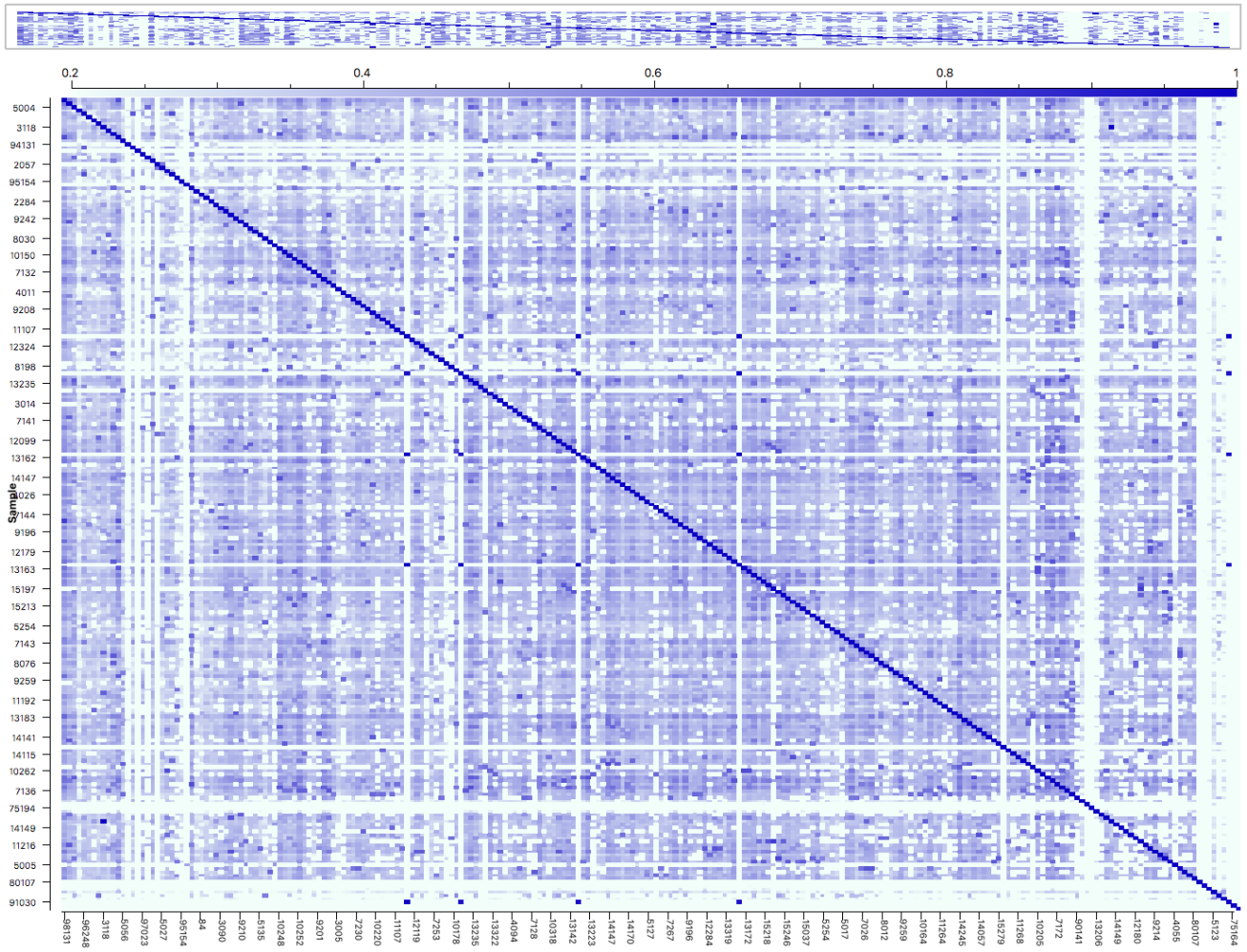


Figure 1. A heatmap showing relatedness of individuals within the Line 4 population. The dark blue diagonal line is individuals plotted against themselves and the darkest blue boxes above or below the diagonal represent individuals that are more related.

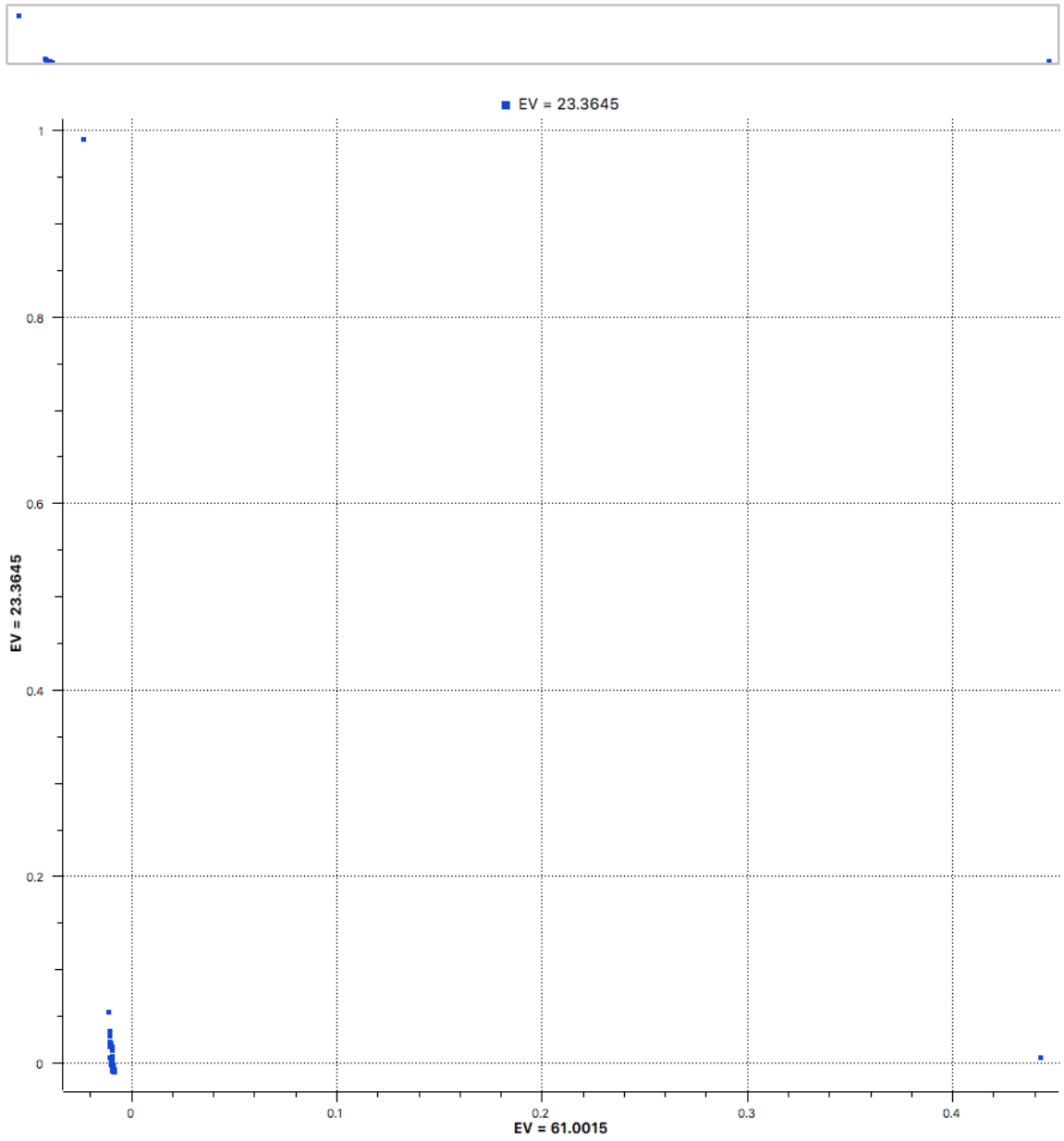


Figure 2. A principle component analysis (PCA) plot containing a scatter plot for individual animals on the first and second principle components.

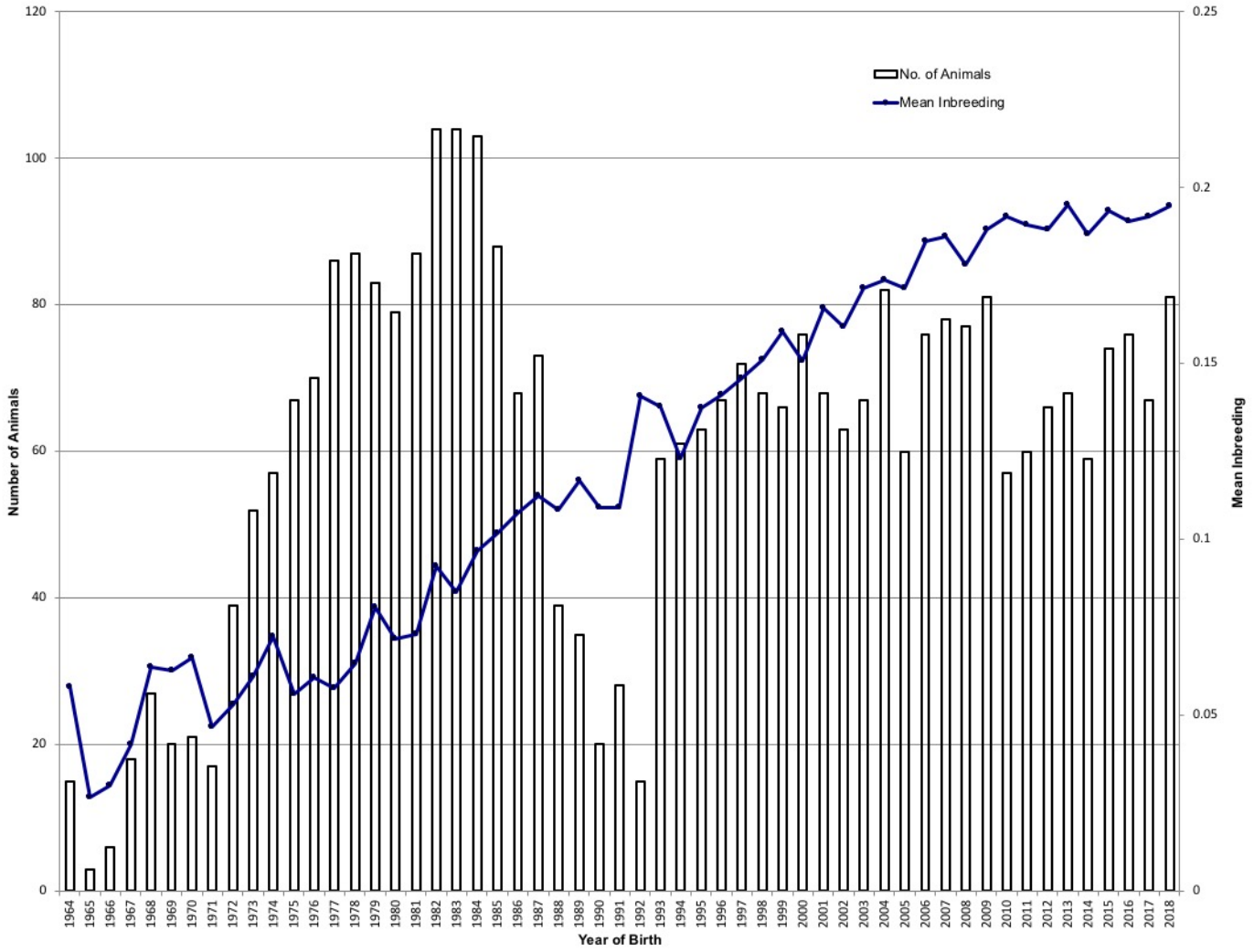


Figure 3. Number of animals by year of birth between 1964 and 2018, and trend of average pedigree inbreeding (blue line).

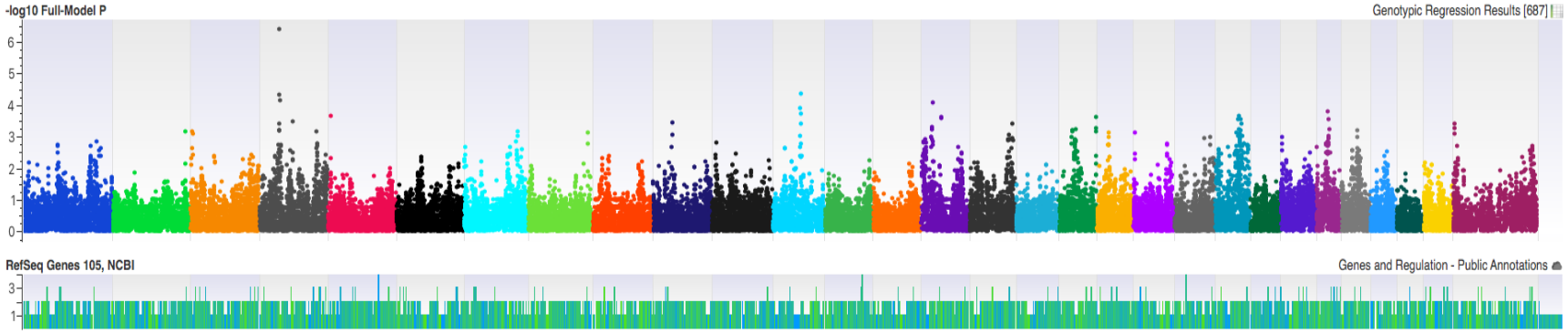


Figure 4. Manhattan plot for birth weight (BW). Genome-side significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

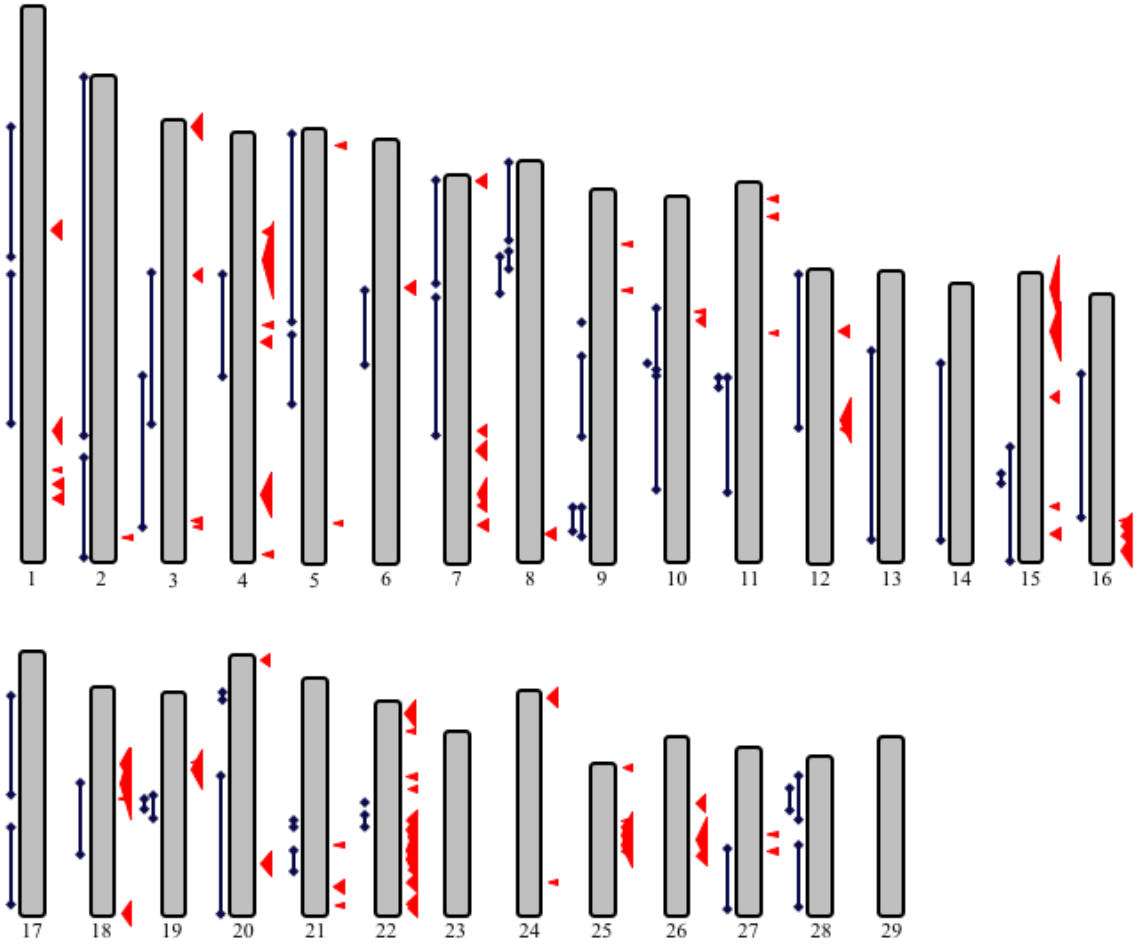


Figure 5. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines) and significant single nucleotide polymorphism (SNP; $p < 0.005$) for birth weight (BW) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

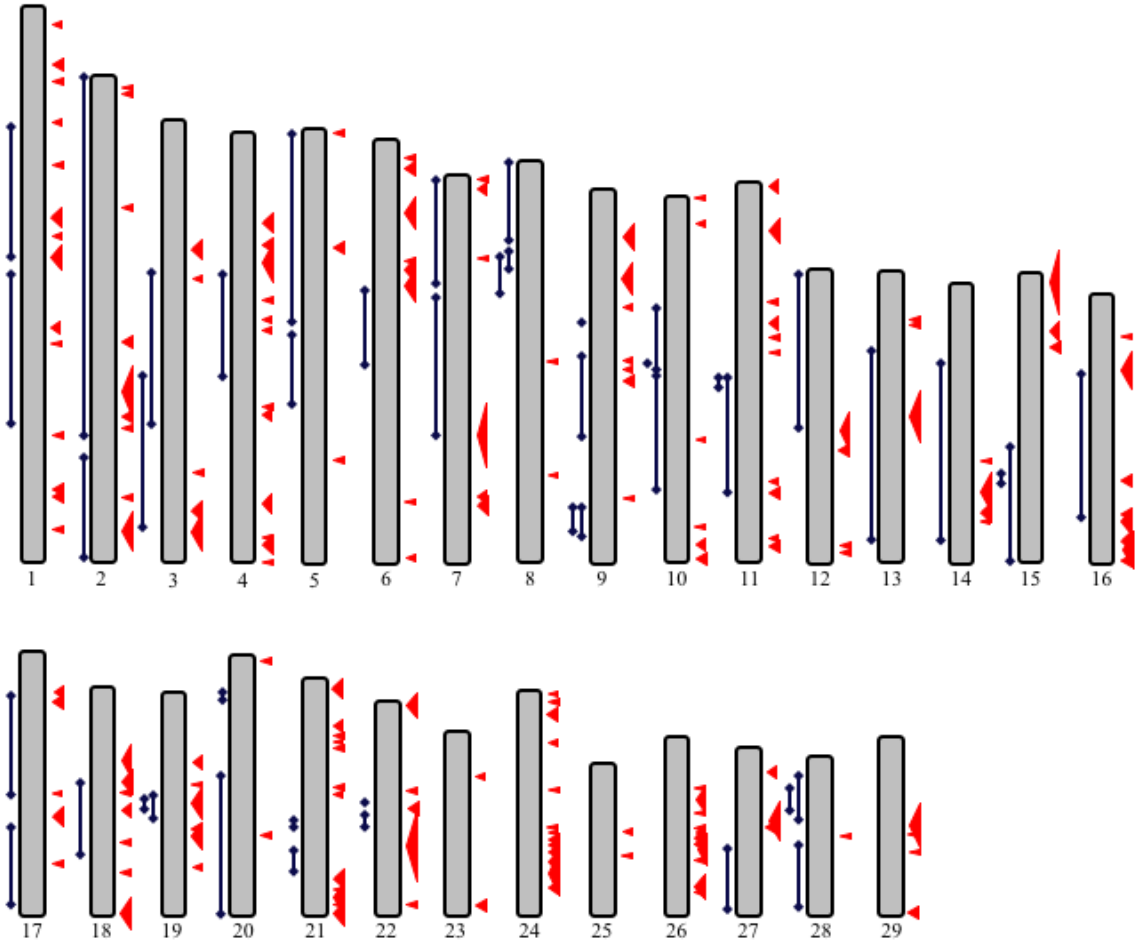


Figure 6. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines). Significant single nucleotide polymorphism (SNP; $p < 0.005$) for weaning weight (WW) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

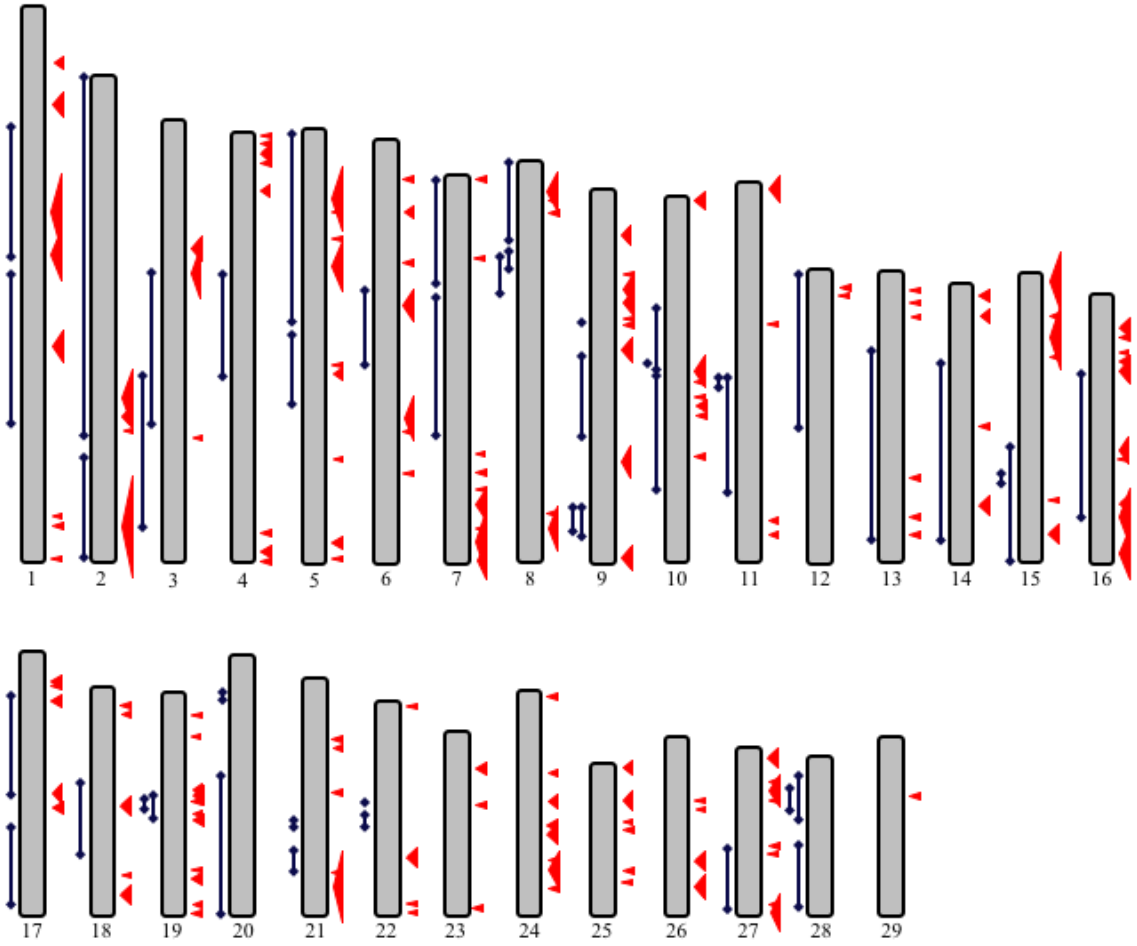


Figure 7. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines). Significant single nucleotide polymorphism (SNP; $p < 0.005$) for yearling weight (YW) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

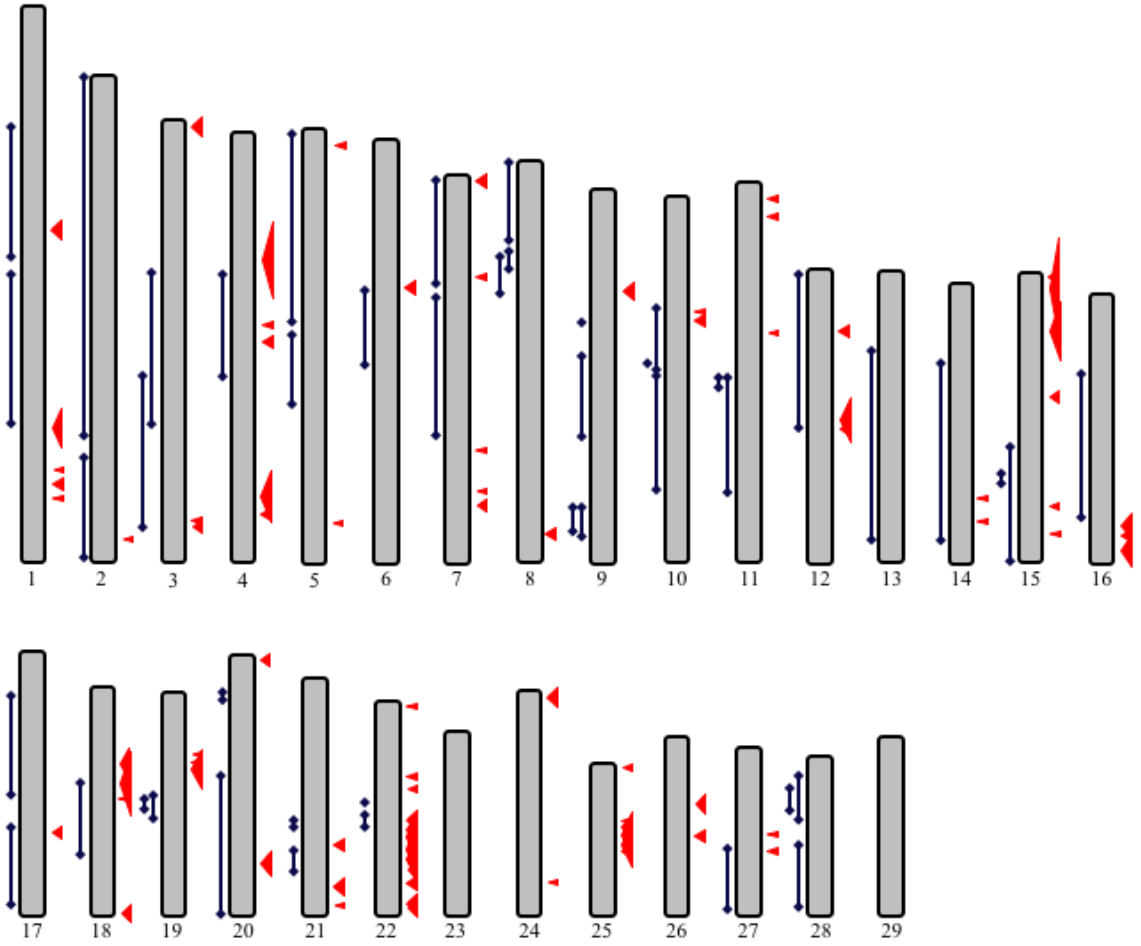


Figure 8. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines). Significant single nucleotide polymorphism (SNP; $p < 0.005$) for calving ease (CE) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

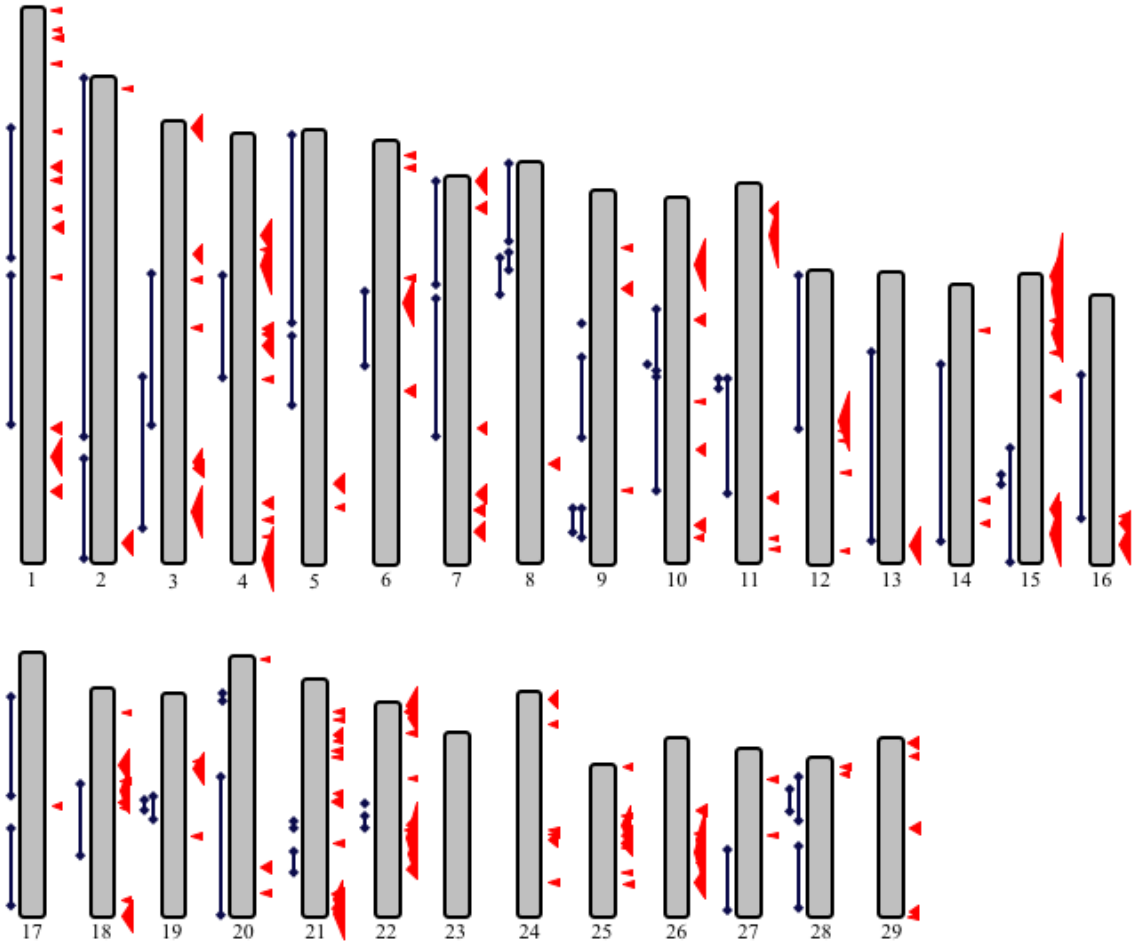


Figure 9. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines). Significant single nucleotide polymorphism (SNP; $p < 0.005$) for age at first calving (AFC) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

CHAPTER THREE

INBREEDING LEVELS OF THE LINE 1 HEREFORD CATTLE POPULATION

Introduction

Inbreeding is defined as the mating of animals that are more closely related than the average of the breed (Brinks and Knapp, 1975; Northcutt et al., 2004). Inbreeding often results in inbreeding depression, or the decline in average phenotypic performance, and its impacts have been well documented including reduced performance, reproduction, and profitability (MacNeil et al., 1989; Burrow, 1993).

Inbreeding is increasing in the beef cattle industry due to increased use of artificial insemination (AI) and embryo transfer (ET; Granleese et al., 2015). There is currently a lack of understanding of the molecular mechanisms involved in inbreeding depression. Pearl (1913; 1915) was the first to develop an inbreeding coefficient, which is now of historical interest only. It was later refined by Wright in 1921 (Lush, 1948), but to date the molecular basis has not been established. Long-term linebred populations, such as the Line 1 Hereford population, offer a unique opportunity to increase the understanding of the molecular consequence of inbreeding (Rumph et al., 2005). The hypothesis of this work is to determine if a combination of runs of homozygosity (ROH) analysis and genome-wide association can be used to identify regions of the genome associated with inbreeding depression. The specific objectives of this chapter were to: 1) understand the effect of individual and maternal inbreeding on growth and maternal traits in the Line 1 Hereford cattle population and 2) utilize high density genotyping data to

identify candidate markers and genes associated with performance decline due to inbreeding.

Materials and Methods

This study used data compiled over several years and did not directly use individual animals. The animals were cared for under a standard operating procedure at the Agriculture Research Service (ARS) Livestock and Range Research Laboratory (LARRL).

Data used in this study were from the Line 1 Hereford population maintained at the United States Department of Agriculture (USDA) – LARRL near Miles City, MT. Line 1 was developed in 1934 when two sons of Advance Domino 13, Advance Domino 20 and Advance Domino 54, were purchased from Fred C. DeBegrard of Kremmling, CO (MacNeil, 2009; Durham, 2010). The two sons were then bred to 50 cows purchased from George M. Miles of Miles City, MT, followed by daughters of Advance Domino 20 being bred to Advance Domino 54 and vice versa (Durham, 2010). Line 1 closed in 1935 and all animals are descendants of those foundation animals (MacNeil, 2009).

The increase in inbreeding per generation that is normally seen in line-bred animals has been reduced in this population as the line's numbers has increased and mating closely related individuals has been avoided. In the 1930s, the Line 1 Herefords were used for research focusing on methods of measuring performance of beef cattle, including progeny testing. The implied breeding objective of the line was economic return above feed costs that came from steer carcasses slaughtered at a live weight of 408 kg (MacNeil, 2009). In the 1940s, the advancement of feeding trial testing procedures

became the focus of the research, which drove the decision to base future Line 1 sire selection on growth to one year of age (MacNeil, 2009).

Pedigree and phenotypic information consisted of phenotype data collected from 1978 – 2016 at USDA – LARRL, from the American Hereford Association Herdbook, and from breeding records dating back to the origin of the line. A pedigree containing 10,680 animals was constructed covering 1926 – 2016, and the following traits were used in this study: birth weight (BW), weaning weight (WW), yearling weight (YW), calving ease (CE), and age at first calving (AFC). Six hundred and seventy-one samples were genotyped. Genotypes were originally genotyped on a variety of single nucleotide polymorphism (SNP) density panels and then imputed to a common 30K SNP panel.

Inbreeding was estimated using a complete pedigree (F_{PED}; PedScope, version 2.5.01ms) and genomic information. Genomic inbreeding (F_G) and pedigree inbreeding (F_{GPED}) were evaluated for 664 genotyped animals, because the identity of six animals could not be verified. Genomic inbreeding coefficients were calculated in Golden Helix SVS software (version 8.7.2-2017-08-11) using Wright's within-subpopulation fixation index and genomic pedigree inbreeding was calculated by taking the pedigree inbreeding values for the genotyped animals from F_{PED} analysis. Average rate of change in inbreeding per year was also evaluated by using the F_{PED} results and manually averaging the inbreeding for each year of birth. Runs of homozygosity analysis was performed in Golden Helix SVS software (v8.8.3) and ROH were defined as a minimum run length of 2,500 kb with a minimum of 250 SNP appearing in 20 samples. This scans the genome with a sliding window of 2,500 kb looking for a minimum of 250 consecutive

homozygous SNP. Regions of the genome with increased homozygosity potentially contributes to inbreeding depression as the size and density of blocks of homozygosity increase with inbreeding depression.

The ROH parameters set are considered short ROH. Ferenčaković et al. (2011) indicate that ROH that are less than one megabase (Mb) are a result of ancient inbreeding. Furthermore, Zhang et al. (2015) found that short ROH regions were shared between all individuals in their cattle population, confirming that short ROH were selected and derived from ancient haplotypes that became fixed in their population. The significant correlation between shared ROH regions and regions consistently passed down from generation to generation with selection suggests that some of the short ROH are a result of both inbreeding and selection. Rather than ROH regions being scattered among the genome, there are regions with dense-ROH peaks that are consistent across individuals (Zhang et al. 2015). When more conventional ROH parameters were used, essentially the whole genome was identified as being homozygous. Due to the goal of identifying regions of the genome that are being impacted by inbreeding depression in the current study, the ROH parameters were adjusted to identify the most consistent and most dense regions of homozygosity. This allowed regions of the genome that could be impacting phenotype to be better pinpointed.

For each trait, expected phenotypes were calculated by adjusting each animal's individual phenotype with the published negative impact of inbreeding depression using the animal's own inbreeding coefficient. Regression values were based upon previous research (Smith et al., 1989; Burrow, 1993; Hinrichs and Thaller, 2011). For every 1%

increase in inbreeding, the review done by Burrow (1993) found BW decreased by 0.06 kg, WW decreased by 0.44 kg, and YW decreased by 0.69 kg, while Hinrichs and Thaller (2011) found CE decreased by 0.1, and Smith et al. (1989) found AFC increased by 0.209 days. The difference between expected phenotype and reported phenotypes was used as a variable in the analysis.

Genotype data quality control was done through SNP filtering (Golden Helix, 2019). First, samples were removed if they had a call rate ≤ 0.95 indicating reduced DNA quality. Data were then pruned to remove markers in linkage disequilibrium. Quality control of markers excluded SNP with spurious position, low call rates (< 90%), a heterozygous deviation > 20% from Hardy-Weinberg equilibrium, or less than 5% minor allele frequency (MAF). This left 10,054 out of 30,815 markers in the downstream analysis.

Samples were then filtered to determine relatedness. An identity by descent (IBD) relationship matrix was created to correct the association analysis for genomic relationship amongst samples and a heatmap was produced. Principal component analysis (PCA) was used to account for cryptic relatedness and the first three eigen vectors represented greater than 55% of the stratification of the SNP data. Calculated relatedness between individuals was used as a covariate in the association analysis.

A regression association analysis in Golden Helix SVS software (Golden Helix, version 8.7.2-2017-08-11) was used on the genotype data while correcting for cryptic relatedness and pedigree structure and then used to generate Manhattan plots. Bonferroni multiple comparison corrections and false discovery rate were used to minimize false-

positive associations. Traditionally, a genome-wide significance level with -log10(*p*-value) is 5 x 10^{-8} (Ehret, 2010) and markers above the level of significance are used to identify regions of the genome being impacted by inbreeding. However, due to this being novel research, the level of significance is unknown and a significance level of (5 x 10^{-4}) was used. Markers above the level of significance were considered strongly significant. Regions with clusters of significantly associated markers were then labeled as putative quantitative trait loci (QTL) and used to identify potential positional candidate genes within each trait.

Results and Discussion

The blue rectangles along the diagonal of the heatmap in Figure 10 are individuals plotted against themselves. The darkest blue rectangles above or below the diagonal line represent individual animals that are more related (higher IBD estimate). More dark blue saturation above or below the diagonal line was expected due to the long-term linebreeding that has occurred over many years in this population. This was further supported by the results of the PCA analysis (Figure 11) where there were different clusters that created a triangle-like shape rather than a tight cluster of points in one location.

Inbreeding ranges were 0 – 71%, 0 – 46%, and 0 – 63% and the average inbreeding was 42.1%, 14.4%, and 31.0% for F_{PED}, F_{G}, and F_{GPED}, respectively. The average rate of change in inbreeding per year was -0.03% over 83 years (Figure 12). There was a sharp decline in average rate of change in inbreeding per year between 1994 and 1996. Two bulls with an inbreeding coefficient of zero appear in the pedigree in 1994

and their first calves appear in 1996. This outcross explains the reduced average rate of change in inbreeding per year from 1999 – 2013.

Fifty regions were identified by ROH (Table 3), indicating that ROH analysis can be used to identify regions of the genome being impacted by inbreeding depression. Although the significance threshold from the regression analyses on the Manhattan plots is unknown due to the novelty of this research, there were 93 SNP across all 5 traits that were above (5×10^{-4}), and those were considered strongly significant SNP (Table 4). Birth weight had 22 strongly significant SNP (Figure 13), WW had 23 strongly significant SNP (Figure B1), YW had 22 strongly significant SNP (Figure B2), CE had 25 strongly significant SNP (Figure B3), and AFC had one strongly significant SNP (Figure B4). There were 18 strongly significant SNP that were strongly significant for BW, WW, YW, and CE, three strongly significant SNP that were strongly significant for BW, WW, and YW, one strongly significant SNP that was strongly significant for WW and CE, and one strongly significant SNP that was strongly significant for BW, and YW. Areas of the chromosome with vertical clusters of markers were of interest as they suggested putative QTL in those regions.

For the significant SNP ($p < 0.005$) of each trait, previously identified genes and their functions were identified using Genome Build Bos taurus UMD 3.1.1 (Tables B1 – B5). Of the identified genes that could potentially be responsible for impaired traits seen with inbreeding depression, two genes were related to carcass and meat quality traits, eight were related to male and female fertility, and one was related to meat, fertility, and milk production.

Changes seen in BW, WW, YW, and CE were highlighted on chromosome 3 (bp position 1,937,626), chromosome 4 (bp positions 33,599,874 and 114,744,308), chromosome 5 (bp position 110,014,606), chromosome 8 (bp position 25,133,019), chromosome 11 (bp position 45,584,828), chromosome 14 (bp position 76,043,148), and chromosome 19 (bp position 33,450,891; also a ROH was identified here). This analysis identified a significant SNP on chromosome 3 (bp position 1,937,626) that Soper et al. (2010) previously identified as maelstrom spermatogenic transposon silencer (*MAEL*) related to reduced spermatogenesis. The analysis presented here also identified a significant SNP on chromosome 4 (bp position 33,599,874) that Araki et al. (2010) previously identified as KIAA1324 like (*KIAA1324L*) and related to embryonic development. Furthermore, a significant SNP was identified on chromosome 4 (bp position 114,744,308) that Wertz and Herrmann (2000) previously identified as WD repeat domain 86 (*WDR86*) and related to gonad development. The current analysis identified a significant SNP on chromosome 5 (bp position 110,014,606) which Okuma et al. (2011) previously identified as galectin 1 (*LGALS1*), expressed during luteal phase and early pregnancy. The current analysis also identified a significant SNP on chromosome 8 (bp position 25,133,019) where perilipin 2 (*PLIN2*) was previously identified by Cheong et al. (2009) in relation to marbling (MARB), by Darwich et al. (2014) in relation to embryo viability, and by Nielsen et al. (1999) in relation to milk fat production. This analysis identified a significant SNP on chromosome 11 (bp position 45,584,828) that was previously identified by Hwang and Horvitz (2002) as UDP-glucuronate decarboxylase 1 (*UXS1*) and related to embryonic development. A

significant SNP on chromosome 14 (bp position 76,043,148) identified in this study was previously identified by Marques et al. (2009) as 2,4-dienoyl-CoA reductase (*DECR1*) and related to ultrasound backfat. Lastly, the current study identified a significant SNP on chromosome 19 (bp position 33,450,891) that was previously identified as Tektin 3 (*TEKT3*) by Golas et al. (2008) in relation to sperm quality and by Roy et al. (2008) in relation to sperm motility.

Changes seen in BW, WW, and YW were highlighted on chromosome 5 (bp position 112,686,649) and chromosome 17 (bp position 71,081,308). This study identified a significant SNP on chromosome 5 (bp position 112,686,649) that was previously identified as ring-box 1 (*RBX1*) by Tan et al. (2009) and they related it to early embryonic death. Further, a significant SNP was identified on chromosome 17 (bp position 71,081,308) that Lin and Wolfner (1989) previously identified as activating signal cointegrator 1 complex subunit 2 (*ASCC2*) in relation to initiation of embryogenesis.

Changes seen in CE were highlighted on chromosome 7 (bp position 98,566,391). This analysis identified a significant SNP in that position that had been previously identified by Schenkel et al. (2006) as calpastatin (*CAST*) to be related to carcass and meat quality traits, including fat and lean yield, hot carcass weight, and ribeye area.

Several of the significant SNP identified have been previously identified as genes related to male and female reproduction and fertility traits. Reduced male fertility results from inbreeding and inbred bulls has been found to have reduced sperm motility (Dorado et al., 2015) and semen concentration and number of spermatozoa (Maximini et al.,

2011). Reduced fertility has also been studied in inbred cows and it has been found that inbred females produce a lower number of transferable embryos and higher rates of unfertilized oocytes (Bezdíček et al., 2014). A few of the significant SNP identified have been previously identified as genes related to carcass and meat traits. Inbreeding depression has little to no effect on carcass traits (Northcutt et al., 2004), however some decreased carcass traits could be a result of decreased growth. Carcass and meat quality traits could be impacted by depressed growth rate associated with inbreeding depression (Burrow, 1993). There was one gene that was identified as a significant SNP in the current study that was linked to milk production. The effects of inbreeding on milk production has been studied in dairy cows; specifically, Pryce et al. (2014) found for every 1% increase in inbreeding there was a 0.73 kg decrease in milk fat yield in Holsteins.

Using the National Center for Biotechnology Information Gene Search, the molecular functions of the previously identified genes that could potentially be responsible for impaired traits seen with inbreeding depression were identified. There are two genes that are transcription factors including *KIAA1324L* and *ASCC2*. These transcription factors regulate the expression of other genes related to immunity, fertility, and growth in this study. Many transcription factors have multiple targets that aren't typically tissue-specific (MacQuarrie et al., 2012). There are three genes associated to immune function including *MAEL*, *LGALS1*, and *RBX1*. These genes could be responsible for reduced viability that is seen with inbreeding depression. The following genes are related to either male or female fertility: *MAEL*, *KIAA1324L, LGALS1*, *RBX1*,

and *ASCC2*. The combination of all of these genes could be impacting the growth retardation, reduced breeding capacity, and reduced viability in these long-term linebred cattle.

Each trait had significant SNP located within ROH identified regions (Figure 14 – 18), further indicating there are regions of the genome being impacted by inbreeding. The highest number of significant SNP were located within ROH for chromosome 2. Birth weight, WW, and YW each had seven significant SNP within a 60,192,869 bp ROH (Table 4). Further research is warranted to further identify the relation of inbreeding depression and heterosis physiology on chromosome 2 and to expand the identified ROH regions to investigate the linkage blocks.

Conclusions

Fifty regions across the genome are impacted by inbreeding depression resulting in inbreeding depression and thus reduced growth and fertility. Ninety-three strongly significant SNP were identified and 23 of those SNP were strongly significant across two to four traits. Three strongly significant SNP identified are located within ROH suggesting increase in allele homozygosity contributed to inbreeding depression. Some of the significant SNP were located within 11 previously identified genes, some of which are transcription factors or associated to immune function. However, a large number of significant SNP identified have not previously been associated with a specific gene. This is the first known research that has located regions of the genome that are potentially explaining phenotypic inbreeding depression. This type of work has potential application to all livestock species where inbreeding is rising due to poor breeding management and

reproductive technology. There are also implications outside of agriculture in wildlife conservation and captive breeding programs and the impacts of inbreeding found with both.

Table 3. Runs of homozygosity (ROH) locations and number of significant single nucleotide polymorphism (SNP) within a ROH for each trait in each location.

Chromosome	Base Pair Start Position	Base Pair End Position	BW[1]	WW[1]	YW[1]	CE[1]	AFC[1]
1	45,157,959	45,614,604	0	0	0	0	0
	107,573,707	161,021,443	3	3	3	4	1
2	39,350,058	99,542,927	7	7	7	5	0
	102,772,529	104,637,671	0	0	0	1	0
3	63,672,814	64,493,554	0	0	0	0	0
	89,233,653	92,175,867	0	0	0	0	0
4	38,257,758	38,548,833	0	0	0	0	0
	67,222,038	67,615,775	1	1	1	1	0
5	11,284,482	18,075,032	1	1	1	1	0
	66,157,408	69,276,358	0	0	0	0	0
6	9,524,226	16,898,895	0	0	0	0	0
	63,137,386	64,059,795	0	0	0	0	0
7	46,981,340	49,104,721	0	0	0	0	0
	77,038,018	82,088,459	1	1	1	1	1
8	25,997,609	26,062,021	0	0	0	0	0
	60,192,438	65,107,050	0	0	0	0	0
9	16,142,291	27,797,201	0	0	0	0	1
	41,989,065	57,536,880	0	0	0	0	0
10	32,485,711	37,995,157	0	0	0	0	0
	61,769,231	63,836,108	0	0	0	0	0
11	14,947,290	20,061,567	0	0	0	0	0
	52,045,971	63,467,507	0	0	0	0	0
12	23,874,869	24,668,970	0	0	0	0	0
	50,451,289	55,333,531	0	0	0	0	0
13	36,197,476	37,429,612	0	0	0	0	0
	47,990,990	63,204,278	1	1	1	0	0
14	22,587,081	23,100,717	0	0	0	0	0
	54,356,138	56,379,138	1	1	1	1	0
15	22,840,299	28,223,909	0	0	0	0	0
	44,584,661	55,488,319	0	0	0	0	0
16	28,644,553	32,458,840	0	0	0	0	0
	51,095,203	60,009,076	0	0	0	0	1
17	22,857,773	24,848,457	0	0	0	0	0
	50,194,955	58,821,993	0	0	0	0	0
18	12,675,262	22,889,138	0	0	0	0	0
	35,388,791	48,241,428	3	3	3	4	0

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

[*]SNP that fall within more than one ROH on the same chromosome

Table 3. Continued.

Chromosome	Base Pair Start Position	Base Pair End Position	BW[1]	WW[1]	YW[1]	CE[1]	AFC[1]
19	22,367,761	39,879,398	2	2	2	2	0
	36,992,354	54,880,876	0	0	0	0	2
20	35,102,203	45,225,619	0	0	0	0	0
	52,124,199	59,070,717	3	3	3	5	1
21	12,051,183	27,296,213	3	3	3	1	1
	38,191,506	48,509,940	4	3	4	1	0
22	21,164,077	33,245,588	2	2	2	1	0
	35,771,697	55,988,937	0	0	0	0	0
24	12,415,668	30,206,723	0	0	0	1*	0
	28,691,752	41,644,404	1	1	1	1*	0
26	7,932,648	20,332,013	2*	2*	2*	3*	0
	18,193,246	32,716,808	2*	2*	2*	2*	0
29	7,276,898	22,380,350	2	2	2	2	1
	22,876,174	33,770,541	0	0	0	0	0

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

*SNP that fall within more than one ROH on the same chromosome

Table 4. Strongly significant single nucleotide polymorphism (SNP; located above -log10(p-value) of 5 x 10^{-4}) on a Manhattan plot.

Trait[1]	Chromosome	Base Pair Position	ROH Overlap[2]
BW	1	90,283,892	
		96,677,750	
	3	1,267,869	
		13,080,516	
		115,659,306	
	5	28,120,980	
		55,263,796	
		57,404,217	
		104,714,350	
	8	66,785,437	
		102,920,161	
	11	37,876,375	
		48,425,269	
	14	12,247,110	
		51,811,945	
		76,043,148	
	17	38,001,105	
	19	8,770,836	
	21	26,181,772	X
	26	1,065,894	
		49,366,950	
	27	14,173,400	
WW	1	90,283,892	
		96,677,750	
	3	1,267,869	
		13,080,516	
		115,659,306	
	5	28,120,980	
		30,960,699	
		55,263,796	
		57,404,217	
		104,714,350	
	8	66,785,437	
		102,920,161	
	11	37,876,375	
		48,425,269	
	14	12,247,110	
		51,811,945	

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

[2]ROH = runs of homozygosity

Table 4. Continued.

Trait[1]	Chromosome	Base Pair Position	ROH Overlap
WW	14	76,043,148	
	15	67,981,902	
	17	38,001,105	
	19	8,770,836	
	21	26,181,772	X
	26	1,065,894	
		49,366,950	
YW	1	90,283,892	
		96,677,750	
	3	1,267,869	
		13,080,516	
		115,659,306	
	5	28,120,980	
		55,263,796	
		57,404,217	
		104,714,350	
	8	66,785,437	
		102,920,161	
	11	37,876,375	
		48,425,269	
	14	12,247,110	
		51,811,945	
		76,043,148	
	17	38,001,105	
	19	8,770,836	
	21	26,181,772	X
	26	1,065,894	
		49,366,950	
	27	14,173,400	
CE	1	90,283,892	
		96,677,750	
	2	135,190,642	
	3	1,267,869	
		13,080,516	
		115,659,306	
	4	90,847,252	
	5	28,120,980	
		30,960,699	

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

[2]ROH = runs of homozygosity

Table 4. Continued.

Trait[1]	Chromosome	Base Pair Position	ROH Overlap
CE	5	55,263,796	
		57,404,217	
		101,124,171	
		104,714,350	
	8	102,920,161	
	10	99,330,554	
	11	37,876,375	
		48,425,269	
	14	3,484,849	
		51,811,945	
		76,043,148	
	17	38,001,105	
	19	8,770,836	
	25	4,779,974	
	26	1,065,894	
		49,366,950	
AFC	5	1,087,211	

[1]BW = birth weight; WW = weaning weight; YW = yearling weight; CE = calving ease; AFC = age at first calving

[2]ROH = runs of homozygosity

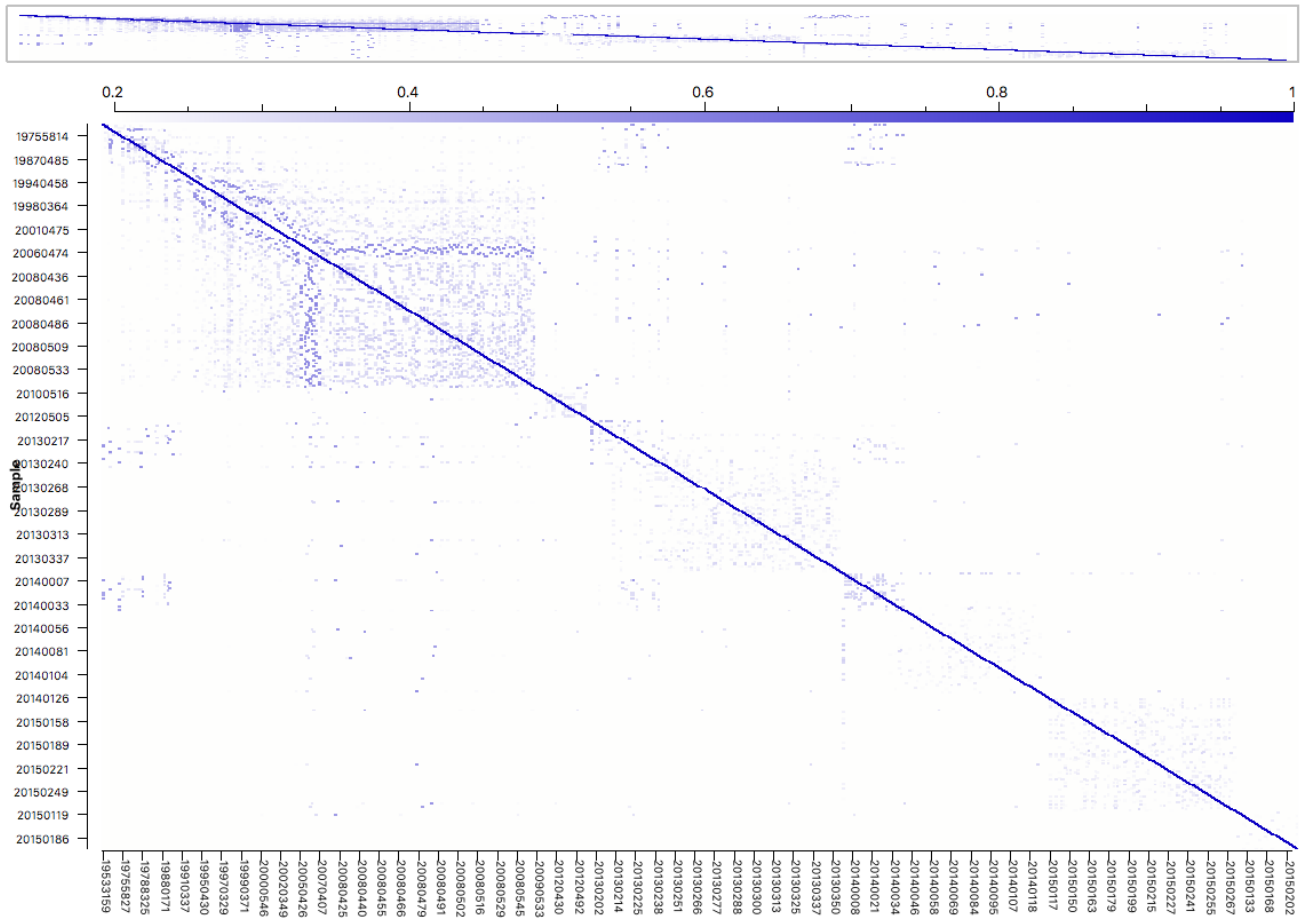


Figure 10. A heatmap showing relatedness of individuals within the Line 1 population. The dark blue diagonal line is individuals plotted against themselves and the darkest blue boxes above or below the diagonal represent individuals that are more related.

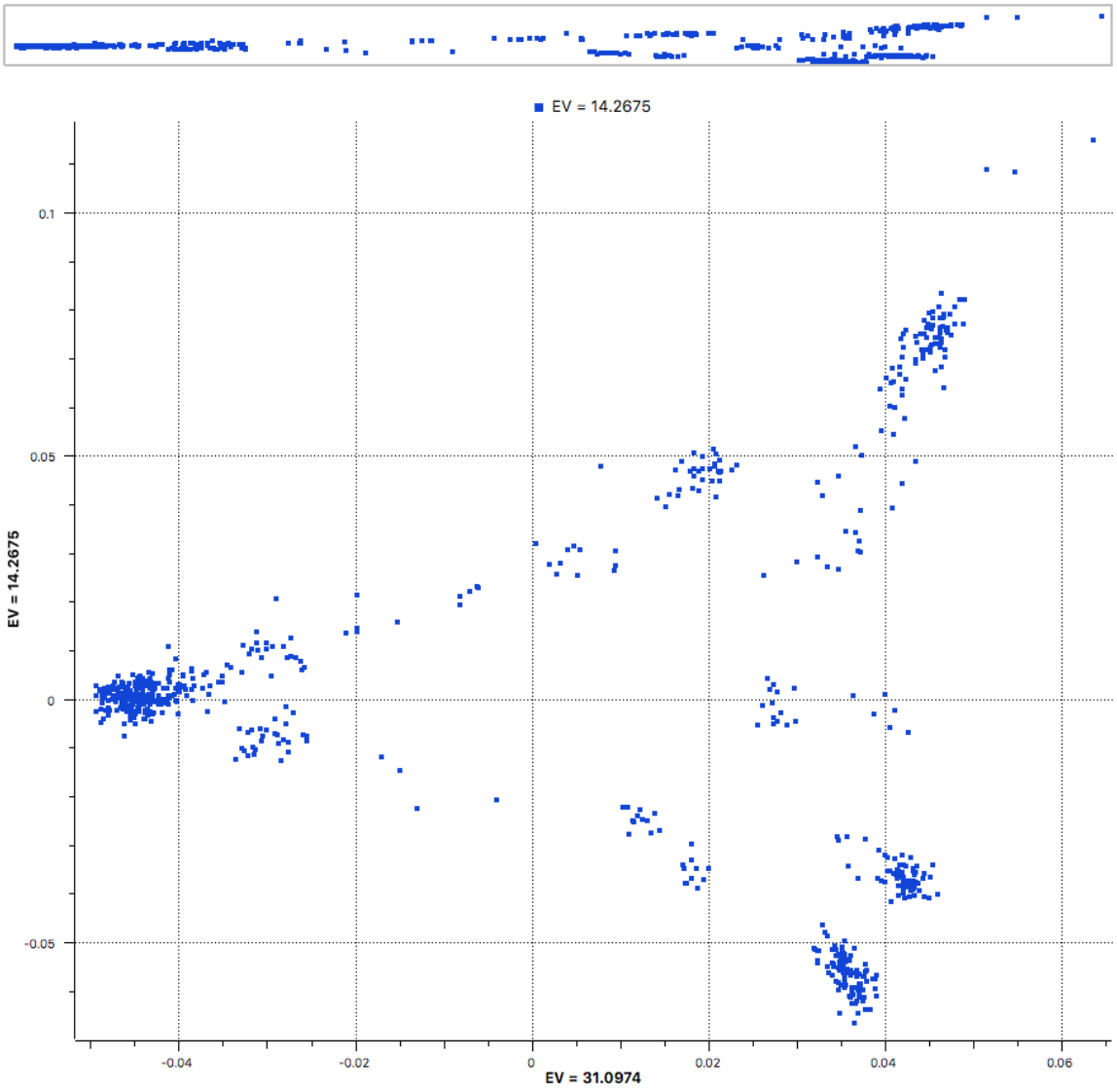


Figure 11. A principle component analysis (PCA) plot containing a scatter plot for individual animals on the first and second principle components.

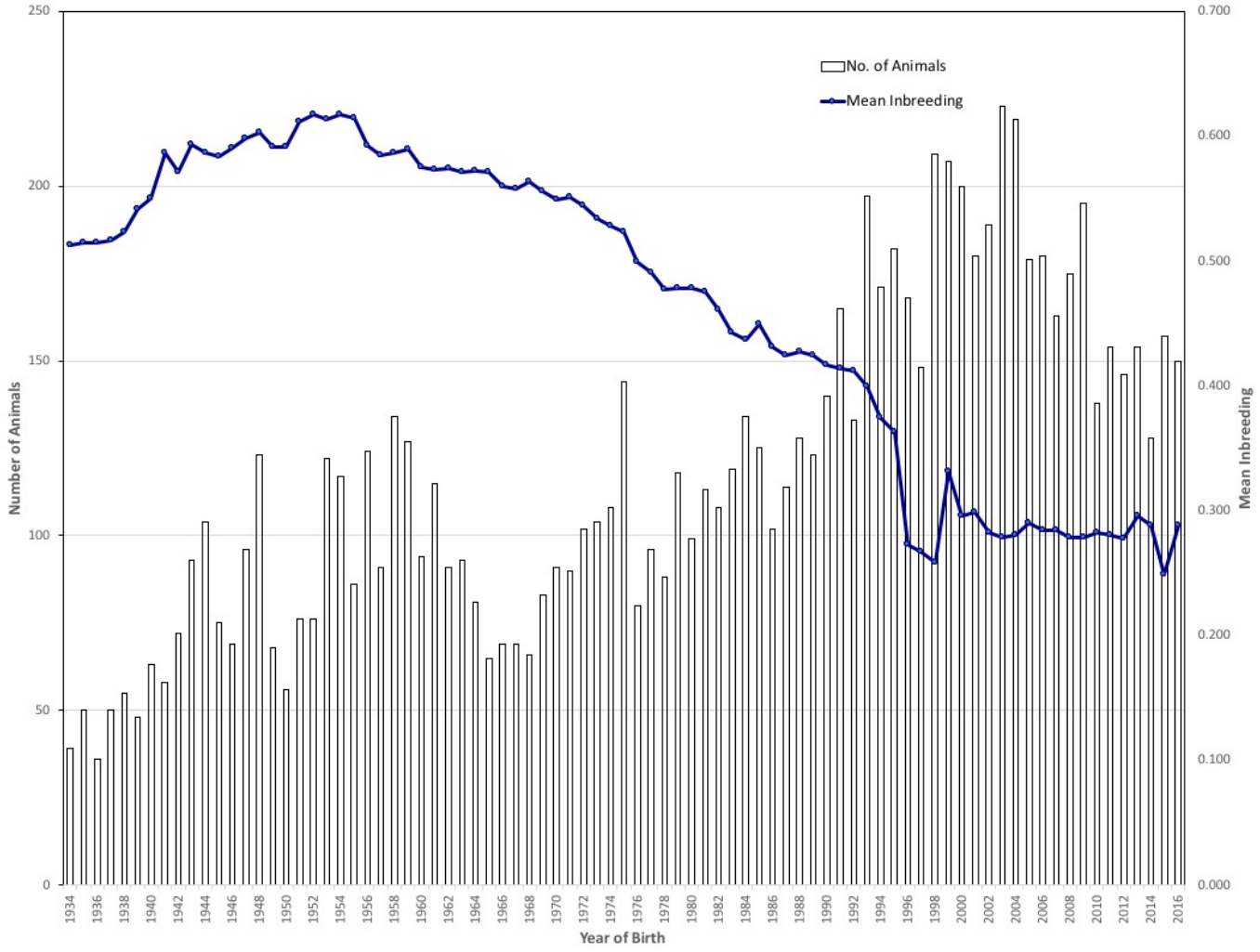


Figure 12. Number of animals by year of birth between 1934 and 2016, and trend of average pedigree inbreeding (blue line).

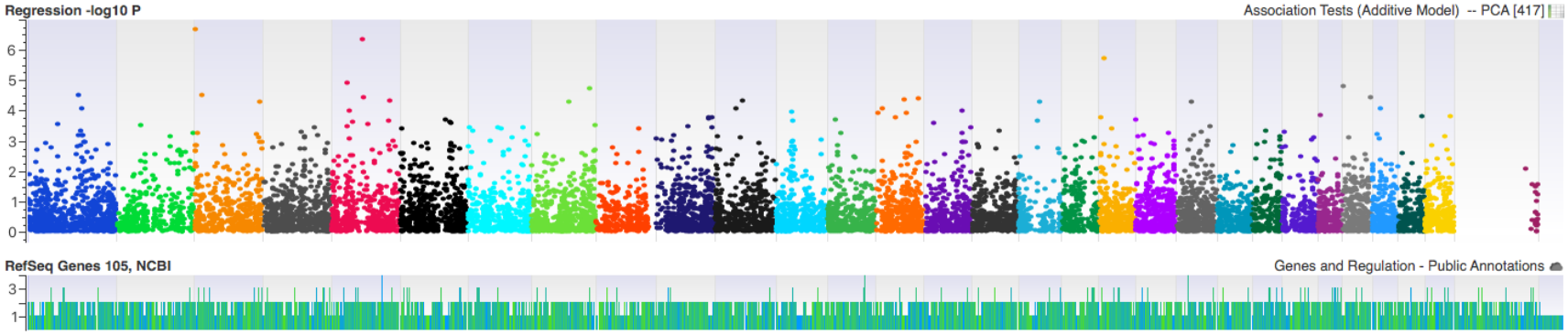


Figure 13. Manhattan plot for birth weight (BW). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-5} and vertical clusters of markers indicate suggestive QTL.

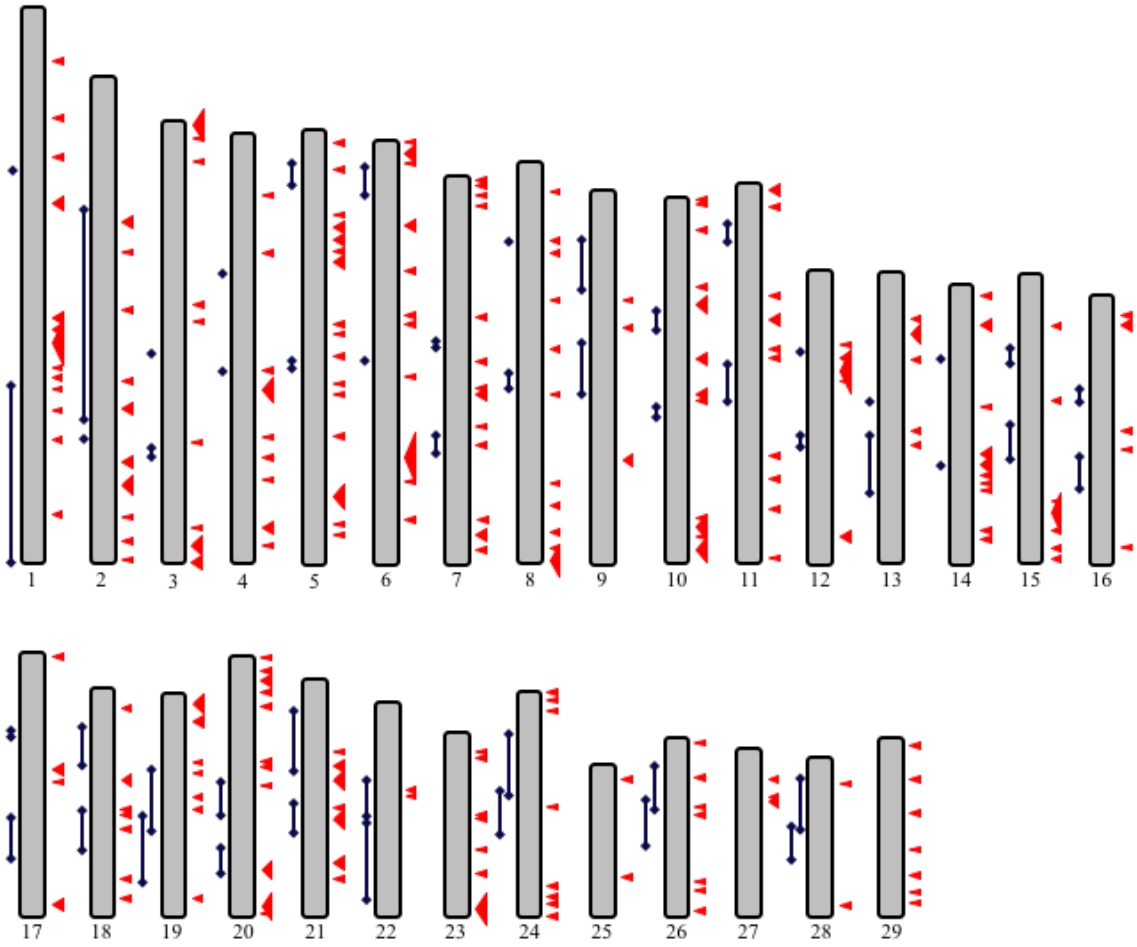


Figure 14. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines) and significant single nucleotide polymorphism (SNP; $p < 0.005$) for birth weight (BW) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

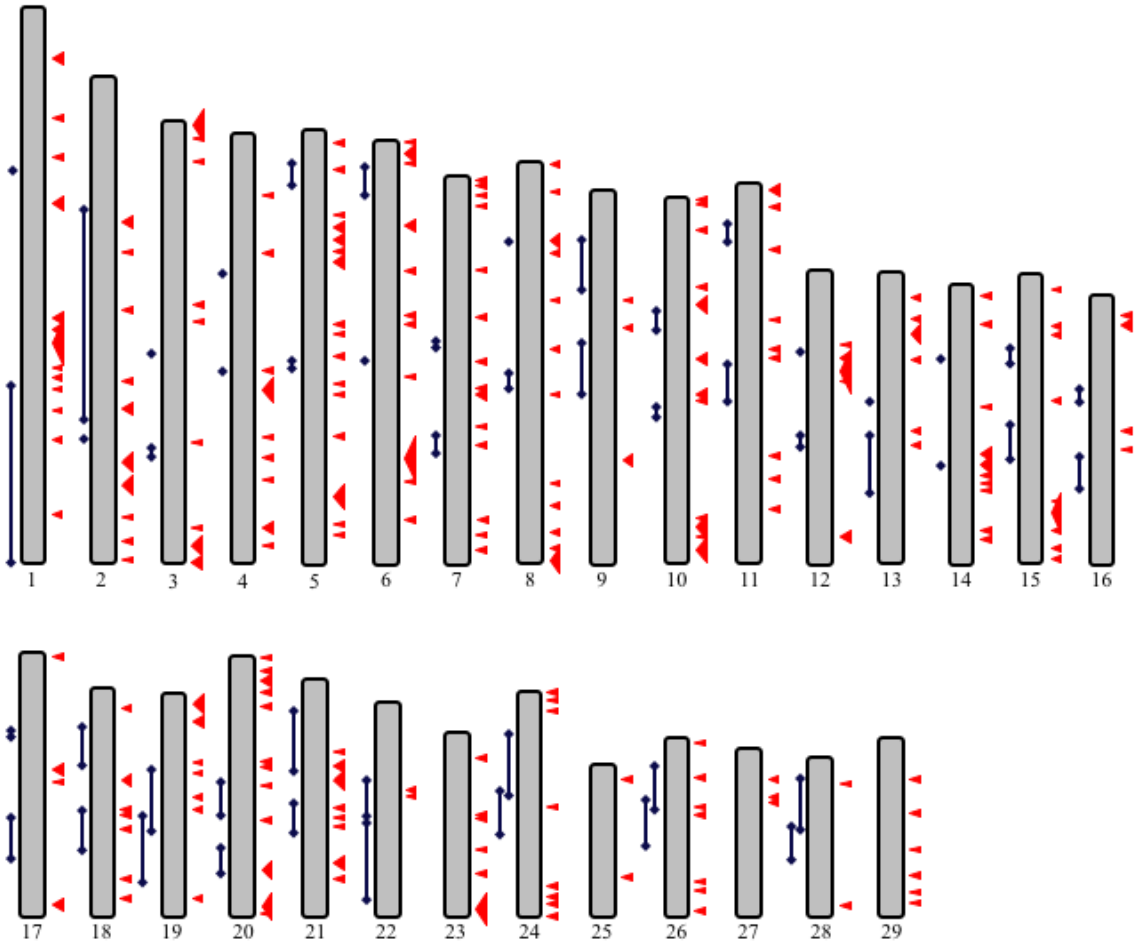


Figure 15. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines) and significant single nucleotide polymorphism (SNP; $p < 0.005$) for weaning weight (WW) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

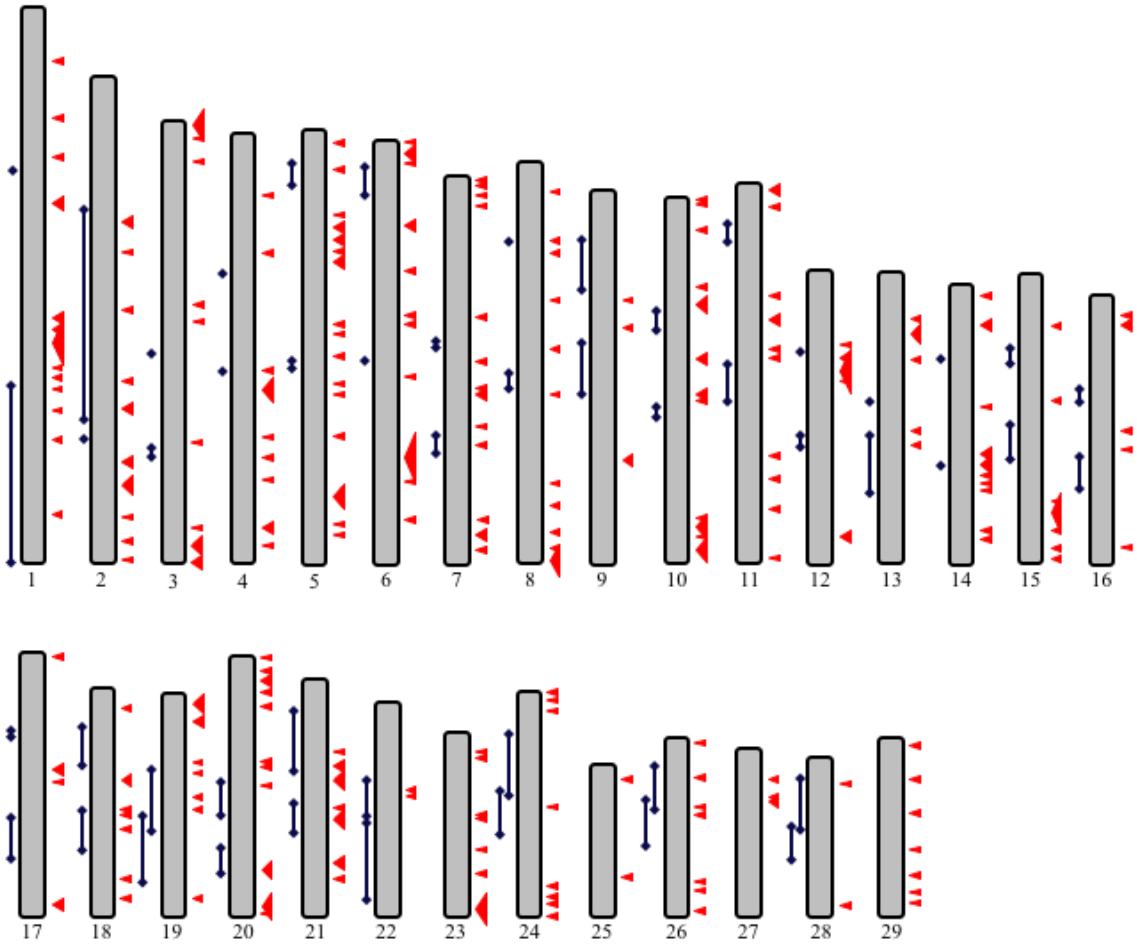


Figure 16. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines) and significant single nucleotide polymorphism (SNP; $p < 0.005$) for yearling weight (YW) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

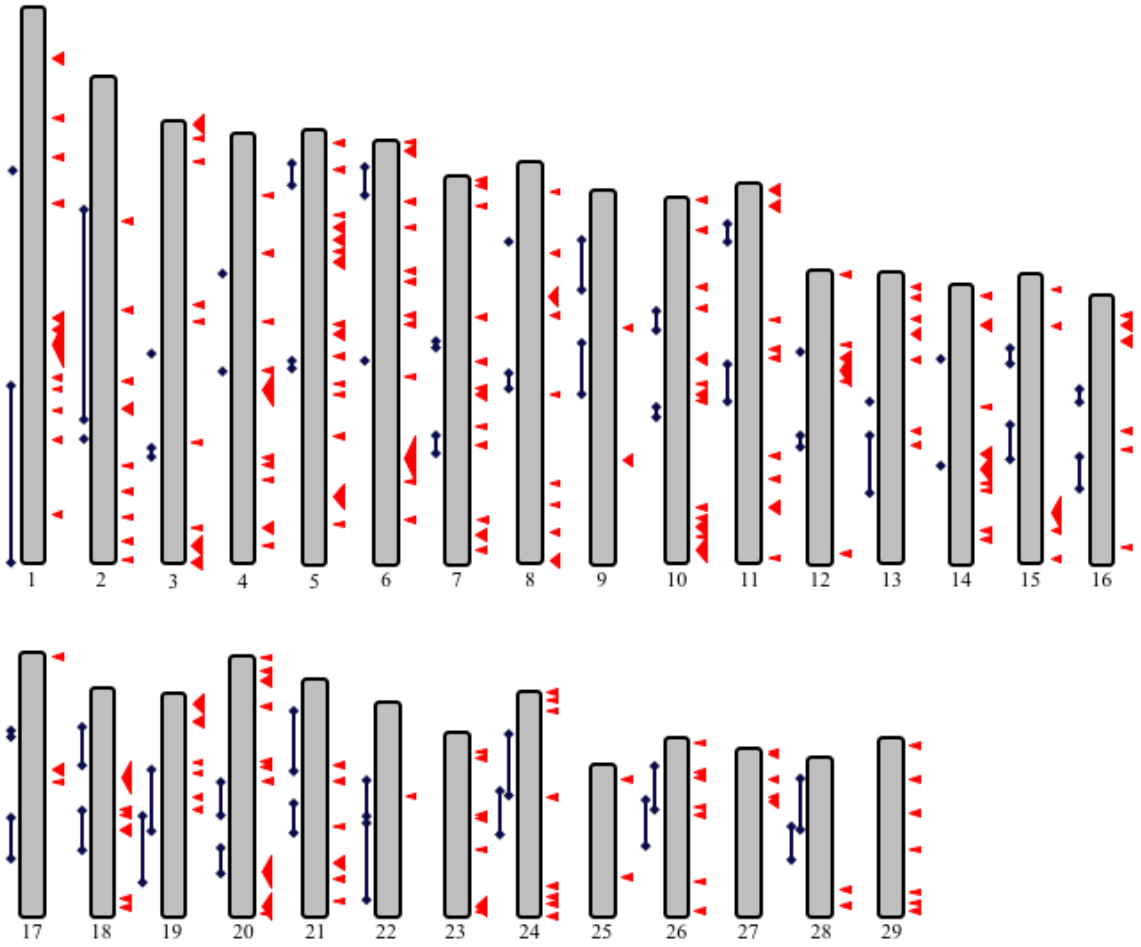


Figure 17. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines) and significant single nucleotide polymorphism (SNP; $p < 0.005$) for calving ease (CE) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

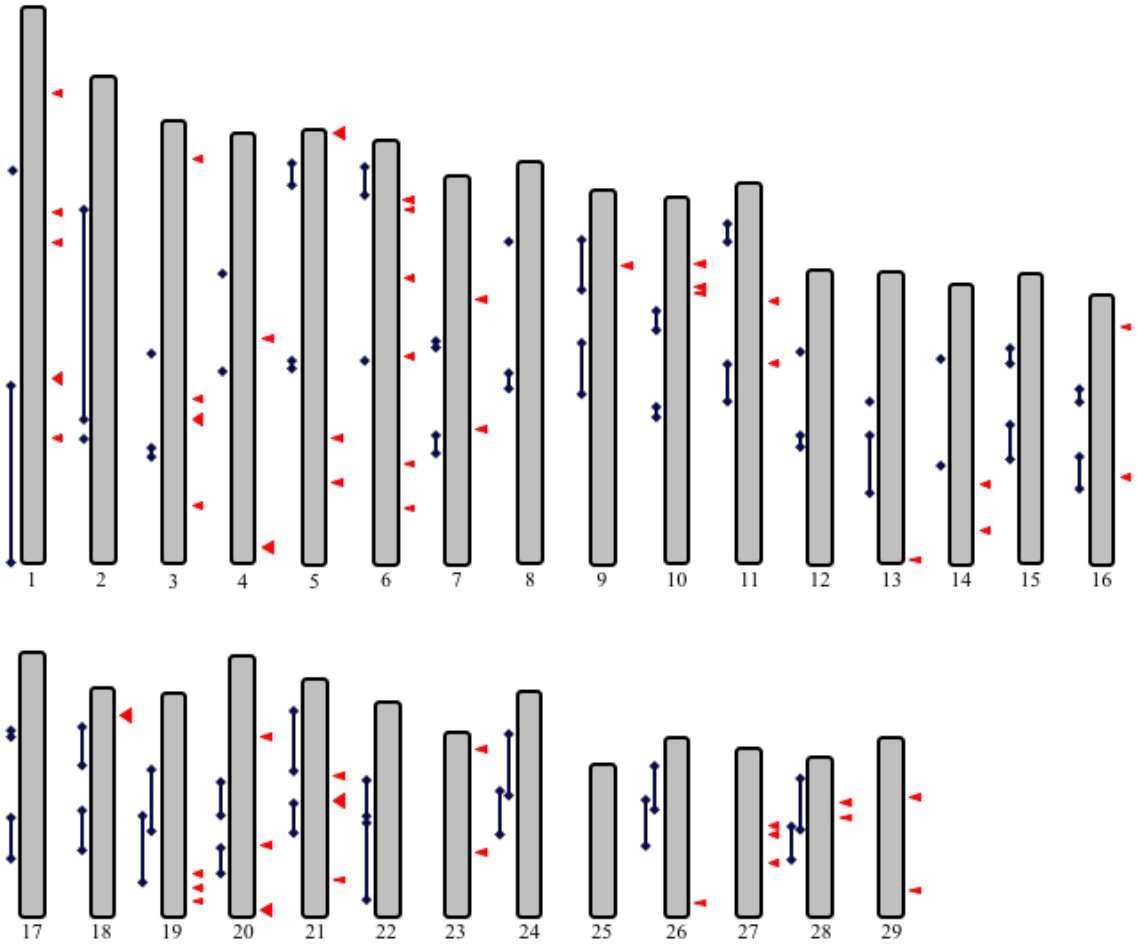


Figure 18. Regions of the genome with runs of homozygosity (ROH) on an individual chromosome basis (left side of chromosomes, blue lines) and significant single nucleotide polymorphism (SNP; $p < 0.005$) for age at first calving (AFC) identified by regression analysis (right side of chromosomes, red arrows). Height of arrow corresponds to number of consecutive significant SNP.

CHAPTER FOUR

IDENTIFICTION OF GENETIC MARKERS AND QTL FOR CARCASS QUALITY TRAITS WITHIN THE AMERICAN SIMMENTAL ASSOCATION CARCASS MERIT PROGRAM

Introduction

With the first matings at the Sheek Ranch in Cabool, MO, in the spring of 1997 the American Simmental Association (ASA) launched a program that has influenced all producers and users of Simmental genetics. Simply known as the Carcass Merit Project (CMP), the enrolled sires of the Simmental and Simbrah breeds have been randomly mated to 35,000 commercial females to collect difficult-to-get progeny carcass information by sire group. Ten thousand carcass records have been collected and carcasses are averaging 74% Choice and a 2.8 yield grade, with tenderness data having been completed. In terms of calving ease (CE), 4,400 British heifers have been mated and resulting calves have an average birth weight (BW) of 78.6 lbs. For feed conversion, 1,318 sire-identified SimAngus™ progeny steers have been used resulting in an average dry matter feed conversion 6.3:1 and an average daily gain of 1.64 kg/day. Data has been collected from 41 different herds across 18 states, with steers fed and harvested in nearly every cattle feeding region in the United States.

These data allowed the ASA to improve the accuracy of expected progeny differences (EPD) used for selection of economically relevant traits. It improved confidence levels of traits from calving assistance all the way to predicting end point

product value. In the last 25 years, a shift has occurred in the U.S. beef industry from a commodity-based market to one that is based on quality or product yield (Moore et al, 2012; Weaber and Miller, 2004). This has been facilitated by increased accuracy of carcass merit EPD. In an effort to reduce product variability and improve profitability, many producers have added marbling (MARB) and carcass yield as selection criteria. This means that a large number of the current cow herds have females that possess merit in the area of MARB or carcass quality. This selection could result in changes in other traits. Previously, researchers have reported negative genetic correlations between maternal performance traits and carcass merit (MacNeil et al.,1984; Crews and Kemp, 1990). As a result, there is interest in how the current carcass-based selection impacts maternal performance and index-based selection criteria. There is still genetic variation that cannot be predicted with current genomic tools. Thus, the objective of this study was to identify genetic markers and quantitative trait loci (QTL) for carcass traits and to evaluate the correlations between carcass merit traits and maternal performance.

Materials and Methods

Data were gathered by the ASA CMP. All records containing calf BW, calving ease direct scores (CED; Beef Improvement Federation, 2018), calving ease maternal scores (CEM), 205-day adjusted weaning weights (WW), 12th rib fat (BF), ribeye area (REA), MARB, hot carcass weight (HCW), and internal fat (KPH) were extracted from the ASA database. Sire EPD, performance, and single nucleotide polymorphism (SNP)50K genotype data were also obtained.

Progeny data were organized into 150 sire families. Performance averages for all traits (n = 1 – 150 progeny per family) were calculated. Sires with either SNP50K or comparable imputed 50K data from higher or lower density SNP chips were used in the overall analysis. Genotype data quality control was done through SNP (Golden Helix, 2017). First, samples were removed with call rates ≤ 0.95 indicating reduced DNA quality. Next, markers were removed if: a call rate was < 0.85, had > 2 alleles, and a minor allele frequency (MAF) < 0.01. Data were then pruned to remove markers in linkage disequilibrium and located on non-autosomal chromosomes. This left 37,552 out of 52,584 markers in the downstream analysis.

Samples were then filtered to determine relatedness. An identity by descent (IBD) relationship matrix was created to correct association analysis for genomic relationship amongst samples. Principal component analysis (PCA) was used to account for cryptic relatedness and the first three eigen vectors represented greater than 50% of the stratification on the SNP data. Identity by descent calculated relatedness between individuals was used as a covariate in the association analysis.

A single-locus mixed linear model (EMMAX; Kang et al., 2010) and a multi-locus mixed linear model (MLMM; Segura et al., 2012) in Golden Helix SVS software (Golden Helix, version 8.7.2-2017-08-11) were used to perform regression-based association analyses on the genotype data while correcting for cryptic relatedness and pedigree structure. Benjamini-Hochberg multiple comparison corrections were used to minimize false-positive associations. A genome-wide significance level utilizing the Benjamini-Hochberg correction with -log10(*p*-value) was 5×10^{-8} (Ehret, 2010) and

markers above the level of significance were used to identify regions of the genome associated with the trait in question. Regions with clusters of significantly associated markers were then labeled as putative QTL and used to identify potential positional candidate genes.

To better understand how carcass-based selection impacts maternal performance, genetic correlations between each carcass trait were correlated to each of the maternal traits. Genetic correlations were estimated using the genomic best linear unbiased prediction (GBLUP) method to perform a bivariate REML analysis in SVS software (Golden Helix, version 8.7.2-2017-08-11). The following parameters were set for the analysis: did not exclude residual covariance, zero for missing values, did not correct for additional covariates, did not account for gene by environment interactions, did not correct for gender, used an IBD genomic relationship matrix, and samples with missing phenotypes were dropped.

We estimated the proportion of phenotypic variance explained for each trait, again using SVS software. Data were exported from SVS and from the first identified marker in each chromosome, markers that fell within 1 Mb were highlighted. The same process was done for all of the identified markers for each chromosome, which created some overlap of highlighted areas, and then the proportion of phenotypic variance for each marker within each highlighted area was totaled. Previously reported significant markers were then cross-referenced with the highlighted areas. For significant markers ($p < 0.001$), the proportion of genetic variation explained by the marker was reported.

Results and Discussion

The dataset consisted of samples from 3,849 individuals. Samples were grouped by sire and 2,745 individuals had known sires, producing 395 sire families. Sire families ranged in size from one to 150 progeny with reported data for carcass traits. Progeny performance averages were constructed.

Single-locus Model

For KPH, chromosomes 11 and 16 each had one significant marker (Figure 19). For progeny average HCW, chromosome 20 had one significant marker, for average MARB, chromosome 16 had one, and for average BF, chromosome 17 had one (Figures C1 – C8).

For KPH, the two significant markers on chromosome 11 and chromosome 16 explained 0.0210 and 0.0262 percent of the phenotypic variation, respectively (Table 5). From the constructed progeny phenotypes, there were only three significant markers. Average HCW had one on chromosome 20 that explained 0.0231 percent of the variation, average MARB had one on chromosome 16 that explained 0.0230 percent, and average BF had one on chromosome 17 that explained 0.0243 percent. These five significant markers only explained 0.1176 percent of the total amount of phenotypic variation.

Although the sire family structure of the data limited the resolution of our association analyses, areas of the chromosomes with vertical clusters of markers were of interest as they suggested putative QTL in those regions. Within a 100,000 base pair (bp) window of each putative QTL region, positional candidate genes were identified using Genome Build Bos taurus UMD 3.1.1. Putative QTL regions were compared to known

QTL using AnimalQTLdb (http://www.animalgenome.org). Both novel and previously identified QTL were identified in this study. Carcass merit trait QTL have been identified in both US and Chinese beef cattle breeds. In a recent study by Saatchi et al. (2014), 10 US beef breeds including Simmental were used to identify several QTL that overlapped with the significant regions in our study, including chromosome 6 for average HCW and chromosome 20 for average BF. In addition to these previously identified regions, we also identified 365 novel regions across all traits were also identified (Tables C1 – C9); 31 for HCW, 28 for MARB, 42 for BF, 33 for REA, 31 for KPH, 26 for average HCW, 50 for average MARB, 63 for average BF, and 61 for average REA.

Of the positional candidate genes found in this study, four genes had been previously identified in other breeds (Tables C1 – C9). Gill et al. (2010) identified protein kinase AMP-activated non-catalytic subunit gamma 3 (*PRKAG3*) on chromosome 2 for HCW in Aberdeen Angus-sired steers. The association between *PRKAG3* and HCW was the only SNP-trait association significantly affected by percent of Angus in breed composition; an increase of Angus in breed composition led to a decrease in HCW (Gill et al., 2010).

For BF on chromosome 1, Kim et al. (2003) detected interferon alpha and beta receptor subunit 1 (*IFNAR1*) in Angus-Brahman cross cattle as a marker with the least suggestive evidence for linkage under their line-cross model. For BF on chromosome 5, Ujan et al. (2011) identified myogenic factor 5 (*MYF5*) in Chinese *Bos taurus* and Baeza et al. (2011) identified signal transducer and activator of transcription 6 (*STAT6*) in

Brangus steers, both of which are transcription factors. In addition to this, 251 novel positional candidate genes were identified across all traits.

Multi-locus Model

For KPH, chromosome 16 had one significant marker (Figure D9). For progeny average HCW, chromosome 20 had one significant marker, average MARB had one significant marker on chromosome 16, and average BF had one on chromosome 17 (Figures D2, D4, and D6).

For KPH, the significant marker on chromosome 16 explained 0.0262 percent of the phenotypic variation (Table 5). From the constructed progeny phenotypes, there were only three significant markers. Average HCW had one marker on chromosome 20 that explained 0.0231 percent, average MARB had one marker on chromosome 16 that explained 0.0230 percent, and average BF had one marker on chromosome 17 that explained 0.0243 percent. These four significant markers only explained 0.0966 percent of the total phenotypic variation in the animals evaluated. The significant markers for KPH, average HCW, average MARB, and average BF are identical in bp position and the proportion of variation explained by four of the significant markers found in the single-locus model.

Similar to the single-locus model, Saatchi et al. (2014) identified several QTL that overlapped with the significant regions in our study, including chromosome 6 for HCW and chromosome 6 for average BF. In addition to these previously identified regions, 393 novel regions were identified across all traits (Tables D1 – D9); 28 for HCW, 34 for

MARB, 38 for BF, 35 for REA, 35 for KPH, 56 for average HCW, 39 for average MARB, 65 for average BF, and 63 for average REA.

Of the positional candidate genes, four genes had been previously identified in other breeds (Tables D1 – D9). Gill et al. (2010) identified protein kinase AMP-activated non-catalytic subunit gamma 3 (*PRKAG3*) on chromosome 2 for HCW in Aberdeen Angus-sired steers. For MARB, retinoic acid receptor-related orphan receptor C (*RORC*) was identified on chromosome 3 by Barendse et al. (2010) in Australian Angus, Brahman, and Hereford and by Barendse et al. (2007) in Angus, Shorthorn, and other taurine breeds. For BF on chromosome 1, Kim et al. (2003) identified interferon alpha and beta receptor subunit 1 (*IFNAR1*) in Angus-Brahman cross cattle and on chromosome 5, Ujan et al. (2011) identified myogenic factor 5 (*MYF5*) in Chinese *Bos taurus*. In addition to these, 283 novel positional candidate genes were identified across all traits.

Genetic Correlations

Table 6 shows the correlations between offspring carcass traits and maternal traits. The strongest negative correlations found in the dataset were between HCW and CED (-0.20), WW and Milk (-0.18), and WW and CEM (-0.17). The correlation between HCW and CED (-0.20) was less than the correlation previously reported (-0.31) by MacNeil et al. (1984) in crossbred steers and heifers. Likewise, the magnitude of previously reported negative correlations between REA, BF, and KPH and maternal traits are no longer as great, indicating reduction in the detrimental effects of selection for these disparate traits. Crews and Kemp (1990) found a correlation of -0.23 for REA and BW in

crossbred steers and heifers compared to the correlation of 0.10 found in this study. In crossbred steers and heifers for BF and CED, MacNeil et al. (1984) found a correlation of -0.36 and Splan et al. (1998) found a correlation of -0.14 compared to the correlation of 0.002 found in this study. Splan et al (1998) also found a correlation of -0.29 for KPH and CED compared to the correlation of -0.01 found in this study. This indicates that multi-trait selection has been successful at decreasing the negative correlations between carcass characteristics and maternal traits in this population.

Conclusions

Five chromosomes harboring QTL for various carcass traits were identified, explaining 0.2142 percent of the total phenotypic variation. Across all traits, 365 novel regions and 251 novel positional candidate genes were identified for the single-locus model and 393 novel regions and 283 novel positional candidate genes were identified for the multi-locus model. Also, the detrimental genetic correlations between carcass characteristics and maternal traits are less than what has been previously reported indicating that multi trait or index-based selection has been effective at reducing the strength of negative genetic relationships between traits.

Table 5. Genome-wide association significant markers (located above -log10(*p*-value) of 5 x 10^{-8}) on a Manhattan plot.

Trait[1]	**Chromosome**	**Base Pair Position**	**Positional Candidate Gene**	**Proportion of Variation Explained**
Single-locus Model				
KPH	11	49,473,033	Bos taurus ELMOD3	0.0210
	16	65,669,824		0.0262
Average[2] HCW	20	9,651,103		0.0231
Average[2] MARB	16	65,669,824		0.0230
Average[2] BF	17	46,357,742		0.0243
Multi-locus Model				
KPH	16	65,669,824		0.0262
Average[2] HCW	20	9,651,103		0.0231
Average[2] MARB	16	65,669,824		0.0230
Average[2] BF	17	46,357,742		0.0243

[1]HCW = hot carcass weight; MARB = marbling; BF = 12th rib fat; KPH = internal fat

[2]Average denotes traits from constructed progeny performance averages

Table 6. Genetic correlations between carcass and maternal traits[1].

	HCW	MARB	BF	REA	KPH	CED	BW	WW	YW	CEM	Milk	MWW	Stay	Doc
HCW		0.53	0.40	0.63	0.37	-0.20	0.22	0.33	0.36	-0.04	-0.06	0.22	-0.04	0.03
MARB			0.35	0.28	0.52	0.07	-0.07	-0.10	-0.07	-0.01	-0.05	-0.12	0.03	0.07
BF				-0.08	0.41	0.002	-0.05	-0.01	-0.01	0.00	-0.01	-0.01	-0.03	0.07
REA					0.13	-0.08	0.10	0.11	0.12	0.00	-0.09	0.04	-0.01	0.00
KPH						-0.01	-0.04	-0.09	-0.08	0.00	-0.01	-0.04	-0.01	-0.01
CED							0.00	0.00	0.00	0.02	0.20	0.00	0.17	0.03
BW								0.60	0.53	0.00	0.00	0.27	0.03	-0.05
WW									0.00	-0.17	-0.18	0.67	-0.02	-0.01
YW										-0.03	-0.03	-0.68	0.01	-0.01
CEM											0.22	0.06	0.00	-0.04
Milk												0.67	0.11	0.03
MWW													0.08	0.02
Stay														0.03
Doc														

[1]HCW = hot carcass weight; MARB = marbling; BF = 12th rib fat; KPH = internal fat; CED = calving ease direct; BW = birth weight; WW = weaning weight; YW = yearling weight; CEM = calving ease maternal; MWW = maternal weaning weight; Stay = stayability; Doc = docility

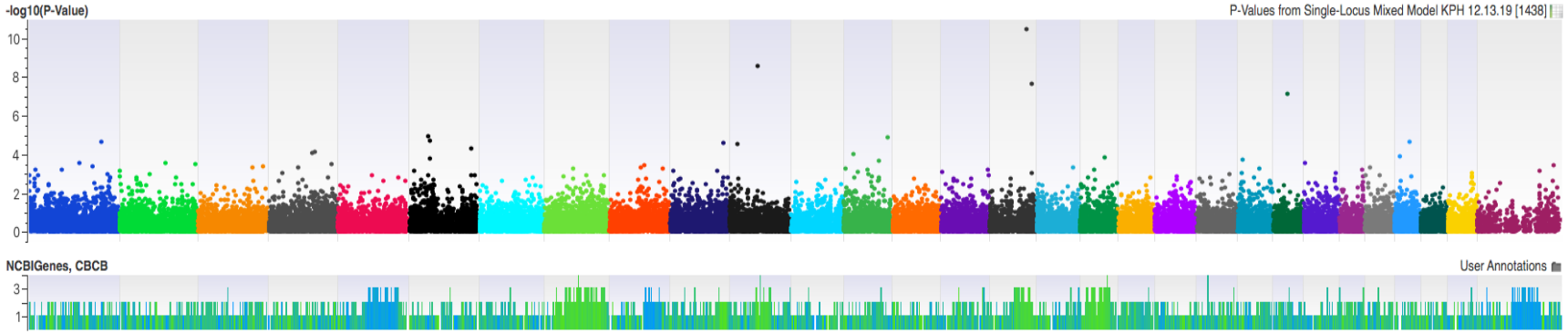


Figure 19. Manhattan plot for single-locus model internal fat (KPH). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

CHAPTER FIVE

CONCLUDING REMARKS

The Line 4 and Line 1 Hereford populations are two long-term linebred populations. While both lines stem from the same genetics as surplus Line 1 females were used as Line 4 foundation females, they have been managed differently based on selection decisions. When established, the implied breeding objective of Line 1 was economic return above feed costs from steer carcasses slaughtered at a live weight of 408 kg. However, in the 1940s, the selection decisions changed to growth to one year of age. In the Line 4 population, from 1976 to 1995, selection decisions were made based on an index for adjusted yearling weight (YW) minus 3.2 times adjusted birth weight (BW). Selection decisions changed from 1995 to 2006 to selection for scrotal circumference, and the current selection is for increased YW while keeping increased inbreeding at a low level.

Within the Line 4 population, individuals were more related than the Line 1 population, which was visually clear in the heatmaps and principle component analysis (PCA) plots (Figures 1, 2, 10, and 11). This could be because no unrelated animals were introduced into the Line 4 population. There are 84 animals that appear in the Line 1 pedigree beginning in 1994 and this could be contributing to the decrease in relatedness in the Line 1.

The high end of the range of pedigree and genomic pedigree inbreeding coefficients for Line 4 were 35% and 35% lower than that of Line 1, respectively. Again, this could be explained by having unrelated animals in the Line 1 dataset. However, the

genomic inbreeding coefficient of Line 4 was 3% higher than Line 1. Average pedigree (F_{PED}), genomic (F_G), and genomic pedigree (F_{GPED}) inbreeding coefficients of Line 1 were 29.5%, 2.1%, and 13.3% higher than Line 4. This is expected as Line 1 is 28 years older than Line 4 and has accumulated more inbreeding. Average rate of change of inbreeding for Line 4 is 0.03% over 55 years and it was a little over 5% in 1964. Average rate of change of inbreeding for Line 1 is -0.03% over 83 years and it was a little over 50% in 1934. Again, this is expected as unrelated bulls appear in the Line 1 dataset in 1994.

In Line 4, 45 runs of homozygosity (ROH) were identified compared to the 50 that were identified in Line 1. When comparing ROH regions for both lines, the largest region where the two lines overlap is on chromosome 2. However, there are more ROH that are different, and one line has ROH on some chromosomes while the other does not. Line 4 had 35 strongly significant SNP that were above the significance level of 5×10^{-4} and five of those SNP were strongly significant across two to four traits versus the 93 strongly significant SNP found with the Line 1 and 23 of those SNP were strongly significant across two to four traits. None of the strongly significant SNP were found in both lines.

Of the genes and functions that were identified that could potentially be responsible for impaired traits observed with inbreeding depression for both lines, there were 12 genes for Line 4 and 11 genes for Line 1. KIAA1324 like (*KIAA1324L*) was the only gene that appeared in both lines and it has been related to embryonic development. There were significant SNP located within ROH-identified regions for each trait for each

line. Line 4 had a greater proportion of significant SNP than Line 1, yet Line 1 has been linebred for longer, has a greater number of animals in the population, and has greater inbreeding coefficients.

Comparison of the results of both lines indicate that selection is impacting the results of inbreeding and the degree to which inbreeding depression is being expressed. Previous research has utilized ROH to study inbreeding, and when ROH analysis is coupled with identifying significant SNP related to changes seen in inbreeding-impacted traits, the results are stronger as it takes the molecular approach farther by identifying genes impacted by inbreeding.

Linebreeding and how it is affecting the genome were evaluated in chapters 2 and 3. Due to the different selection decisions that have been made with the two lines, it is clear that linebred animals go above and beyond ancient DNA that fix regions of the genome through selection, contributing to inbreeding depression. These results agree with Zhang et al. (2015) as they found short sections of ROH were passed down from generation to generation as a result of inbreeding and selection. As short ROH have been selected through making selection decisions, those ancient haplotypes are being fixed in populations and are continually passed down.

In chapter 4, a single-locus and a multi-locus model were used to perform regression-based association analyses on the genotype data of the American Simmental Association Carcass Merit Program. The single-locus model identified five significant markers that were above the significance threshold of 5×10^{-8}, while the multi-locus model identified four. The four markers found in the multi-locus model were found in the

single-locus model. The five significant markers for the single-locus model explained only 0.1176 percent of the total phenotypic variation while 0.0966 percent was explained in the multi-locus model.

While there were a low number of significant markers, there were vertical clusters in areas of the chromosomes that were of interest as they suggested putative quantitative trait loci (QTL) in those regions. Saatchi et al. (2014) previously identified several QTL that overlapped with significant regions in the current study, including chromosome 6 for average hot carcass weight (HCW) and chromosome 20 for average 12^{th} rib fat (BF) for both models. Three hundred sixty-five novel regions were identified across all nine traits for the single-locus model and 393 were identified for the multi-locus model. Four genes for both models were previously identified, three of which overlapped in both regions leaving one gene independent of each model. For the single-locus model, 251 novel positional candidate genes were identified across all traits while 283 were identified for the multi-locus model.

Previous research has reported negative correlations between carcass characteristics and maternal traits as a result of single-trait selection. Genetic correlations were analyzed for the carcass characteristics and maternal traits in the study. The negative impact of previously reported correlations was not found in this population, indicating multi-trait selection has been successful in decreasing the negative correlations between carcass and maternal traits.

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APPENDICES

APPENDIX A

LINE 4 SUPPLEMENTARY TABLES AND FIGURES

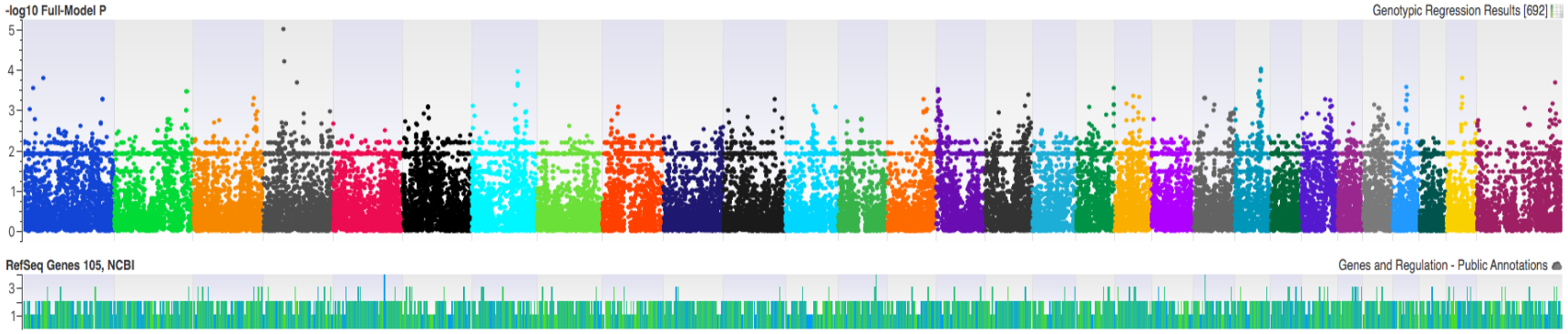


Figure A1. Manhattan plot for weaning weight (WW). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

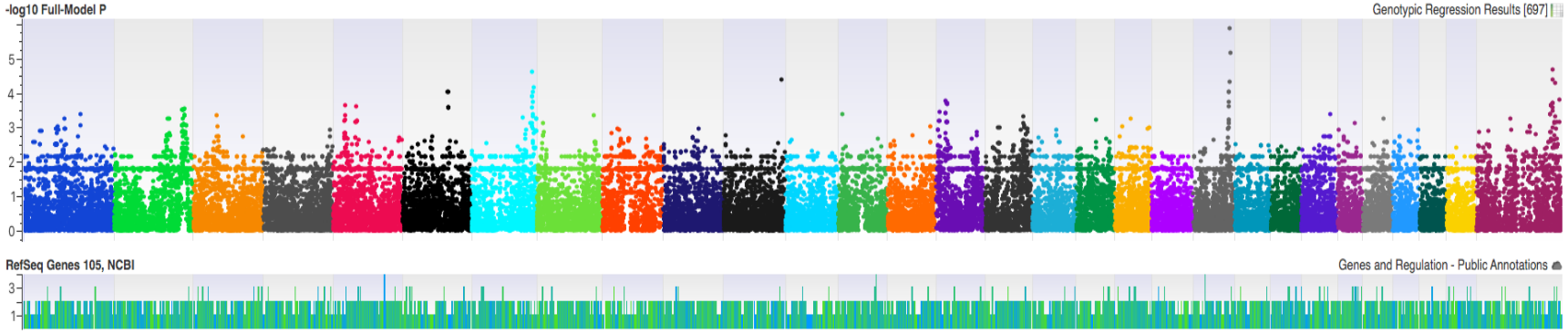


Figure A2. Manhattan plot for yearling weight (YW). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

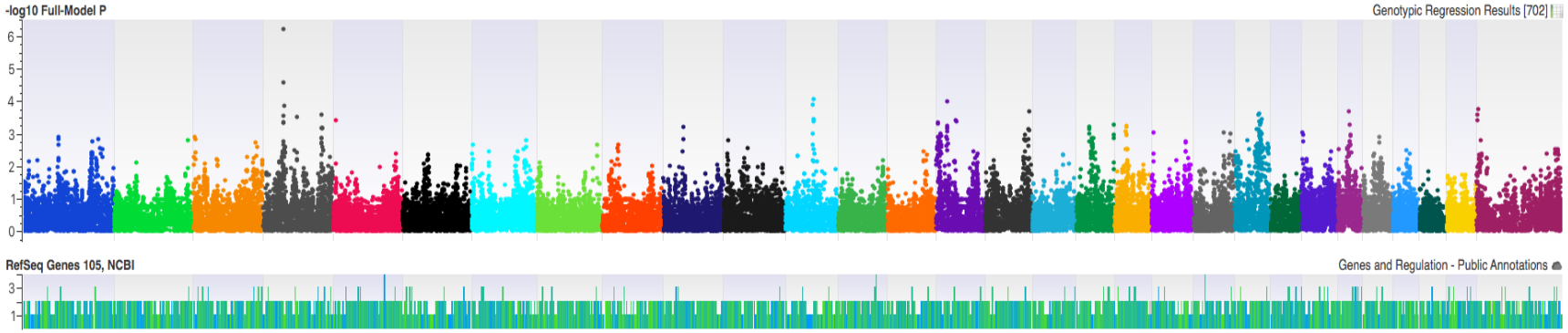


Figure A3. Manhattan plot for calving ease (CE). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

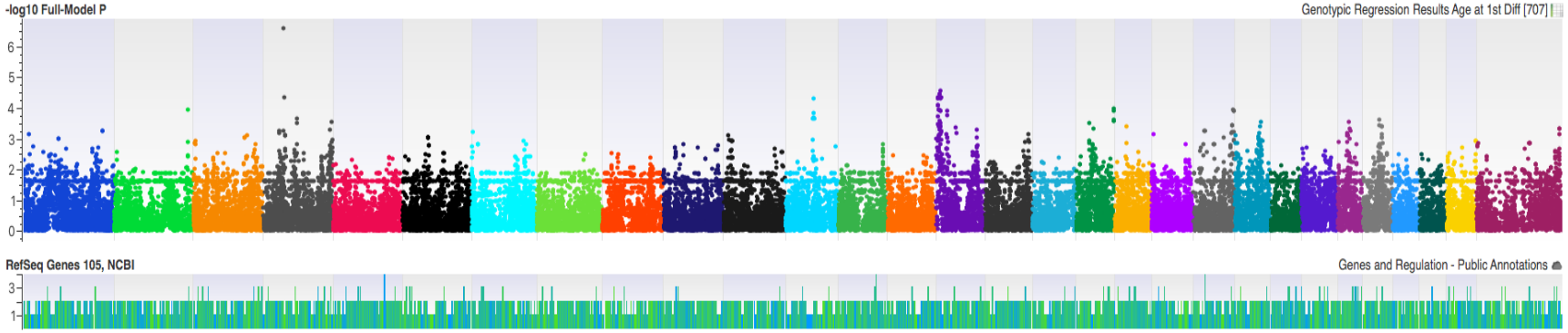


Figure A4. Manhattan plot for age at first calving (AFC). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

Table A1. Significant birth weight (BW) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
1	61,172,245	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	61,540,639	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	61,806,466				X
	119,544,478	Bos taurus WWTR1	Enhances osteogenic differentiation and suppresses adipogenic differentiation	doi:10.1111/j.1476-5381.2011.01664.x	
	120,109,716	Bos taurus GYG1	Muscle specific regulatory domain	doi:10.1016/s0378-1119(99)00211-5	
	120,315,919				
	120,479,376	Bos taurus AGTR1	Potent vasopressor hormone; primary regulator of aldosterone secretion; important effector controlling blood pressure and volume of cardiovascular system	GeneCards	
	131,163,604				
	134,937,491				
	135,580,651	Bos taurus EPHB1	Stimulates osteo-adipogenic progenitor proliferation resulting in increased adipogenesis in cell cultures	10.1016/j. prostaglandins.2012.01.001	
	138,510,793				
	138,519,398				
2	129,008,096	Bos taurus RCAN3	Neurotransmitter that influences development	NCBI	X
3	2,624,552				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
3	3,231,882				
	3,331,788				
	4,183,635				
	41,416,136				
	41,519,979	Bos taurus OLFM3	Regulation of collagen development	doi:10.1007/s12035-009-8076-x	
	108,444,081				X
	111,585,046				
4	28,117,205				
	28,215,295				
	33,059,396				
	33,636,014	Bos taurus KIAA1324L	Embryo development	doi:10.1074/jbc.M110.177907	
	33,966,904	Bos taurus GRM3	Major excitatory neurotransmitter in the central nervous system; activates ionotropic and metabotropic glutamate receptors; involved in most aspects of normal brain function	GeneCards	
	34,693,882				
	34,723,945				
	34,738,011				
	34,867,416				
	35,183,415				
	35,558,998				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
4	35,605,434	Bos taurus SEMA3D	Encodes a member of the semaphorin III family of secreting signaling proteins that are involved in axon guidance during neuronal development	GeneCards	
	35,705,474	Bos taurus SEMA3D	Encodes a member of the semaphorin III family of secreting signaling proteins that are involved in axon guidance during neuronal development	GeneCards	
	36,182,094				
	36,354,506				
	36,533,621				
	38,486,244	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,548,833	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,571,065	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
4	38,573,157	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,680,360	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	54,097,830	Bos taurus FOXP2	Essential for proper development of speech and language regions of the brain during embryogenesis; may be involved in variety of biological pathways and cascades that influence language development	GeneCards	X
	58,540,307				X
	58,563,766				X
	101,523,850				
	101,790,675	Bos taurus PTN	Significant roles in cell growth and survival, cell migration, angiogenesis, and tumorigenesis	GeneCards	
	102,432,527	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,433,510	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,447,483	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,513,433	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
4	103,092,493				
	103,484,220				
	117,308,096	Bos taurus DPP6	Associated with autosomal dominant microcephaly and mental retardation; sclerosis	doi:10.1016/j.ejmg.2013.06.008; doi:10.1016/j.neurobiolaging.2009.05.014	
5	5,120,813				X
	5,400,651				X
6	43,517,549				X
	43,649,345				X
7	765,687				
	1,263,597				
	76,497,957				X
	77,023,177				X
	80,717,275				
	80,819,058				
	80,885,006				
	91,484,380				
	92,744,435				
	92,817,550				
	92,917,772				
	93,355,753				
	94,562,555				
	94,767,287				
	100,413,608				
	102,328,838				
8	105,946,838				
	106,241,362				
9	16,465,867				
	28,257,531				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
10	32,955,493				X
	35,036,509				X
	35,086,759				X
11	5,964,756	Bos taurus NPAS2	Important regulator of physiological functions including metabolism, sleep, body temperature, blood pressure, endocrine, immune, cardiovascular, and renal	GeneCards	
	7,712,524				
	42,102,223				
12	21,441,958				X
	21,472,748				X
	47,858,784				X
	47,915,012				X
	48,036,822				X
	48,131,404				X
	48,902,740	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	48,933,612	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	48,984,802	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
12	49,095,991	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	49,123,661	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	50,324,576				X
15	3,051,938				
	3,369,565				
	3,416,019				
	3,462,006				
	4,094,542				
	4,149,756				
	4,478,076				
	5,342,417				
	5,674,820				
	6,180,970				
	6,938,962	Bos taurus CFAP300	Plays a role in axonemal structure organization and motility	GeneCards	
	6,962,261				
	7,728,537				
	7,944,599				
	7,989,843				
	8,836,147				
	8,937,081				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
15	9,125,948	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	17,768,941	Bos taurus RAB39A	Plays a role in maturation and acidification of phagosomes that engulf pathogens	GeneCards	
	18,137,423	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	18,218,536	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	19,377,108				
	19,409,074				
	19,529,491				
	19,605,113				
	19,959,252				
	20,171,885				
	21,061,865	Bos taurus ARHGAP20	Impacts neurite outgrowth	GeneCards	
	35,143,414	Bos taurus SERGEF	Regulator of chromosome condensation	NCBI	
	35,606,202	Bos taurus ABCC8	Transport various molecules across extra- and intra-cellular membranes	NCBI	
	65,235,259				X
	72,027,612				X
	72,624,841				X
16	66,254,679				X
	68,714,893	Bos taurus HMCN1	Age-related macular degeneration	doi:10.1002/humu.20464	

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
16	68,857,193				
	68,981,703	Bos taurus ODR4	Protein expression	doi:10.1076/opge.24.141.15604	
	69,010,341	Bos taurus PDC	Phosphoprotein from photoreceptor cells	Lee et al., 1990. J. Biol. Chem. 265:15867-15873	
	70,674,332	Bos taurus PTPN14	Cell growth	doi:10.1074/jbc.274.18.12905	
	71,485,655				
	71,625,483				
	74,958,644				
	75,465,698	Bos taurus HSD11B1	Conversion of cortisol to cortisone and cortisone to cortisol	GeneCards	
	76,059,261				
	76,423,682				
	76,606,285				
18	22,339,904	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,379,853	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,760,455				
	22,956,535				
	23,025,804				
	26,282,975				
	26,362,767				
	26,380,950	Bos taurus NDRG4	Cell cycle progression	doi:10.1074/jbc.M109.012484	
	27,101,515				
	27,121,621				
	27,410,770				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
18	27,579,708				
	27,719,066				
	27,769,678				X
	27,870,868				X
	28,030,835				X
	28,096,476				X
	28,286,346				X
	28,324,801				X
	28,372,073				X
	28,608,495				X
	28,670,292				X
	28,734,924				X
	28,843,447				X
	29,078,437				X
	29,466,879				X
	29,583,082				X
	29,594,472	Bos taurus CDH8	Mediates calcium-dependent cell-cell adhesion	GeneCards	X
	29,882,606				X
	30,018,259				X
	32,855,646	Bos taurus CDH11	Promotes the metastasis of cancer cells to bone	doi:10.1158/1541-7786.MCR-08-0077; doi:10.3892/ijo.33.1.17	X
	65,423,598				
	65,456,096				
	65,460,377				
	65,463,329				
19	20,123,437				
	21,432,208	Bos taurus CORO6	Related to actin filament binding	GeneCards	

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
19	21,434,766	Bos taurus CORO6	Related to actin filament binding	GeneCards	
	21,470,659				
	21,510,144				
	21,579,655				
	21,878,635				
	22,304,690	Bos taurus ABR	Encodes a GTPase-activating	GeneCards	
20	2,523,465	Bos taurus KCNIP1	Target recognition of neuronal calcium sensor proteins	doi:10.1016/j.bbagen.2011.10.003	
	2,647,934				
	59,016,802				X
	59,235,834				X
	59,615,805				X
	59,712,991				X
21	52,816,464				
	63,286,443	Bos taurus VRK1	Loss of spermatogonia	doi:10.1095/biolreprod.109.079095	
	64,152,628				
	68,216,653				
22	5,266,853	Bos taurus GADL1	Metabolism and amino acid synthesis	GeneCards	
	5,365,596	Bos taurus GADL1	Metabolism and amino acid synthesis	GeneCards	
	5,883,048				
	6,064,248				
	9,716,846				
	21,599,195				
	24,876,308				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
22	34,629,577				X
	34,965,607				
	34,979,445				
	35,730,548				
	36,797,671				
	36,992,517	Bos taurus ADAMTS9	Control of organ shape during development	GeneCards	
	37,455,074				
	37,858,827				
	39,122,937	Bos taurus C22H3orf14	Influence immune response associated with mastitis resistance	doi:10.1073/pnas.0601015103	
	39,702,951	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	
	39,725,145	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	
	40,232,132	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	X
	40,748,442	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	41,827,325	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	42,137,230				X
	42,270,737				X
	42,284,451				X
	42,616,545				X
	42,639,967				X
	43,534,982	Bos taurus PXK	Epidermal growth factors receptor	doi:10.1128/MCB.01105-09	X
	43,664,444				X

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
22	43,693,452	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,723,207	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,744,791	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,747,725	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	
	43,767,521	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	
	43,777,202	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	
	44,912,994	Bos taurus TASOR	Mediates epigenetic repression	GeneCards	
	44,939,749	Bos taurus TASOR	Mediates epigenetic repression	GeneCards	
	45,455,314	Bos taurus ERC2	Component of HUSH complex – multiprotein complex that mediates epigenetic repression	GeneCards	
	45,556,690				
	45,696,332				
	45,954,406				
	46,465,290				
	46,533,857	Bos taurus CACNA2D3	Tumor suppression	doi:10.1002/ijc.28252	
	47,440,100				
	47,632,083				
	51,180,659				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
22	51,484,825	Bos taurus QARS1	tRNA synthetases	doi:10.1074/jbc.C113.490599	
	51,607,887	Bos taurus ARIH2	Nucleic acid binding and ubiquitin-protein transferase activity	GeneCards	
	56,805,439				
	56,927,672	Bos taurus IFT122	Cell cycle progression, signal transduction, apoptosis, and gene regulation	GeneCards	
	56,943,056	Bos taurus IFT122	Cell cycle progression, signal transduction, apoptosis, and gene regulation	GeneCards	
	58,201,716				
	58,210,660				
	58,345,168				
24	2,393,800				
	3,052,873				
	3,143,836				
	52,336,155				
25	1,011,670				
	16,345,048				
	16,704,949				
	17,166,118				
	17,197,385				
	17,316,731	Bos taurus VPS35L	Obesity	doi:10.1371/journal.pgen.1000976	
	19,173,376				
	19,674,506				
	19,807,341				
	19,995,956				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
25	20,114,319				
	20,123,753	Bos taurus EEF2K	Tumor suppressor	doi:10.1371/journal.pone.0041171	
	21,419,593				
	21,440,612				
	21,486,414	Bos taurus UBFD1	Polyubiquitin binder	doi:10.1016/j.bbapap.2009.02.013	
	21,533,984	Bos taurus PALB2	Tumor suppressor	doi:10.1002/gcc.22045	
	21,633,170				
	21,789,204	Bos taurus PRKCB	B cell activation, apoptosis induction, endothelial cell proliferation, and intestinal sugar absorption	GeneCards	
	22,045,818	Bos taurus PRKCB	B cell activation, apoptosis induction, endothelial cell proliferation, and intestinal sugar absorption	GeneCards	
	22,728,704				
	23,899,904				
26	19,097,135				
	19,109,907				
	19,327,984				
	27,751,543				
	27,967,463	Bos taurus SORCS1	Encodes domain-containing receptor proteins	GeneCards	
	28,001,988	Bos taurus SORCS1	Encodes domain-containing receptor proteins	GeneCards	
	28,780,553				

Table A1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
26	28,930,038				
	28,988,511				
	29,068,665				
	29,287,851				
	29,330,013				
	29,871,678				
	30,209,142				
	31,439,013				
	31,442,262				
	31,980,622				
27	23,928,751				
	29,037,564				X

Table A2. Significant weaning weight (WW) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	11,342,712				
	17,598,522				
	19,518,752				
	22,187,222				
	35,367,693				X
	45,067,210	Bos taurus ZNF596	Nucleic acid binding	GeneCards	X
	61,172,245	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	61,540,639	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	61,958,256				X
	66,058,664	Bos taurus GTF2E1	Sequence-specific DNA binding	GeneCards	X
	71,468,501	Bos taurus PCYT1A	Regulation of phosphatidylcholine biosynthesis	doi:10.1074/jbc.M113.526970	X
	72,178,742				
	72,801,931	Bos taurus ACAP2	GTPase activator	GeneCards	
	74,713,515				
	93,631,890	Bos taurus NLGN1	Neuronal surface	doi:10.1002/0471142301.ns0219s64	X
	93,632,358	Bos taurus NLGN1	Neuronal surface	doi:10.1002/0471142301.ns0219s64	X
	99,597,502				X
	120,315,919				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	135,580,651	Bos taurus EPHB1	Stimulates osteo-adipogenic progenitor proliferation resulting in increased adipogenesis in cell cultures	10.1016/j. prostaglandins.2012.01.001	
	136,029,972				
	138,510,793				
	138,519,398				
	146,433,117	Bos taurus HSF2BP	Testis development	doi:10.1016/s0378-1119(98)00208-x	
2	4,262,209				X
	7,492,224				X
	36,438,945	Bos taurus PLA2R1	Membranous nephropathy	doi:10.3760/cma.j.issn.1003-9406.2013.06.016	X
	75,723,421				X
	75,739,854				X
	89,978,495	Bos taurus ORC2	Origin recognition complex	doi:10.1074/jbc.M111.338467	X
	90,112,552				X
	90,647,574				X
	90,949,696				
	91,103,892	Bos taurus KIAA2012	Unknown	NCBI	X
	91,117,564	Bos taurus KIAA2012	Unknown	NCBI	X
	91,392,375	Bos taurus BMPR2	Bone formation; embryogenesis	NCBI; doi:10.1016/j.anireprosci.2012.08.017	X
	91,411,176	Bos taurus BMPR2	Bone formation; embryogenesis	NCBI; doi:10.1016/j.anireprosci.2012.08.017	X

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	92,514,726				X
	92,777,435				X
	92,796,573				X
	92,939,225				X
	92,971,754				X
	96,774,579				X
	97,003,581	Bos taurus PIKFYVE	Early embryonic development	doi:10.1074/jbc.M111.222364	X
	99,136,417				X
	118,932,435				X
	124,922,135	Bos taurus MECR	Mitochondrial fatty acid synthase	doi:10.1111/j.1574-6968-2009.01688.x	X
	125,853,355				X
	126,186,383				X
	126,317,625				X
	126,703,382	Bos taurus SLC9A1	Regulates pH homeostasis, cell migration, and cell volume	GeneCards	X
	127,720,203	Bos taurus PAFAH2	Metabolism	GeneCards	X
	129,008,096	Bos taurus RCAN3	Neurotransmitter that influences development	NCBI	X
3	35,441,056				
	36,035,377	Bos taurus NTNG1	Guides axon growth during neuronal development	GeneCards	
	36,088,792	Bos taurus NTNG1	Guides axon growth during neuronal development	GeneCards	
	45,227,223				X
	93,467,125				X

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
3	104,578,840				X
	105,822,792	Bos taurus CTPS1	Immune function	GeneCards	X
	106,322,730	Bos taurus SMAP2	Spermiogenesis	doi:10.1091/mbc.E13-05-0234	X
	108,444,081				X
	109,157,709				X
	110,001,844				
	110,003,750				
	110,449,617	Bos taurus AGO3	RNA interference	GeneCards	
	110,587,057				
	111,585,046				
4	27,570,681				
	28,117,205				
	28,215,295				
	31,934,622	Bos taurus KLHL7	Retinitis pigmentosa – difficulty seeing at night and loss of peripheral vision	doi:10.1001/archophthalmol.2010.98	
	32,126,035	Bos taurus IGF2BP3	Skin cancer; eye cancer	doi:10.4081/ejh.2013.e6; doi:10.1016/j.humpath.2012.12.003	
	33,966,904	Bos taurus GRM3	Major excitatory neurotransmitter in the central nervous system; activates ionotropic and metabotropic glutamate receptors; involved in most aspects of normal brain function	GeneCards	
	35,183,415				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	35,558,998				
	36,533,621				
	38,435,198	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	39,567,241				X
	39,700,613				X
	48,408,626				X
	54,063,010				X
	58,563,766				X
	68,658,134	Bos taurus JAZF1	Uterus cancer	doi:10.1158/0008-5472.CAN-05-2485	X
	70,320,578				X
	70,643,370				X
	101,790,675	Bos taurus PTN	Significant roles in cell growth and survival, cell migration, angiogenesis, and tumorigenesis	GeneCards	
	102,433,510	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,513,433	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	112,551,883				
	115,138,746				
	117,132,194	Bos taurus DPP6	Associated with autosomal dominant microcephaly and mental retardation; sclerosis	doi:10.1016/j.ejmg.2013.06.008; doi:10.1016/j.neurobiolaging.2009.05.014	

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	117,308,096	Bos taurus DPP6	Associated with autosomal dominant microcephaly and mental retardation; sclerosis	doi:10.1016/j.ejmg.2013.06.008; doi:10.1016/j.neurobiolaging.2009.05.014	
	120,611,981				
5	557,709				
	32,874,507				
	33,078,266				
	91,107,601				
6	4,399,364				
	10,199,636				
	10,242,400				
	22,880,226				
	22,967,387				
	23,009,696				
	23,039,055				
	23,437,153	Bos taurus MANBA	Severe neurodegenerative lysosomal storage disease	doi:10.1007/s003359901179	
	23,562,312	Bos taurus NFKB1	Mastitis	doi:10.1016/j.micpath.2016.02.013	
	24,709,428				
	36,889,292				
	38,293,497	Bos taurus MEPE	Bone softening	doi:10.1007/s00223-009-9313-z	
	38,599,667	Bos taurus LAP3	Milk production	doi:10.1007/s11033-010-0524-1	
	38,599,864	Bos taurus LAP3	Milk production	doi:10.1007/s11033-010-0524-1	

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
6	38,599,993	Bos taurus LAP3	Milk production	doi:10.1007/s11033-010-0524-1	
	42,239,393				X
	42,633,407				X
	43,517,549				X
	43,649,345				X
	43,989,905				X
	44,023,813				X
	45,216,251				X
	45,300,844				X
	100,644,801				
	117,548,224				
7	1,140,600	Bos taurus RNF130	Embryonic development	GeneCards	
	2,069,225	Bos taurus ADAMTS2	Dermatosparaxis – extremely fragile skin	doi:10.1086/302504	
	5,054,492				
	26,266,887	Bos taurus SLC27A6	Fatty acid composition of milk	doi:10.3168/jds.2013-6703	X
	75,960,737	Bos taurus GABRG2	Epilepsy	doi:10.1016/j.seizure.2012.10.007	X
	76,497,957				X
	76,719,459				X
	76,946,359				X
	77,023,177				X
	78,623,925				
	78,672,889				
	79,444,757				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
7	80,165,783				
	80,573,481				
	80,717,275				
	80,819,058				
	80,885,006				
	92,817,550				
	93,355,753				
	94,562,555				
	94,767,287				
	94,881,428				
8	57,026,214				
	88,021,995	Bos taurus AUH	RNA binding	GeneCards	
9	14,807,106				
	15,732,102	Bos taurus MYO6	Structural integrity of inner ear hair cells	doi:10.1523/jneurosci.4559-12.2013	
	15,972,347				
	16,465,867				
	26,034,690				
	26,772,343	Bos taurus NKAIN2	Lymphoma	GeneCards	
	26,785,284	Bos taurus NKAIN2	Lymphoma	GeneCards	
	27,728,622				
	28,257,531				
	34,681,064				
	49,239,943				X
	51,098,615				X

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
9	53,922,487				X
	54,710,988				X
	86,992,806				
10	1,360,826				
	10,122,128				
	70,596,269				
	92,073,773	Bos taurus NRXN3	Behavioral issues	GeneCards	
	99,858,925				
	100,562,628				
	102,972,150	Bos taurus NRDE2	Life span	doi:10.18632/aging.100191	
	104,193,801				
11	7,781,564				
	9,181,976				
	13,429,329				
	13,450,833				
	14,362,410	Bos taurus SRD5A2	Semen quality	doi:10.3892/mmr.2012.965	
	15,726,355	Bos taurus LTBP1	Fibrillin proteins and latent TGF-beta binding proteins affect TGF-beta availability in the ovary	doi:10.1016/j.mce.2009.03.002	
	35,444,897				
	42,283,105				
	42,330,073				
	45,073,303				
	49,557,164				
	86,751,976				X

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
11	88,958,700				X
	89,236,308				X
	100,817,959	Bos taurus ASS1	Argininosuccinate synthetase deficiency – symptoms include convulsions, hyperventilation, ataxia, hypothermia, lethargy, and poor feeding	doi:10.1073/pnas.86.20.7947	
	102,657,358				
	102,704,292	Bos taurus DDX31	Embryogenesis and spermatogenesis	GeneCards	
12	48,131,404				X
	48,786,733				X
	48,902,740	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	48,956,332	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	48,984,802	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	49,668,909				X
	50,324,576				X
	54,279,558				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
12	54,979,593	Bos taurus NDFIP2	WW domain binding	GeneCards	
	83,777,475				
	87,193,223	Bos taurus FAM155A	Psychiatric disorders	doi:10.1016/S0140-6736(12)62129-1	
13	15,027,093				
	16,332,940	Bos taurus ITIH5	Breast cancer	doi:10.1038/sj.onc.1210669	
	39,901,603	Bos taurus NAA20	Ogden syndrome – an X-lined neurodevelopment disorder, symptoms include growth failure and dysmorphic features	GeneCards	X
	39,961,667				X
	40,379,747				X
	40,606,621				X
	40,986,903	Bos taurus XRN2	Corneal dystrophies	GeneCards	X
	41,083,814				X
	41,303,962				X
	41,748,693				X
14	51,010,240	Bos taurus TRPS1	Breast cancer	doi:10.1007/s12672-010-0008-8	X
	62,478,242				X
	62,478,242				X
	62,830,899				X
	63,777,156	Bos taurus AZIN1	Corpus luteum cysts	GeneCards	X
	63,869,311				X

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
14	64,541,527				X
	67,871,897	Bos taurus STK3	Hippo pathway – organ size	doi:10.1016/j.ydbio.2013.01.030	X
	68,578,968	Bos taurus MATN2	Formation of filamentous networks in the extracellular matrices of various tissues	doi:10.1074/jbc.274.19.13353	X
	68,962,221				X
	70,503,098				X
15	495,098				
	2,922,907				
	3,051,938				
	3,061,918				
	3,078,493				
	3,369,565				
	3,462,006				
	4,094,542				
	4,221,234				
	4,478,076				
	5,367,143				
	5,674,820				
	5,791,533				
	5,904,969				
	6,938,962	Bos taurus CFAP300	Plays a role in axonemal structure organization and motility	GeneCards	
	6,962,261				
	7,306,679				
	7,728,537				
	7,780,636				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	7,929,048				
	7,944,599				
	9,125,948	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	9,327,786	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	9,414,414	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	9,516,602	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	18,725,299	Bos taurus DDX10	RNA binding	GeneCards	
	18,924,675	Bos taurus DDX10	RNA binding	GeneCards	
	19,529,491				
	21,430,642				
	21,869,917				
16	15,247,073				
	22,272,329				
	23,134,140				
	23,186,830				
	23,278,638				
	23,289,551				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
16	24,366,950	Bos taurus RAB3GAP2	Warburg Micro syndrome and Martsolf syndrome – mental retardation, bone and joint anomalies, and genital hypoplasia	doi:10.1042/BST20120169	
	58,045,996				X
	58,900,478				X
	66,653,859				X
	66,755,320				X
	68,006,066				X
	68,063,376				X
	68,069,139				X
	69,010,341	Bos taurus PDC	Phosphoprotein from photoreceptor cells	Lee et al., 1990. J. Biol. Chem. 265:15867-15873	
	72,764,450				
	73,148,406	Bos taurus PPP2R5A	Cardiac dysfunction	doi:10.1093/cvr/cvp037	
	73,226,170				
	74,951,756				
	74,958,644				
	75,465,698	Bos taurus HSD11B1	Conversion of cortisol to cortisone and cortisone to cortisol	GeneCards	
	76,059,261				
	76,423,682				
	76,606,285				
	79,778,212				
	80,172,768				
17	14,133,474				X

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
17	14,243,062	Bos taurus GYPA	Anemia and autoimmune hemolytic	GeneCards	X
	16,441,272				X
	16,751,408				X
	41,882,666				
	48,407,009				
	48,485,869				
	48,994,043				
	59,661,066	Bos taurus KSR2	Obesity and insulin resistance	doi:10.1016/j.cell.2013.09.058	X
18	22,339,904	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,379,853	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,760,455				
	22,956,535				
	23,025,804				
	28,030,835				X
	28,608,495				X
	28,734,924				X
	28,843,447				X
	32,497,164				X
	37,522,665				X
	38,132,252				X
	39,990,553				X
	53,132,012	Bos taurus CLASRP	Paranasal sinus sarcoma and paralytic lagophthalmos – inability to close eyelids	GeneCards	

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
18	65,423,598				
	65,433,421				
	65,456,096				
	65,460,377				
	65,463,329				
19	21,434,766	Bos taurus CORO6	Related to actin filament binding	GeneCards	
	21,470,659				
	27,157,287	Bos taurus MINK1	Brain development	doi:10.1016/s0014-5793(00)01247-3	
	31,638,453				XX*
	32,025,866				XX*
	32,867,556	Bos taurus HS3ST3B1	Herpes virus	doi:10.1016/s0092-8674(00)80058-6	XX*
	32,982,224				X
	33,175,863				X
	41,577,655				
	42,199,423				
	42,996,553	Bos taurus STAT5B	Mastitis and somatic cells	doi:10.1017/S0022029911000148	
	43,755,425	Bos taurus BRCA1	Mastitis	doi:10.1007/s11033-012-1467-5	
	43,856,171				
	44,431,617				
	50,125,452	Bos taurus PSMD12	Mental disabilities	GeneCards	
20	2,523,465	Bos taurus KCNIP1	Target recognition of neuronal calcium sensor proteins	doi:10.1016/j.bbagen.2011.10.003	

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
20	50,387,798				X
21	10,565,190				
	10,712,478				
	10,944,434				
	12,095,049				
	12,181,960				
	17,568,377				
	17,679,035				
	18,787,164				
	21,042,466	Bos taurus ABHD2	Sperm activation	doi:10.1126/science.aad6887	
	22,690,957				
	35,640,578	Bos taurus STXBP6	Deafness	GeneCards	
	36,578,144				
	62,140,403				
	62,656,572				
	62,709,685	Bos taurus BDKRB2	Vasodilation, edema, smooth muscle spasm, and pain fiber stimulation	GeneCards	
	64,152,628				
	65,160,222				
	65,198,296				
	65,198,296				
	66,310,479				
	67,220,188				
	68,461,213	Bos taurus PPP2R5C	Tumor suppressor	doi:10.1074/jbc.M111.334094	

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
21	69,545,389				
	70,182,028				
	70,182,980				
	70,769,579				
22	1,305,852				
	1,370,907				
	2,314,019				
	2,332,558				
	25,575,807				
	30,819,495				
	30,894,155				
	39,122,937	Bos taurus C22H3orf14	Influence immune response associated with mastitis resistance	doi:10.1073/pnas.0601015103	
	40,232,132	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	X
	40,748,442	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	41,171,245	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	42,270,737				X
	42,284,451				X
	42,304,410				X
	42,616,545				X
	42,826,746				X
	43,094,806				X
	43,133,215				X
	43,490,927	Bos taurus PXK	Epidermal growth factors receptor	doi:10.1128/MCB.01105-09	X

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
22	43,534,982	Bos taurus PXK	Epidermal growth factors receptor	doi:10.1128/MCB.01105-09	X
	43,744,791	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	44,083,638				
	44,860,043				
	45,047,902				
	45,225,119	Bos taurus ERC2	Component of HUSH complex – multiprotein complex that mediates epigenetic repression	GeneCards	
	45,455,314	Bos taurus ERC2	Component of HUSH complex – multiprotein complex that mediates epigenetic repression	GeneCards	
	45,696,332				
	45,954,406				
	45,966,034				
	46,465,290				
	46,533,857	Bos taurus CACNA2D3	Tumor suppression	doi:10.1002/ijc.28252	
	47,327,649	Bos taurus CACNA2D3	Tumor suppression	doi:10.1002/ijc.28252	
	47,736,966	Bos taurus CACNA1D	Brain function	doi:10.1159/000054692	
	58,201,716				
23	13,484,531				
	48,577,286				
	48,579,646				
24	2,393,800				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
24	5,410,963	Bos taurus NETO1	Memory	GeneCards	
	9,760,206				
	10,343,062				
	17,179,801				
	29,605,711				
	39,629,608				
	41,143,699				
	42,420,755				
	43,061,787				
	45,497,032				
	45,601,179				
	46,901,718	Bos taurus ST8SIA5	Protein metabolism	GeneCards	
	46,907,845	Bos taurus ST8SIA5	Protein metabolism	GeneCards	
	47,859,057				
	48,553,409				
	48,566,369				
	48,593,796				
	48,847,947				
	49,813,314				
	50,391,320				
	50,412,323				
	50,413,079				
	50,568,228				
	50,911,996	Bos taurus ME2	Epilepsy	doi:10.1086/426735	

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
24	51,267,320				
	51,671,282				
	52,336,155				
	53,946,649				
	54,134,726				
25	20,123,753	Bos taurus EEF2K	Tumor suppressor	doi:10.1371/journal.pone.0041171	
	27,028,950				
26	15,604,631	Bos taurus PLCE1	Esophagus cancer	doi:10.1111/amp.12095	
	19,097,135				
	19,109,907				
	19,771,726				
	19,973,761				
	23,024,262	Bos taurus SUFU	Early development	GeneCards	
	27,006,638				
	27,967,463	Bos taurus SORCS1	Encodes domain-containing receptor proteins	GeneCards	
	28,001,988	Bos taurus SORCS1	Encodes domain-containing receptor proteins	GeneCards	
	29,068,665				
	29,217,369				
	29,871,678				
	31,442,262				
	31,980,622				
	32,766,500				
	33,066,487				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
26	33,161,627				
	33,349,780				
	34,053,110				
	36,650,431				
	42,134,297				
	42,178,883				
	42,204,081				
	42,229,222				
	43,453,685				
27	10,764,825				
	22,555,911				
	23,040,097				
	23,399,753				
	23,598,119				
	23,688,304				
	23,928,751				
	24,588,014				
	25,392,013	Bos taurus SARAF	Regulatory factor of calcium homeostasis	NCBI	
28	23,694,498	Bos taurus CTNNA3	Cardiomyopathy	doi:10.1093/eurheartj/ehs373	
		Bos taurus LRRTM3	Autism	doi:10.1186/2040-2392-1-7	
29	25,252,506				
	25,348,969				

*SNP that fall within more than one ROH on the same chromosome

Table A2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
29	25,997,272	Bos taurus CSRP3	Cardiomyopathy	doi:10.1093/hmg/ddn160	
	26,009,040	Bos taurus CSRP3	Cardiomyopathy	doi:10.1093/hmg/ddn160	
	26,019,088				
	26,697,399				
	26,751,704				
	27,563,511				
	32,925,700	Bos taurus ARHGAP32	Regulation of dendritic spine morphology	doi:10.1111/j.1471-4159.2008.05335.x	
	50,569,383	Bos taurus TSPAN4	Deafness	GeneCards	
	50,600,689				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Significant yearling weight (YW) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	17,598,522				
	19,518,752				
	28,990,475				
	29,004,968				
	29,109,257				
	31,173,269				
	55,784,222				X
	55,930,246				X
	56,279,860				X
	56,666,304				X
	56,669,858				X
	56,705,107				X
	56,923,157				X
	57,170,980				X
	57,403,359				X
	57,660,748				X
	57,920,148				X
	58,268,848				X
	58,480,973				X
	58,620,225	Bos taurus SPICE1	Cell division	doi:10.1242/jcs.069963	X
	58,639,595	Bos taurus SPICE1	Cell division	doi:10.1242/jcs.069963	X
	58,695,977	Bos taurus SIDT1	RNA transmembrane transporter activity	GeneCards	X
	59,123,524				X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	59,309,948	Bos taurus DRD3	Tremors	GeneCards	X
	60,158,712				X
	61,958,256				X
	66,058,664	Bos taurus GTF2E1	Sequence-specific DNA binding	GeneCards	X
	69,244,252	Bos taurus KALRN	Synaptic function	doi:10.1007/s12035-011-8223-z	X
	71,015,840				X
	71,104,778				X
	71,468,501	Bos taurus PCYT1A	Regulation of phosphatidylcholine biosynthesis	doi:10.1074/jbc.M113.526970	X
	71,676,702				
	72,178,742				
	72,801,931	Bos taurus ACAP2	GTPase activator	GeneCards	
	74,713,515				
	95,979,250	Bos taurus FNDC3B	Adipogenesis	doi:10.1016/j.febslet.2004.09.062	X
	96,507,612				X
	96,905,786				X
	99,597,502				X
	99,642,111				X
	143,614,490				
	146,433,117	Bos taurus HSF2BP	Testis development	doi:10.1016/s0378-1119(98)00208-x	
	158,090,253				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	89,978,495	Bos taurus ORC2	Origin recognition complex	doi:10.1074/jbc.M111.338467	X
	90,112,552				X
	90,647,574				X
	90,949,696				X
	91,084,672	Bos taurus KIAA2012	Unknown	NCBI	X
	91,103,892	Bos taurus KIAA2012	Unknown	NCBI	X
	91,117,564	Bos taurus KIAA2012	Unknown	NCBI	X
	91,357,390	Bos taurus BMPR2	Bone formation; embryogenesis	NCBI; doi:10.1016/j.anireprosci.2012.08.017	X
	91,392,375	Bos taurus BMPR2	Bone formation; embryogenesis	NCBI; doi:10.1016/j.anireprosci.2012.08.017	X
	91,411,176	Bos taurus BMPR2	Bone formation; embryogenesis	NCBI; doi:10.1016/j.anireprosci.2012.08.017	X
	92,514,726				X
	92,777,435				X
	92,796,573				X
	92,828,714				X
	92,939,225				X
	92,943,252				X
	92,971,754				X
	96,774,579				X
	96,799,132				X
	97,003,581	Bos taurus PIKFYVE	Early embryonic development	doi:10.1074/jbc.M111.222364	X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	99,136,417				X
	118,259,844				X
	118,517,271				X
	118,773,633	Bos taurus FBXO36	Unknown	NCBI	X
	118,932,435				X
	118,953,961				X
	119,155,003				X
	119,564,531				X
	119,576,421				X
	119,768,964				X
	119,777,560				X
	120,008,794				X
	120,487,760	Bos taurus DIS3L2	Wilms tumor – cancer that starts in the kidneys at an early age	doi:10.1002/ajmg.c.31358	X
	120,542,406	Bos taurus DIS3L2	Wilms tumor – cancer that starts in the kidneys at an early age	doi:10.1002/ajmg.c.31358	X
	120,775,372	Bos taurus DIS3L2	Wilms tumor – cancer that starts in the kidneys at an early age	doi:10.1002/ajmg.c.31358	X
	120,886,359				X
	121,387,324				X
	121,418,332	Bos taurus AZIN2	Corpus luteum cysts	GeneCards	X
	121,618,105				X
	121,707,643	Bos taurus YARS1	Nerve damage	GeneCards	X
	121,738,562				X
	121,777,578				X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	121,847,018				X
	122,177,338	Bos taurus IQCC	Unknown	NCBI	X
	122,935,290				X
	123,045,219				X
	123,103,934	Bos taurus PUM1	Protects spermatogenesis	doi:10.1016/j.cub.2012.01.039	X
	123,107,094	Bos taurus PUM1	Protects spermatogenesis	doi:10.1016/j.cub.2012.01.039	X
	123,128,752	Bos taurus PUM1	Protects spermatogenesis	doi:10.1016/j.cub.2012.01.039	X
	123,615,442				X
	124,231,499				X
	124,922,135	Bos taurus MECR	Mitochondrial fatty acid synthase	doi:10.1111/j.1574-6968-2009.01688.x	X
	125,248,041	Bos taurus OPRD1	Opioid dependence	doi:10.1016/j.drugalcdep.2012.06.023	X
	125,707,849	Bos taurus SESN2	Cellular response to stress	doi:10.1038/cdd.2012.157	X
	125,716,884				X
	125,853,355				X
	126,375,615				X
	126,548,259				X
	126,703,382	Bos taurus SLC9A1	Regulates pH homeostasis, cell migration, and cell volume	GeneCards	X
	126,721,147	Bos taurus SLC9A1	Regulates pH homeostasis, cell migration, and cell volume	GeneCards	X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	127,047,563	Bos taurus ARID1A	Tumor progression	doi:10.1097/PAS.ob013e3182889dc3	X
	127,532,867	Bos taurus FAM110D	Unknown	NCBI	X
3	34,080,566				
	34,083,582	Bos taurus SYPL2	Myopathy	doi:10.1083/jcb.147.7.1473	
	35,441,056				
	35,698,990				
	40,646,601	Bos taurus COL11A1	Fibrochondrogenesis	doi:10.1016/j.ajhg.2010.20.009	
	41,265,596				
	41,519,979	Bos taurus OLFM3	Regulation of collagen development	doi:10.1007/s12035-009-8076-x	
	41,671,262				
	43,023,823				X
	43,939,238				X
	43,940,802				X
	44,172,303				X
	45,227,223				X
	86,570,007				X
4	190,619				
	4,741,200				
	6,035,725				
	6,049,251				
	6,078,027				
	10,494,415	Bos taurus VPS50	Endocytic recycling	GeneCards	

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	17,943,164				
	18,293,340				
	112,551,883				
	117,132,194	Bos taurus DPP6	Associated with autosomal dominant microcephaly and mental retardation; sclerosis	doi:10.1016/j.ejmg.2013.06.008; doi:10.1016/j.neurobiolaging.2009.05.014	
	117,308,096	Bos taurus DPP6	Associated with autosomal dominant microcephaly and mental retardation; sclerosis	doi:10.1016/j.ejmg.2013.06.008; doi:10.1016/j.neurobiolaging.2009.05.014	
	120,611,981				
5	19,949,248				X
	19,983,794				X
	20,187,722				X
	20,236,905				X
	20,451,667				X
	20,627,843				X
	20,724,589				X
	20,859,221				X
	21,124,142				X
	21,389,684				X
	21,509,243				X
	21,768,260				X
	21,829,834				X
	21,907,909				X
	22,726,676				X
	22,943,453				X
	24,141,472	Bos taurus PLXNC1	Melanoma	doi:10.1002/humu.21017	X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
5	25,425,554				X
	32,874,507				X
	38,918,719				X
	39,218,185				X
	39,223,986				X
	39,720,278	Bos taurus PDZRN4	Ubiquitin-protein transferase activity and ubiquitin protein ligase activity	GeneCards	X
	40,058,566	Bos taurus CNTN1	Central nervous system	doi:10.1073/pnas.1313769110	X
	41,415,525	Bos taurus SLC2A13	Myo-inositol: proton symporter activity	doi:10.1038/sj.emboj.7600072	X
	41,830,903				X
	42,024,923	Bos taurus KIF21A	Congenital fibrosis of the extraocular muscles	doi:10.3892/ijmm.2011.759	X
	42,188,101				X
	42,488,128	Bos taurus CPNE8	Calcium-dependent phospholipid binding	doi:10.1021/bi0019949	X
	44,885,503				X
	63,160,794	Bos taurus APAF1	Apoptosis	doi:10.1016/j.str.2011.05.013	X
	68,420,453	Bos taurus CHST11	Coordinate skeletal movement	doi:1242/dev.019950	X
	68,614,168	Bos taurus CHST11	Coordinate skeletal movement	doi:1242/dev.019950	X
	91,107,601				
	115,296,185				
	116,167,919				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
5	120,687,427				
6	16,145,912	Bos taurus ENPEP	Hypertension	doi:10.1007/s10741-007-9065-7	
	25,834,687				
	26,377,975	Bos taurus MTTP	Abetalipoproteinemia – interferes with normal absorption of fat and fat-soluble vitamins from food	doi:10.1194/jlr.M031658	
	38,825,835				X
	49,130,874				X
	50,567,007				X
	50,593,861				X
	51,247,362				X
	51,439,843				X
	78,302,761				
	78,334,666				
	78,862,493	Bos taurus ADGRL3	Attention-deficit/hyperactivity disorder	doi:10.1016/j.euroneuro.2012.11.001	
	79,006,685	Bos taurus ADGRL3	Attention-deficit/hyperactivity disorder	doi:10.1016/j.euroneuro.2012.11.001	
	79,063,882	Bos taurus ADGRL3	Attention-deficit/hyperactivity disorder	doi:10.1016/j.euroneuro.2012.11.001	
	79,166,927	Bos taurus ADGRL3	Attention-deficit/hyperactivity disorder	doi:10.1016/j.euroneuro.2012.11.001	
	79,203,343	Bos taurus ADGRL3	Attention-deficit/hyperactivity disorder	doi:10.1016/j.euroneuro.2012.11.001	
	81,169,373				
	82,965,163				
	93,674,959				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
7	715,134				
	26,266,887	Bos taurus SLC27A6	Fatty acid composition of milk	doi:10.3168/jds.2013-6703	X
	80,885,006				
	85,220,722				
	89,967,934				
	92,817,550				
	93,355,753				
	94,284,572				
	94,562,555				
	94,767,287				
	102,328,838				
	104,961,250				
	105,035,315	Bos taurus NUDT12	Metabolism of water-soluble vitamins	GeneCards	
	105,243,639				
	105,263,914				
	105,422,685				
	105,621,232				
	105,974,829				
	106,730,109				
	106,738,136				
	107,527,276				
	107,706,815				
	107,735,569				
	107,837,688				
	107,894,858				
	107,921,509				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
7	108,125,984				
	108,598,522				
	110,397,885				
	111,782,120				
	111,931,788				
	112,393,056				
	112,538,624				
	112,552,708				
	112,594,442				
8	9,021,297				X
	9,047,553				X
	10,203,115	Bos taurus ZNF395	Huntington's disease	doi:10.1074/jbc.M310726200	X
	10,566,477	Bos taurus ELP3	Neurological disorders	doi:10.1016/j.molmed.2009.11.002	X
	10,723,864	Bos taurus SCARA5	Prostate sarcoma	GeneCards	X
	10,733,848	Bos taurus SCARA5	Prostate sarcoma	GeneCards	X
	12,657,766				X
	16,188,404				X
	99,176,833				
	101,044,054	Bos taurus PALM2	Hypertrichosis	GeneCards	
	101,796,474				
	101,936,668	Bos taurus MUSK	Muscle weakness	doi:10.1371/journal.pone.0053826	

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
8	102,111,609	Bos taurus LPAR1	Pulmonary fibrosis	GeneCards	
	103,067,461				
	103,250,620				
	103,305,018				
	104,404,915				
	111,931,788				
	112,393,056				
	112,538,624				
	112,552,708				
	112,594,442	Bos taurus GSN	Amyloidosis	doi:10.1007/s10048-012-0330-0	
9	15,312,685				
	15,368,823				
	15,732,102	Bos taurus MYO6	Structural integrity of inner ear hair cells	doi:10.1523/jneurosci.4559-12.2013	
	26,034,690				
	28,979,477	Bos taurus PKIB	Brain cancer	doi:10.1023/a:1015079705841	
	29,049,570				
	29,244,257				
	29,292,408				
	29,421,267				
	32,142,930	Bos taurus MAN1A1	Protein metabolism	GeneCards	
	32,173,083	Bos taurus MAN1A1	Protein metabolism	GeneCards	
	33,050,144				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
9	33,688,782				
	36,707,200	Bos taurus HS3ST5	Mental retardation	GeneCards	
	38,339,200				
	45,246,969	Bos taurus PREP	Celiac disease	GeneCards	
	45,581,923				
	46,045,008				
	47,208,243				
	77,302,555				
	77,384,381				
	77,541,646				
	77,576,301				
	103,728,559				
	104,154,509				
	104,161,265				
	104,994,550				
10	238,014				
	1,250,058				
	1,268,686				
	51,671,253	Bos taurus ADAM10	Alzheimer's disease	doi:10.1073/pnas.96.7.3922	X
	51,735,816	Bos taurus ADAM10	Alzheimer's disease	doi:10.1073/pnas.96.7.3922	X
	51,803,725	Bos taurus LIPC	Hepatic lipase deficiency	GeneCards	X
	51,827,797	Bos taurus LIPC	Hepatic lipase deficiency	GeneCards	X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
10	51,839,164	Bos taurus LIPC	Hepatic lipase deficiency	GeneCards	X
	54,082,665				X
	57,611,774				X
	60,198,169				X
	60,394,494				X
	61,709,905				X
	72,999,985				X
11	2,903,136				
	3,016,909	Bos taurus ZAP70	Immunodeficiency	doi:10.1016/j.gene.2012.10.062	
	3,045,232	Bos taurus ZAP70	Immunodeficiency	doi:10.1016/j.gene.2012.10.062	
	4,199,727				
	42,102,223				
	95,637,394				X
	100,817,959	Bos taurus ASS1	Argininosuccinate synthetase deficiency – symptoms include convulsions, hyperventilation, ataxia, hypothermia, lethargy, and poor feeding	doi:10.1073/pnas.86.20.7947	
12	7,608,159				
	10,719,656				X
13	7,248,447	Bos taurus TASP1	Tumor suppressor	doi:10.1158/0008-5472.CAN-11-2584	
	9,269,676	Bos taurus MACROD2	Hypogonadism – male testes or female ovaries produce little to no sex hormones	GeneCards	
	12,737,871				
	59,101,909				X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
13	69,794,006				X
	75,742,150				X
14	6,276,199				
	6,463,583				
	12,190,775				
	13,214,504				
	45,406,866	Bos taurus MRPS28	Mitochondrial translation	doi:10.1093/nar/gks774	X
	75,964,148				X
	76,067,415				X
	76,202,934				X
15	3,061,918				
	3,078,493				
	3,369,565				
	3,462,006				
	4,094,542				
	4,478,076				
	5,367,143				
	5,674,820				
	5,791,533				
	5,904,969				
	7,306,679				
	15,434,044				
	16,817,080	Bos taurus GUCY1A2	Heme protein receptor	GeneCards	
	16,937,958	Bos taurus GUCY1A2	Heme protein receptor	GeneCards	

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	16,989,950	Bos taurus GUCY1A2	Heme protein receptor	GeneCards	
	17,080,803	Bos taurus GUCY1A2	Heme protein receptor	GeneCards	
	17,107,459				
	17,199,655	Bos taurus ALKBH8	Intellectual development disorder	GeneCards	
	17,768,941	Bos taurus RAB39A	Plays a role in maturation and acidification of phagosomes that engulf pathogens	GeneCards	
	18,137,423	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	18,218,536	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	19,377,108				
	19,529,491				
	19,605,113				
	19,906,629				
	19,959,252				
	20,171,885				
	21,207,529				
	21,430,642				
	21,869,917				
	25,586,735				X
	63,010,760	Bos taurus DNAJC24	Wilms tumor – cancer that starts in the kidneys at an early age	GeneCards	X
	71,904,712				X
	71,909,775				X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	72,071,828				X
16	13,479,918				
	13,695,211				
	15,537,023				
	20,688,106				
	22,272,329				
	22,314,631				
	24,102,165				
	24,116,365				
	24,366,950	Bos taurus RAB3GAP2	Warburg Micro syndrome and Martsolf syndrome – mental retardation, bone and joint anomalies, and genital hypoplasia	doi:10.1042/BST20120169	
	24,613,337				X
	47,987,928				X
	48,412,158				X
	48,658,207				X
	48,821,912				X
	49,822,747				X
	62,054,237				X
	62,790,846				X
	63,626,640	Bos taurus STX6	Neuropathy	GeneCards	X
	64,971,348				X
	65,815,981				X
	66,653,859				X
	66,755,320				X
	66,883,771				X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
16	67,068,198	Bos taurus C16H1orf21	Prostate cancer	doi:10.1006/geno.2001.6500	X
	67,159,362				X
	67,607,778	Bos taurus RNF2	Angelman syndrome	GeneCards	X
	67,703,949				X
	67,757,664				X
	67,767,956	Bos taurus IVNS1ABP	Influenza	Wolff et al., 1998. J. Virol. 72:7170-80	X
	67,888,290				X
	67,995,016				X
	69,010,341	Bos taurus PDC	Phosphoprotein from photoreceptor cells	Lee et al., 1990. J. Biol. Chem. 265:15867-15873	
	71,485,655				
	71,625,483				
	72,319,661	Bos taurus RPS6KC1	Periventricular leukomalacia – brain injury that affects premature infants	GeneCards	
	72,322,411	Bos taurus RPS6KC1	Periventricular leukomalacia – brain injury that affects premature infants	GeneCards	
	73,148,406	Bos taurus PPP2R5A	Cardiac dysfunction	doi:10.1093/cvr/cvp037	
	73,226,170				
	73,425,409	Bos taurus INTS7	Gastric cancer	GeneCards	
	73,596,503	Bos taurus LPGAT1	Cardiomyopathy	GeneCards	

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
16	73,787,623				
	79,360,604				
	80,891,186				
17	9,891,448	Bos taurus NR3C2	Mineralocorticoid receptor	doi:10.3389/fnbeh.2013.00056	
	10,416,957	Bos taurus ARHGAP10	GTPase activator activity	Lancaster et al. 1994. J. Biol. Chem. 269:1137-42	
	11,828,433				
	16,441,272				X
	16,751,408				X
	41,686,505	Bos taurus TMEM144	Carbohydrate transmembrane transporter activity	GeneCards	
	41,778,876	Bos taurus GASK1B	Unknown	NCBI	
	41,882,666				
	46,090,458	Bos taurus EP400	Epilepsy	GeneCards	
	47,203,601				
18	5,751,720	Bos taurus WWOX	Epileptic encephalopathy	GeneCards	
	7,704,404				
	34,598,746				X
	34,935,487	Bos taurus KIAA0895L	Urogenital and caudal dysgenesis	doi:10.1093/hmg.ddi011	X
	34,992,628	Bos taurus FHOD1	Cerebral amyloid angiopathy	GeneCards	X

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
18	53,132,012	Bos taurus CLASRP	Paranasal sinus sarcoma and paralytic lagophthalmos – inability to close eyelids	GeneCards	
	58,008,113				
	58,463,665				
	59,284,273				
19	8,889,398	Bos taurus MRPS23	Colorectal cancer	GeneCards	
	13,184,140	Bos taurus MYO19	Hyperkalemic periodic paralysis	GeneCards	
	26,881,051				
	26,926,279				
	29,007,477				X
	29,767,462				X
	30,226,608				X
	31,592,333				XX*
	35,755,815				
	37,437,821				
	38,392,511				
	50,125,452	Bos taurus PSMD12	Mental disabilities	GeneCards	
	58,642,115				
	58,751,768				
	60,811,182				
	63,943,069				
21	18,787,164				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
21	21,042,466	Bos taurus ABHD2	Sperm activation	doi:10.1126/science.aad6887	
	35,640,578	Bos taurus STXBP6	Deafness	GeneCards	
	58,256,729	Bos taurus ITPK1	Neural tube defects	GeneCards	
	59,644,071				
	59,793,553	Bos taurus SERPINA5	Thrombosis	GeneCards	
	60,588,824				
	61,055,832	Bos taurus LOC784932	Alzheimer's disease	doi:10.1007/s11033/012-1472-8	
		Bos taurus KRTCAP2	Granulomatous disease	GeneCards	
	61,068,120	Bos taurus LOC784932	Alzheimer's disease	doi:10.1007/s11033/012-1472-8	
		Bos taurus KRTCAP2	Granulomatous disease	GeneCards	
	61,319,019	Bos taurus LOC784932	Alzheimer's disease	doi:10.1007/s11033/012-1472-8	
		Bos taurus KRTCAP2	Granulomatous disease	GeneCards	

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
21	61,355,008	Bos taurus LOC784932	Alzheimer's disease	doi:10.1007/s11033/012-1472-8	
		Bos taurus KRTCAP2	Granulomatous disease	GeneCards	
	61,409,227	Bos taurus LOC784932	Alzheimer's disease	doi:10.1007/s11033/012-1472-8	
		Bos taurus KRTCAP2	Granulomatous disease	GeneCards	
	61,412,716	Bos taurus LOC784932	Alzheimer's disease	doi:10.1007/s11033/012-1472-8	
		Bos taurus KRTCAP2	Granulomatous disease	GeneCards	
	61,503,433	Bos taurus LOC784932	Alzheimer's disease	doi:10.1007/s11033/012-1472-8	
		Bos taurus KRTCAP2	Granulomatous disease	GeneCards	
	62,245,543				
	62,257,313				
	62,414,563				
	62,450,328				
	62,502,588				
	62,656,572				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
21	63,286,443	Bos taurus VRK1	Loss of spermatogonia	doi:10.1095/biolreprod.109.079095	
	64,152,628				
22	1,243,288				
	45,455,314	Bos taurus ERC2	Component of HUSH complex – multiprotein complex that mediates epigenetic repression	GeneCards	
	45,696,332				
	45,954,406				
	58,201,716				
	60,543,119				
23	11,745,700	Bos taurus ZFAND3	Spermatogenesis	doi:10.1006/excr.1999.4482	
	12,056,387	Bos taurus BTBD9	Restless leg syndrome	doi:10.1136/jmg.2010.087858	
	18,338,751	Bos taurus SUPT3H	Dysostosis	GeneCards	
	49,137,925	Bos taurus FARS2	Mitochondrial phenylalanyl-tRNA synthetase	doi:10.1073/pnas.88.19.8387	
24	2,393,800				
	22,403,126				
	31,544,758				
	31,734,641	Bos taurus ZNF521	Cell cancer	GeneCards	
	39,304,066				
	39,629,608				
	41,143,699				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
24	41,579,956				
	42,582,505				
	47,859,057				
	48,999,628				
	49,813,314				
	50,255,173				
	50,412,323				
	50,413,079				
	50,911,996	Bos taurus ME2	Epilepsy	doi:10.1086/426735	
	55,656,457				
25	1,011,670				
	1,352,670				
	10,526,660				
	11,022,673	Bos taurus SNX29	Monoclonal paraproteinemia	GeneCards	
	11,248,699	Bos taurus SNX29	Monoclonal paraproteinemia	GeneCards	
	15,885,509				
	18,490,646				
	30,269,233				
	32,755,073				
26	17,577,730				
	20,490,701				
	36,650,431				
	36,757,615				
	37,495,624				

*SNP that fall within more than one ROH on the same chromosome

Table A3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
26	42,134,297				
	42,178,883				
	42,204,081				
	42,229,222				
27	2,995,076				
	3,069,501				
	3,076,246				
	10,338,431				
	11,342,766				
	11,657,439				
	11,715,052				
	11,862,558				
	12,199,787				
	13,665,873				
	28,368,840	Bos taurus FUT10	Fucosyltransferase activity	doi:10.1074/jbc.M100573200	X
	30,201,519				X
	42,344,117				X
	44,507,101				
	44,610,312				
	44,629,833				
	44,795,496				
	44,943,382				
	45,217,020				
29	16,291,872				

*SNP that fall within more than one ROH on the same chromosome

Table A4. Significant calving ease (CE) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	61,172,245	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	61,540,639	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	61,806,466				X
	119,544,478	Bos taurus WWTR1	Enhances osteogenic differentiation and suppresses adipogenic differentiation	doi:10.1111/j.1476-5381.2011.01664.x	
	120,109,716	Bos taurus GYG1	Muscle specific regulatory domain	doi:10.1016/s0378-1119(99)00211-5	
	120,315,919				
	120,326,805				
	120,479,376	Bos taurus AGTR1	Potent vasopressor hormone; primary regulator of aldosterone secretion; important effector controlling blood pressure and volume of cardiovascular system	GeneCards	
	131,163,604				
	134,937,491				
	135,580,651	Bos taurus EPHB1	Stimulates osteo-adipogenic progenitor proliferation resulting in increased adipogenesis in cell cultures	10.1016/j. prostaglandins.2012.01.001	
	138,519,398				
2	129,008,096	Bos taurus RCAN3	Neurotransmitter that influences development	NCBI	X
3	2,624,552				
	3,231,882				
	3,331,788				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
3	108,444,081				X
	110,449,617	Bos taurus AGO3	RNA interference	GeneCards	
	111,585,046				
4	33,636,014	Bos taurus KIAA1324L	Embryo development	doi:10.1074/jbc.M110.177907	
	33,966,904	Bos taurus GRM3	Major excitatory neurotransmitter in the central nervous system; activates ionotropic and metabotropic glutamate receptors; involved in most aspects of normal brain function	GeneCards	
	34,693,882				
	34,723,945				
	34,738,011				
	34,867,416				
	35,183,415				
	35,558,998				
	35,605,434	Bos taurus SEMA3D	Encodes a member of the semaphorin III family of secreting signaling proteins that are involved in axon guidance during neuronal development	GeneCards	
	35,705,474	Bos taurus SEMA3D	Encodes a member of the semaphorin III family of secreting signaling proteins that are involved in axon guidance during neuronal development	GeneCards	
	36,182,094				
	36,354,506				
	36,533,621				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	38,486,244	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,548,833	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,571,065	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,573,157	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,680,360	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	54,097,830	Bos taurus FOXP2	Essential for proper development of speech and language regions of the brain during embryogenesis; may be involved in variety of biological pathways and cascades that influence language development	GeneCards	X
	58,540,307				X
	58,563,766				X
	101,523,850				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	101,617,832				
	101,790,675	Bos taurus PTN	Significant roles in cell growth and survival, cell migration, angiogenesis, and tumorigenesis	GeneCards	
	102,432,527	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,433,510	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,447,483	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,513,433	Bos taurus CREB3L2	Form homodimers; transcriptional activator	GeneCards	
	102,877,319				
	103,092,493				
	103,484,220				
	105,345,171				
	105,392,433				
5	5,120,813				X
	109,655,733	Bos taurus BID	Bladder transitional cell papilloma	GeneCards	
6	43,517,549				X
	43,649,345				X
7	765,687				
	1,263,597				
	29,791,340				X
	80,885,006				
	91,484,380				
	94,562,555				
	94,767,287				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
8	105,946,838				
	106,241,362				
9	26,772,343	Bos taurus NKAIN2	Lymphoma	GeneCards	
	27,728,622				
	28,257,531				
10	32,955,493				X
	35,036,509				X
	35,086,759				X
11	5,964,756	Bos taurus NPAS2	Important regulator of physiological functions including metabolism, sleep, body temperature, blood pressure, endocrine, immune, cardiovascular, and renal	GeneCards	
	7,712,524				
	42,102,223				
12	21,441,958				X
	21,472,748				X
	47,915,012				X
	48,036,822				X
	48,131,404				X
	48,902,740	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	48,984,802	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
12	49,095,991	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	49,123,661	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	50,324,576				X
14	64,541,527				X
	70,503,098				X
15	1,363,910				
	1,579,240				
	2,922,907				
	3,051,938				
	3,061,918				
	3,078,493				
	3,369,565				
	3,416,019				
	3,462,006				
	3,482,264	Bos taurus CASP4	Mastitis	doi:10.1007/s00335-001-2145-4 and GeneCards	
	3,745,000				
	4,094,542				
	4,149,756				
	4,478,076				
	4,692,182	Bos taurus PDGFD	Ovarian cancer	Wang et al., 2011. Asian Pac. J. Cancer Prev. 12:3367-70	
	4,789,493				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	4,836,419				
	4,887,219				
	5,342,417				
	5,674,820				
	6,180,970				
	6,740,672				
	6,938,962	Bos taurus CFAP300	Plays a role in axonemal structure organization and motility	GeneCards	
	6,962,261				
	7,728,537				
	7,780,636				
	7,929,048				
	7,944,599				
	7,989,843				
	8,836,147				
	8,905,048				
	8,937,081				
	9,125,948	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	17,768,941	Bos taurus RAB39A	Plays a role in maturation and acidification of phagosomes that engulf pathogens	GeneCards	
	18,137,423	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	18,218,536	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	19,377,108				
	19,409,074				
	19,529,491				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	19,605,113				
	19,906,629				
	19,959,252				
	20,171,885				
	21,061,865	Bos taurus ARHGAP20	Impacts neurite outgrowth	GeneCards	
	35,143,414	Bos taurus SERGEF	Regulator of chromosome condensation	NCBI	
	35,606,202	Bos taurus ABCC8	Transport various molecules across extra- and intra-cellular membranes	NCBI	
	65,235,259				X
	72,624,841				X
16	68,714,893	Bos taurus HMCN1	Age-related macular degeneration	doi:10.1002/humu.20464	
	68,857,193				
	68,981,703	Bos taurus ODR4	Protein expression	doi:10.1076/opge.24.141.15604	
	69,010,341	Bos taurus PDC	Phosphoprotein from photoreceptor cells	Lee et al., 1990. J. Biol. Chem. 265:15867-15873	
	71,485,655				
	71,625,483				
	74,958,644				
	75,465,698	Bos taurus HSD11B1	Conversion of cortisol to cortisone and cortisone to cortisol	GeneCards	
	76,059,261				
	76,423,682				
	76,606,285				
17	52,587,482				X
	52,698,842				X

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
18	22,339,904	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,379,853	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,760,455				
	22,956,535				
	23,025,804				
	26,282,975				
	26,362,767				
	26,380,950	Bos taurus NDRG4	Cell cycle progression	doi:10.1074/jbc.M109.012484	
	27,101,515				
	27,121,621				
	27,410,770				
	27,579,708				
	27,719,066				
	27,769,678				X
	27,870,868				X
	28,030,835				X
	28,372,073				X
	28,608,495				X
	28,734,924				X
	28,843,447				X
	29,078,437				X
	29,466,879				X
	30,018,259				X
	32,855,646	Bos taurus CDH11	Promotes the metastasis of cancer cells to bone	doi:10.1158/1541-7786.MCR-08-0077; doi:10.3892/ijo.33.1.17	X
	65,456,096				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
18	65,460,377				
	65,463,329				
19	18,943,093				
	20,123,437				
	21,432,208	Bos taurus CORO6	Related to actin filament binding	GeneCards	
	21,434,766	Bos taurus CORO6	Related to actin filament binding	GeneCards	
	21,470,659				
	21,510,144				
	21,579,655				
	21,878,635				
	22,304,690	Bos taurus ABR	Encodes a GTPase-activating	GeneCards	
20	2,523,465	Bos taurus KCNIP1	Target recognition of neuronal calcium sensor proteins	doi:10.1016/j.bbagen.2011.10.003	
	2,647,934				
	59,016,802				X
	59,235,834				X
	59,615,805				X
	59,712,991				X
21	52,816,464				
	52,911,310				
	62,709,685	Bos taurus BDKRB2	Vasodilation, edema, smooth muscle spasm, and pain fiber stimulation	GeneCards	
	63,286,443	Bos taurus	Loss of spermatogonia	doi:10.1095/biolreprod.109.079095	
	64,152,628				
	68,216,653				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
22	1,305,852				
	21,599,195				
	24,876,308				
	34,629,577				X
	34,965,607				
	34,979,445				
	35,730,548				
	36,797,671				
	36,992,517	Bos taurus ADAMTS9	Control of organ shape during development	GeneCards	
	37,455,074				
	37,858,827				
	39,122,937	Bos taurus C22H3orf14	Influence immune response associated with mastitis resistance	doi:10.1073/pnas.0601015103	
	39,643,501				
	39,702,951	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	
	39,725,145	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	
	40,232,132	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	X
	40,520,132				X
	40,748,442	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	41,827,325	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	42,137,230				X
	42,270,737				X
	42,284,451				X

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
22	42,616,545				X
	42,639,967				X
	42,826,746				X
	43,133,215				X
	43,534,982	Bos taurus PXK	Epidermal growth factors receptor	doi:10.1128/MCB.01105-09	X
	43,664,444				X
	43,693,452	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,723,207	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,744,791	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,747,725	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	
	43,767,521	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	
	43,777,202	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	
	44,083,638				
	44,860,043				
	44,912,994	Bos taurus TASOR	Mediates epigenetic repression	GeneCards	
	44,939,749	Bos taurus TASOR	Mediates epigenetic repression	GeneCards	
	45,455,314	Bos taurus ERC2	Component of HUSH complex – multiprotein complex that mediates epigenetic repression	GeneCards	
	45,556,690				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
22	45,696,332				
	45,954,406				
	45,966,034				
	46,465,290				
	46,533,857	Bos taurus CACNA2D3	Tumor suppression	doi:10.1002/ijc.28252	
	47,440,100				
	47,632,083				
	47,736,966	Bos taurus CACNA1D	Brain function	doi:10.1159/000054692	
	51,180,659				
	51,484,825	Bos taurus QARS1	tRNA synthetases	doi:10.1074/jbc.C113.490599	
	56,805,439				
	56,927,672	Bos taurus IFT122	Cell cycle progression, signal transduction, apoptosis, and gene regulation	GeneCards	
	56,943,056	Bos taurus IFT122	Cell cycle progression, signal transduction, apoptosis, and gene regulation	GeneCards	
	58,201,716				
	58,210,660				
	58,345,168				
24	2,393,800				
	3,052,873				
	3,143,836				
	52,336,155				
25	1,011,670				
	16,345,048				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
25	17,166,118				
	17,197,385				
	17,316,731	Bos taurus VPS35L	Obesity	doi:10.1371/journal.pgen.1000976	
	19,173,376				
	19,674,506				
	19,807,341				
	19,995,956				
	20,114,319				
	20,123,753	Bos taurus EEF2K	Tumor suppressor	doi:10.1371/journal.pone.0041171	
	21,419,593				
	21,440,612				
	21,486,414	Bos taurus UBFD1	Polyubiquitin binder	doi:10.1016/j.bbapap.2009.02.013	
	21,533,984	Bos taurus PALB2	Tumor suppressor	doi:10.1002/gcc.22045	
	21,633,170				
	21,789,204	Bos taurus PRKCB	B cell activation, apoptosis induction, endothelial cell proliferation, and intestinal sugar absorption	GeneCards	
	22,045,818	Bos taurus PRKCB	B cell activation, apoptosis induction, endothelial cell proliferation, and intestinal sugar absorption	GeneCards	
	22,728,704				
	23,899,904				
26	19,097,135				
	19,109,907				
	19,973,761				

Table A4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
26	28,930,038				
	28,988,511				
27	23,928,751				
	29,037,564				X

Table A5. Significant age at first calving (AFC) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	16,947				
	9,283,006	Bos taurus CYYR1	Unknown	NCBI	
	11,342,712				
	17,598,522				
	35,367,693				X
	45,067,210	Bos taurus ZNF596	Nucleic acid binding	GeneCards	X
	45,592,209				X
	47,856,002				X
	55,404,685				X
	61,172,245	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	61,540,639	Bos taurus LSAMP	Immunoglobulin	NCBI	X
	74,713,515				
	120,315,919				
	120,479,376	Bos taurus AGTR1	Potent vasopressor hormone; primary regulator of aldosterone secretion; important effector controlling blood pressure and volume of cardiovascular system	GeneCards	
	126,606,801	Bos taurus SLC9A9	Autism	GeneCards	
	128,117,807				
	128,166,812				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	128,862,780	Bos taurus SPSB4	Innate immune system	GeneCards	
	128,908,587				
	131,163,604				
	138,510,793				
	138,519,398				
2	4,262,209				X
	128,255,368				X
	128,529,102				X
	128,876,176				X
	129,008,096	Bos taurus RCAN3	Neurotransmitter that influences development	NCBI	X
3	2,624,552				
	3,231,882				
	3,331,788				
	4,183,635				
	34,080,566				
	34,083,582	Bos taurus SYPL2	Myopathy	doi:10.1083/jcb.147.7.1473	
	35,441,056				
	41,519,979	Bos taurus OLFM3	Regulation of collagen development	doi:10.1007/s12035-009-8076-x	
	55,354,686	Bos taurus PKN2	Protein kinase activity	doi:10.1074/jbc.M001753200	X
	89,833,054	Bos taurus C8A	Complement component 8	Schreck et al., 1998. J. Immunol. 161:311-18	X
	89,891,332				X
	91,930,742	Bos taurus TMEM61	Unknown	NCBI	X

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
3	92,168,493	Bos taurus MROH7	Kleefstra syndrome	GeneCards	X
	93,467,125				X
	94,364,377				X
	94,473,231	Bos taurus TUT4	Perlman syndrome	GeneCards	X
	104,578,840				X
	105,822,792	Bos taurus CTPS1	Immune function	GeneCards	X
	107,681,790	Bos taurus RHBDL2	Intramembrane proteases	doi:10.1016/s0092-8674(01)00525-6	X
	107,722,825	Bos taurus RRAGC	Cardiomyopathy	GeneCards	X
	108,444,081				X
	109,157,709				X
	110,001,844				
	110,449,617	Bos taurus AGO3	RNA interference	GeneCards	
	111,585,046				
4	28,117,205				
	28,215,295				
	28,227,229				
	29,039,442				
	29,193,739	Bos taurus ITGB8	Arteriovenous malformation	GeneCards	
	32,126,035	Bos taurus IGF2BP3	Skin cancer; eye cancer	doi:10.4081/ejh.2013.e6; doi:10.1016/j.humpath.2012.12.003	

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	33,966,904	Bos taurus GRM3	Major excitatory neurotransmitter in the central nervous system; activates ionotropic and metabotropic glutamate receptors; involved in most aspects of normal brain function	GeneCards	
	34,867,416				
	35,183,415				
	35,558,998				
	36,533,621				
	38,486,244	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,548,833	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,571,065	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	38,573,157	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	38,680,360	Bos taurus CACNA2D1	Effects milk somatic cell; association with carcass and meat traits; growth; feed intake and efficiency	doi:10.1007/s11033-010-0667-0; doi:10.1007/s11033-010-0117-z; doi:10.2527/2001.794854x; doi: 10.2527/jas.2008-0876	X
	39,567,241				X
	39,700,613				X
	54,063,010				X
	54,097,830	Bos taurus FOXP2	Essential for proper development of speech and language regions of the brain during embryogenesis; may be involved in variety of biological pathways and cascades that influence language development	GeneCards	X
	56,409,650				X
	56,674,807				X
	58,540,307				X
	58,563,766				X
	58,813,567				X
	58,920,558				X
	70,643,370				X
	101,677,815				
	101,790,675	Bos taurus PTN	Significant roles in cell growth and survival, cell migration, angiogenesis, and tumorigenesis	GeneCards	
	107,732,347				
	112,551,883				
	116,059,779				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
4	117,132,194	Bos taurus DPP6	Associated with autosomal dominant microcephaly and mental retardation; sclerosis	doi:10.1016/j.ejmg.2013.06.008; doi:10.1016/j.neurobiolaging.2009.05.014	
	117,308,096	Bos taurus DPP6	Associated with autosomal dominant microcephaly and mental retardation; sclerosis	doi:10.1016/j.ejmg.2013.06.008; doi:10.1016/j.neurobiolaging.2009.05.014	
	117,900,355				
	118,416,451				
	118,873,541				
	120,001,970				
	120,082,962				
	120,133,228				
	120,408,007				
	120,532,487				
	120,553,881				
	120,611,981				
5	97,785,971				
	98,102,349				
	104,391,116	Bos taurus TNFRSF1A	Periodic fever	GeneCards	
		Bos taurus SCNN1A	Pseudohypoaldosteronism – electrolyte metabolism	doi:10.1371/journal.pone.0065676	
6	4,399,364				
	10,199,636				
	39,823,153				X
	43,517,549				X
	43,649,345				X
	43,989,905				X

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
6	44,023,813				X
	45,216,251				X
	45,300,844				X
	45,479,538				X
	70,497,638	Bos taurus SCFD2	Unknown	GeneCards	
	72,759,395	Bos taurus EXOC1	West Nile Virus	GeneCards	
		Bos taurus NMU	Robinow syndrome – short-limbed dwarfism and head, face, and external genitalia	GeneCards	
7	233,662				
	765,687				
	1,263,597				
	2,069,225	Bos taurus ADAMTS2	Dermatosparaxis – extremely fragile skin	doi:10.1086/302504	
	9,947,479				
	10,067,277				
	76,497,957				X
	77,023,177				X
	91,484,380				
	92,744,435				
	92,917,772				
	94,562,555				
	94,767,287				
	100,413,608				
	102,328,838				
8	84,979,655	Bos taurus CTSV	Enkephalin peptide neurotransmitter	doi:10.1073/pnas.1531542100	

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
8	85,107,568	Bos taurus OMD	Teeth development	doi:10.1016/s8756-3282(00)00310-0	
9	15,972,347				
	26,772,343	Bos taurus NKAIN2	Lymphoma	GeneCards	
	28,257,531				
	84,616,437	Bos taurus GRM1	Cerebellar function	doi:10.1523/jneurosci.3542-13.2014	
10	20,219,262	Bos taurus NPTN	Retrograde amnesia	GeneCards	
	20,248,381	Bos taurus NPTN	Retrograde amnesia	GeneCards	
	20,291,547				
	21,105,172				
	21,722,554				
	21,861,572	Bos taurus SLC7A7	Lysinuric protein intolerance	doi:10.1016/j.ymgme.2012.01.008	
	21,865,155	Bos taurus OXA1L	Mitochondrial disorders	GeneCards	
	21,986,516				
	22,302,625				
	35,036,509				X
	35,086,759				X
	60,198,169				X
	73,551,579				X
	73,642,900				X
	92,073,773	Bos taurus NRXN3	Behavioral issues	GeneCards	
	93,682,987				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
10	96,392,179				
11	7,712,524				
	7,781,564				
	9,181,976				
	11,915,408	Bos taurus EXOC6B	Exocytosis	GeneCards	
	11,978,713	Bos taurus EXOC6B	Exocytosis	GeneCards	
	11,993,676	Bos taurus EXOC6B	Exocytosis	GeneCards	
	12,109,902				
	12,478,437				
	13,429,329				
	13,450,833				
	13,585,633				
	14,391,315	Bos taurus SRD5A2	Semen quality	doi:10.3892/mmr.2012.965	
	15,115,350	Bos taurus BIRC6	Retardation of early embryonic development and blastocyst formation in vitro	doi:10.1071/RD09112	
	15,726,355	Bos taurus LTBP1	Fibrillin proteins and latent TGF-beta binding proteins affect TGF-beta availability in the ovary	doi:10.1016/j.mce.2009.03.002	
	15,790,857	Bos taurus LTBP1	Fibrillin proteins and latent TGF-beta binding proteins affect TGF-beta availability in the ovary	doi:10.1016/j.mce.2009.03.002	
	88,958,700				X
	89,236,308				X

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
11	100,817,959	Bos taurus ASS1	Argininosuccinate synthetase deficiency – symptoms include convulsions, hyperventilation, ataxia, hypothermia, lethargy, and poor feeding	doi:10.1073/pnas.86.20.7947	
	102,657,358				
12	47,858,784				X
	47,915,012				X
	48,036,822				X
	48,131,404				X
	48,786,733				X
	48,902,740	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	48,933,612	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	48,984,802	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	49,095,991	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
12	49,123,661	Bos taurus KLF12	Developmentally regulated transcription factor; regulator of gene expression during vertebrate development and carcinogenesis	doi:10.3109/03009742.2011/608715 and doi:10.1038/ng.522	X
	50,324,576				X
	54,279,558				
	63,757,564				
	87,193,223	Bos taurus FAM155A	Psychiatric disorders	doi:10.1016/S0140-6736(12)62129-1	
13	78,282,460	Bos taurus KCNB1	Regulates neurotransmitter release, heart rate, insulin secretion, neuronal excitability, epithelial electrolyte transport, smooth muscle contraction, and cell volume	GeneCards	
	78,701,126				
	78,724,361				
	78,886,198	Bos taurus TMEM189	Encodes a fusion protein comprised of sequence sharing identity with each individual gene product	GeneCards	
	79,109,584				
	79,125,065				
14	10,066,419	Bos taurus KCNQ3	Epilepsy; neonatal convulsions	doi:10.1007/s00232-008-9097-5; doi:10.1016/j.eplepsyres.2007.12.005	
	64,541,527				X
	70,503,098				X
15	367,617				
	495,098				
	1,363,910				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	1,472,593				
	1,579,240				
	1,589,960				
	2,922,907				
	3,051,938				
	3,061,918				
	3,078,493				
	3,369,565				
	3,416,019				
	3,462,006				
	3,482,264	Bos taurus CASP4	Mastitis	doi:10.1007/s00335-001-2145-4 and GeneCards	
	3,745,000				
	4,094,542				
	4,149,756				
	4,172,524				
	4,221,234				
	4,478,076				
	4,692,182	Bos taurus PDGFD	Ovarian cancer	Wang et al., 2011. Asian Pac. J. Cancer Prev. 12:3367-70	
	4,789,493				
	4,836,419				
	4,887,219				
	5,153,883				
	5,225,448				
	5,342,417				
	5,367,143				
	5,674,820				
	5,791,533				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	5,904,969				
	5,981,185				
	6,180,970				
	6,302,487	Bos taurus MMP20	Enamel development	doi:10.1177.0022034513506581	
	6,461,480				
	6,740,672				
	6,827,569				
	6,938,962	Bos taurus CFAP300	Plays a role in axonemal structure organization and motility	GeneCards	
	6,962,261				
	7,306,679				
	7,521,856				
	7,549,611				
	7,728,537				
	7,780,636				
	7,880,793				
	7,929,048				
	7,944,599				
	7,989,843				
	8,362,960				
	8,836,147				
	8,905,048				
	8,937,081				
	9,125,948	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	9,708,615	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	9,832,372	Bos taurus CNTN5	Mediate cell surface interactions during nervous system development	GeneCards	
	11,321,038				
	14,060,810				
	17,768,941	Bos taurus RAB39A	Plays a role in maturation and acidification of phagosomes that engulf pathogens	GeneCards	
	18,137,423	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	18,218,536	Bos taurus ATM	Cell cycle kinase that phosphorylates	GeneCards	
	19,377,108				
	19,409,074				
	19,529,491				
	19,605,113				
	19,959,252				
	20,171,885				
	21,061,865	Bos taurus ARHGAP20	Impacts neurite outgrowth	GeneCards	
	23,102,438				
	35,143,414	Bos taurus SERGEF	Regulator of chromosome condensation	NCBI	
	35,606,202	Bos taurus ABCC8	Transport various molecules across extra- and intra-cellular membranes	NCBI	
	63,867,678				X
	64,752,653	Bos taurus HIPK3	Amyotrophic lateral sclerosis	GeneCards	X
	65,052,346				X

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	65,071,060				X
	65,235,259				X
	70,508,381				X
	70,921,852				X
	71,049,932				X
	71,559,650				X
	71,904,712				X
	71,909,775				X
	72,027,612				X
	72,071,828				X
	72,285,510				X
	72,624,841				X
	72,771,875				X
	72,880,886				X
16	66,653,859				X
	68,006,066				X
	68,063,376				X
	68,069,139				X
	69,010,341	Bos taurus PDC	Phosphoprotein from photoreceptor cells	Lee et al., 1990. J. Biol. Chem. 265:15867-15873	
	74,123,978	Bos taurus KCNH1	Regulates neurotransmitter release, heart rate, insulin secretion, neuronal excitability, epithelial electrolyte transport, smooth muscle contraction, and cell volume	GeneCards	
	74,958,644				
	75,465,698	Bos taurus HSD11B1	Conversion of cortisol to cortisone and cortisone to cortisol	GeneCards	
	76,059,261				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
16	76,423,682				
	76,606,285				
17	46,090,458	Bos taurus EP400	Epilepsy	GeneCards	
18	7,704,404				
	22,339,904	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,379,853	Bos taurus FTO	Increased fat mass	doi:10.1007/s12041-013-0298-z	
	22,760,455				
	22,956,535				
	23,025,804				
	26,380,950	Bos taurus NDRG4	Cell cycle progression	doi:10.1074/jbc.M109.012484	
	27,769,678				X
	28,030,835				X
	28,608,495				X
	28,734,924				X
	28,843,447				X
	29,594,472	Bos taurus CDH8	Mediates calcium-dependent cell-cell adhesion	GeneCards	X
	29,882,606				X
	30,018,259				X
	32,855,646	Bos taurus CDH11	Promotes the metastasis of cancer cells to bone	doi:10.1158/1541-7786.MCR-08-0077; doi:10.3892/ijo.33.1.17	X
	32,973,426				X
	34,598,746				X
	60,710,597				
	65,423,598				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
18	65,433,421				
	65,456,096				
	65,460,377				
	65,463,329				
19	20,123,437				
	21,432,208	Bos taurus CORO6	Related to actin filament binding	GeneCards	
	21,434,766	Bos taurus CORO6	Related to actin filament binding	GeneCards	
	21,470,659				
	21,510,144				
	21,579,655				
	42,199,423				
20	2,523,465	Bos taurus KCNIP1	Target recognition of neuronal calcium sensor proteins	doi:10.1016/j.bbagen.2011.10.003	
	58,864,888				
	59,712,991				
	65,099,050				
21	10,944,434				
	12,181,960				
	17,568,377				
	17,679,035				
	18,787,164				
	21,042,466	Bos taurus ABHD2	Sperm activation	doi:10.1126/science.aad6887	
	22,690,957				
	35,640,578	Bos taurus STXBP6	Deafness	GeneCards	
	36,578,144				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
21	36,844,728				
	52,816,464				
	63,286,443	Bos taurus VRK1	Loss of spermatogonia	doi:10.1095/biolreprod.109.079095	
	64,152,628				
	65,160,222				
	65,198,296				
	66,310,479				
	67,220,188				
	67,242,115				
	68,216,653				
	68,236,325				
	68,461,213	Bos taurus PPP2R5C	Tumor suppressor	doi:10.1074/jbc.M111.334094	
	69,545,389				
	69,554,017				
	69,587,749				
	70,155,265				
	70,182,028				
	70,182,980				
	70,521,657				
	70,769,579				
	70,783,456				
22	996,796				
	1,061,747				
	1,305,852				
	1,370,907				
	2,314,019				
	2,332,558				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
22	3,216,278				
	4,226,071				
	5,266,853	Bos taurus GADL1	Metabolism and amino acid synthesis	GeneCards	
	5,365,596	Bos taurus GADL1	Metabolism and amino acid synthesis	GeneCards	
	5,883,048				
	6,064,248				
	9,716,846				
	21,599,195				
	36,992,517	Bos taurus ADAMTS9	Control of organ shape during development	GeneCards	
	37,455,074				
	37,858,827				
	39,122,937	Bos taurus C22H3orf14	Influence immune response associated with mastitis resistance	doi:10.1073/pnas.0601015103	
	40,232,132	Bos taurus PTPRG	Tumor suppressor	doi:10.1158/0008-5472.CAN-10-0258	X
	40,748,442	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	41,171,245	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	41,827,325	Bos taurus FHIT	Tumor suppressor	doi:10.1186/1478-811X-11-59	X
	42,270,737				X
	42,284,451				X
	42,304,410				X
	42,616,545				X
	42,826,746				X

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
22	43,133,215				X
	43,490,927	Bos taurus PXK	Epidermal growth factors receptor	doi:10.1128/MCB.01105-09	X
	43,534,982	Bos taurus PXK	Epidermal growth factors receptor	doi:10.1128/MCB.01105-09	X
	43,664,444				X
	43,693,452	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,723,207	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,744,791	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	X
	43,767,521	Bos taurus FLNB	Actin binding	doi:10.1016/j.jmb.2009.06.009	
	44,083,638				
	44,860,043				
	44,912,994	Bos taurus TASOR	Mediates epigenetic repression	GeneCards	
	44,939,749	Bos taurus TASOR	Mediates epigenetic repression	GeneCards	
	45,047,902				
	45,455,314	Bos taurus ERC2	Component of HUSH complex – multiprotein complex that mediates epigenetic repression	GeneCards	
	45,696,332				
	45,954,406				
	46,465,290				
	47,327,649	Bos taurus CACNA2D3	Tumor suppression	doi:10.1002/ijc.28252	

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
22	47,440,100				
	47,736,966	Bos taurus CACNA1D	Brain function	doi:10.1159/000054692	
24	2,393,800				
	3,052,873				
	3,143,836				
	9,760,206				
	39,629,608				
	41,143,699				
	42,357,366	Bos taurus VAPA	Amyotrophic lateral sclerosis	GeneCards	
	42,420,755				
	52,336,155				
25	1,011,670				
	14,893,789				
	16,345,048				
	16,704,949				
	16,730,758				
	17,166,118				
	17,197,385				
	17,316,731	Bos taurus VPS35L	Obesity	doi:10.1371/journal.pgen.1000976	
	19,674,506				
	19,807,341				
	20,123,753	Bos taurus EEF2K	Tumor suppressor	doi:10.1371/journal.pone.0041171	
	21,419,593				
	21,440,612				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
25	21,486,414	Bos taurus UBFD1	Polyubiquitin binder	doi:10.1016/j.bbapap.2009.02.013	
	21,533,984	Bos taurus PALB2	Tumor suppressor	doi:10.1002/gcc.22045	
	22,728,704				
	30,269,233				
	32,755,073				
26	19,097,135				
	19,109,907				
	27,006,638				
	27,967,463	Bos taurus SORCS1	Encodes domain-containing receptor proteins	GeneCards	
	28,001,988	Bos taurus SORCS1	Encodes domain-containing receptor proteins	GeneCards	
	28,780,553				
	28,930,038				
	28,988,511				
	29,068,665				
	29,217,369				
	29,546,661				
	29,871,678				
	29,951,748				
	30,209,142				
	31,442,262				
	31,650,452	Bos taurus RBM20	Cardiomyopathy	doi:10.1161/circgenetics.113.000011	
	32,392,411				
	32,766,500				
	32,892,811				

Table A5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
26	32,915,658				
	33,066,487				
	33,153,900				
	33,161,627				
	33,349,780				
	33,605,534				
	34,053,110				
	35,526,836				
	36,650,431				
	41,956,121				
	42,134,297				
	42,178,883				
	42,204,081				
	42,229,222				
27	9,808,734				
	23,598,119				
28	3,233,982				
	4,270,798				
29	1,291,655				
	1,951,595				
	4,525,995				
	26,697,399				
	26,751,704				
	50,860,475	Bos taurus TALDO1	Transaldolase deficiency	doi:10.1093/ndt/gfs061	
	50,941,547				
	51,484,561				

APPENDIX B

LINE 1 SUPPLEMENTARY TABLES AND FIGURES

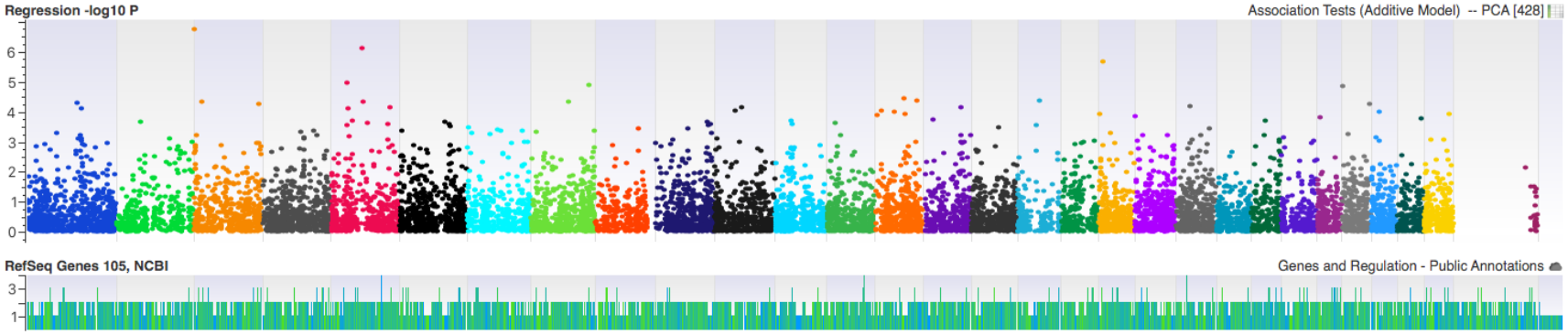


Figure B1. Manhattan plot for weaning weight (WW). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

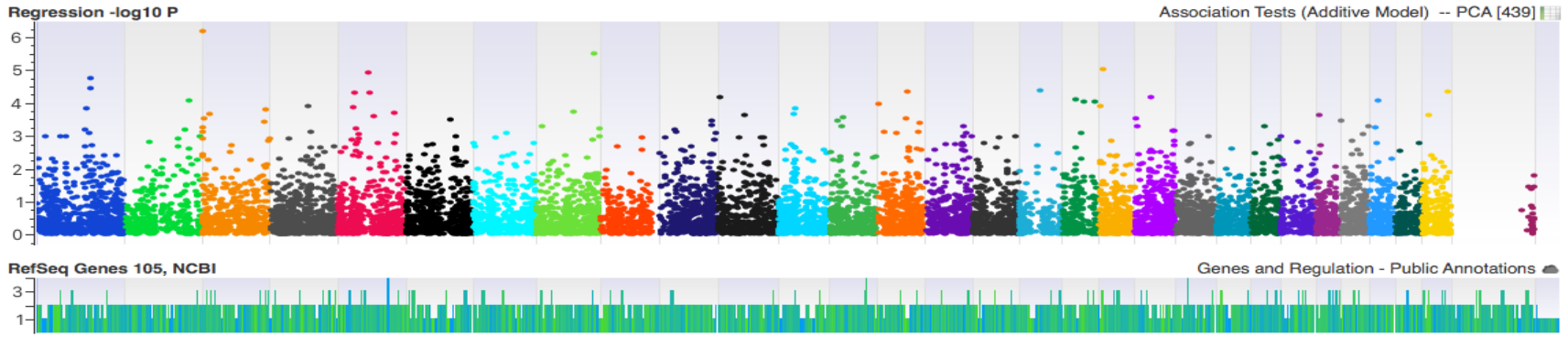


Figure B2. Manhattan plot for yearling weight (YW). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

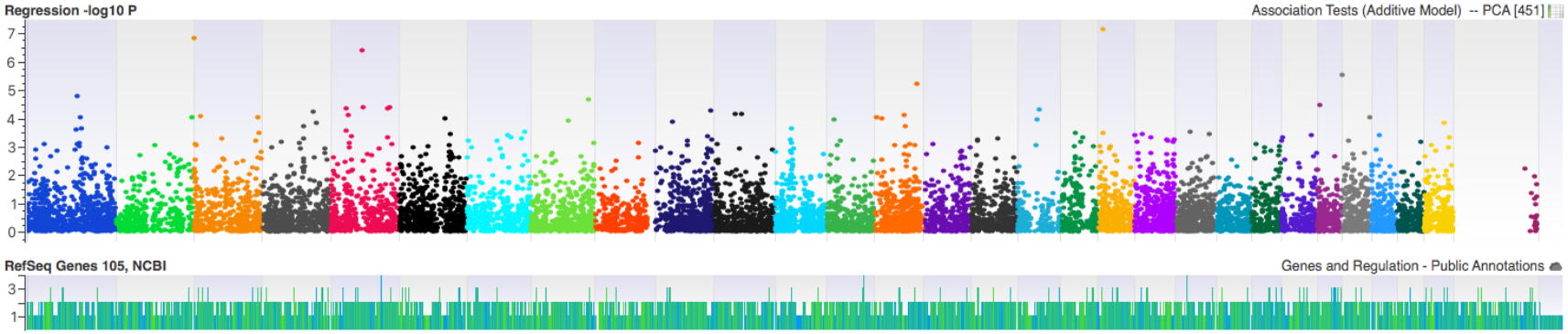


Figure B3. Manhattan plot for calving ease (CE). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

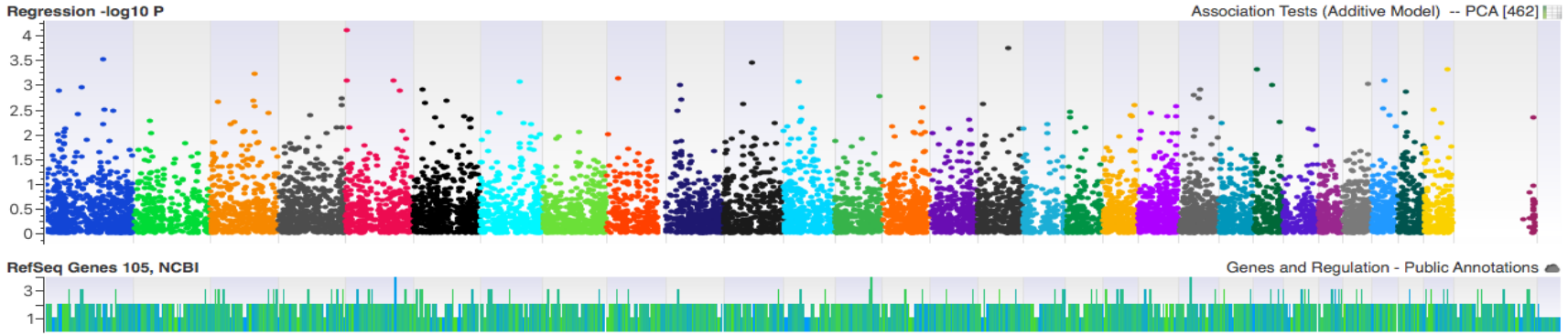


Figure B4. Manhattan plot for age at first calving (AFC). Genome-wide significance threshold was -log10(*p*-value) of 5 x 10^{-4} and vertical clusters of markers indicate suggestive QTL.

Table B1. Significant birth weight (BW) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	16,119,771				
	31,269,020				
	42,227,217				
	52,953,518				
	53,706,235				
	87,161,990				
	87,941,018	Bos taurus PEX5L	Accessory subunit of HCN channels	doi:10.1016/j.neuron.2009.05.009	
	90,283,892				
	90,689,913				
	94,860,836				
	94,952,782				
	96,677,750				
	97,160,730				
	97,458,910				
	97,906,442	Bos taurus PRKCI	Cell cancer	doi:10.1158/1541-7786.MCR-10-0359	
	99,597,502				
	99,689,088				
	103,463,199				
	107,384,385	Bos taurus PPM1L	Protein phosphatase	doi:10.1016/j.febslet.2012.06.050	
	114,907,147				X
	122,814,776				X
	143,788,237				X
2	41,592,409				X

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	42,424,807	Bos taurus GALNT13	Tricuspid valve insufficiency	doi:10.1164/rccm.201201-0057OC	X
	50,130,815				X
	68,231,252	Bos taurus DPP10	Inflammatory disease	doi:10.1016/j.mrfmmm.2004.06.061	X
	88,925,365				X
	94,702,739				X
	94,865,712				X
	108,529,237				
	110,642,302				
	113,946,668				
	114,710,664				
	115,092,998				
	121,847,018				
	129,882,579				
	135,190,642				
3	709,349	Bos taurus DCAF6	Tumor promoter and tumor suppressor	GeneCards	
	1,267,869	Bos taurus CD247	Rheumatoid arthritis	doi:10.1371/journal.pone.0068295	
	1,582,296				
	1,937,626	Bos taurus MAEL	Loss of spermatogenesis	doi:10.1016/j.devcel.2008.05.015	
	2,449,969				
	4,861,761				
	13,080,516				
	49,551,407	Bos taurus ABCA4	Photoreceptor-specific transporter	doi:10.1074/jbc.M405216200	

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
3	53,495,709	Bos taurus LRRC8D	Involved in B cell development	doi:10.1016/S0014-5793(04)00332-1	
	88,456,810				
	111,430,815	Bos taurus SMIM12	Protein coding	GeneCards	
	115,395,556				
	115,659,306				
	117,232,908				
	120,446,774				
	120,573,628				
4	16,393,988				
	33,599,874	Bos taurus KIAA1324L	Embryo development	doi:10.1074/jbc.M110.177907	
	66,830,563	Bos taurus SCRN1	Colorectal cancer; gastric cancer	doi:10.1002/jso.21459; doi:10.1111/j.1349-7006.2006.00194.x	
	67,615,775				X
	73,131,030				
	73,367,338				
	73,597,885	Bos taurus ZNF804B	Gene expression	GeneCards	
	74,460,194				
	84,648,999				
	90,847,252				
	97,185,364				
	110,740,163				
	110,839,255				
	114,744,308	Bos taurus WDR86	Gonad development	doi:10.1016/S0925-4773(00)00452-4	

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
5	4,677,157				
	12,725,994				X
	25,775,985				
	27,869,236				
	28,120,980				
	30,960,699				
	32,310,418	Bos taurus ASB8	Uterine carcinosarcoma	GeneCards	
	33,953,799				
	37,573,018				
	37,804,312				
	55,263,796				
	57,404,217	Bos taurus ANKRD52	Corneal dystrophy	GeneCards	
	64,503,182	Bos taurus UHRF1BP1L	Cell carcinoma	GeneCards	
	72,618,051				
	76,019,053				
	86,997,963	Bos taurus SOX5	Intellectual disability	doi:10.1016/j.ejmg.2012.11.001	
	101,124,171				
	101,974,400				
	103,821,233				
	104,714,350	Bos taurus VWF	Hypoxia	doi:1161/ATVBAHA.113.301359	
	110,014,606	Bos taurus LGALS1	Luteal phase and early pregnancy	doi:10.1152/physiolgenomics.00251.2010	

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
5	112,686,649	Bos taurus RBX1	Early embryonic death	doi:10.1073/pnas.0812425106	
6	1,040,062				
	3,404,563	Bos taurus BBS7	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1016/j.gde.2005.04.006	
	3,526,170				
	4,890,621				
	7,151,738				
	24,495,145				
	25,713,466				
	37,501,365	Bos taurus HERC3	Gastric and colorectal carcinomas	doi:10.1097/PAT.0b013e32834c7e78	
	48,025,306				
	50,442,769				
	80,915,917				
	87,715,723				
	88,242,415	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	88,442,145	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	88,822,266				
	90,217,183				
	90,486,780				
	90,989,420				
	92,497,641				
	93,039,499				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
6	96,037,952				
	106,158,668				
7	428,335				
	2,948,577				
	5,903,128	Bos taurus MYO9B	Celiac disease	doi:10.4321/s1130-01082012001100003	
	8,491,850				
	40,136,380	Bos taurus MXD3	Perianal hematoma	GeneCards	
	53,989,891				
	59,731,620				
	63,052,639				
	64,109,318				
	73,549,865				
	78,672,889				X
	98,194,828				
	102,564,643				
	102,658,777				
	108,575,314				
8	10,013,895	Bos taurus FZD3	Schizophrenia	doi:10.1016/j.neulet.2011.10.023	
	23,448,920	Bos taurus KIAA1797	Tumor suppressor in gliomas	doi:10.1093/brain/aws045	
	25,133,019	Bos taurus PLIN2	Marbling; embryo viability; milk fat production	doi:10.5483/bmbrep.2009.42.8.529; doi:10.1016/j.anireprosci.2014.01.0101; doi:10.3168/jds.S0022-0302(99)75508-6	
	38,518,604	Bos taurus GLDC	Nonketotic hyperglycinemia	doi:10.1136/jmg.2006.043448	

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
8	54,044,256				
	66,785,437				
	90,480,558				
	96,266,647				
	102,920,161				
	108,772,548				
	111,768,601	Bos taurus CDK5RAP2	Microcephaly	doi:10.1186/1750-1172-8-59	
	112,571,608				
	113,190,754				
	113,252,230				
9	29,977,009				
	36,440,319				
	76,316,163				
	76,346,736				
10	961,339				
	2,847,964				
	9,558,767				
	26,973,237				
	29,787,321				
	31,162,777				
	31,574,360				
	47,601,270				
	48,225,546				
	57,611,774				
	58,004,357				
	59,761,240				
	90,906,002				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
10	93,019,985				
	93,246,483				
	93,275,196				
	94,425,952				
	96,065,191				
	99,330,554				
	99,731,658				
	100,288,306				
	100,523,095				
11	2,851,698				
	4,110,773				
	7,585,747				
	31,519,537				
	37,876,375	Bos taurus CCDC88A	Metastasis predictor of breast cancer	doi:10.1007/s12032-011-0087-6	
	38,512,409				
	45,584,828	Bos taurus UXS1	Vulval morphogenesis and embryonic development	doi:10.1073/pnas.172522199	
	48,425,269	Bos taurus REEP1	Spastic paraplegia	doi:10.1007/s10048-008-0163-z	
	78,001,260				
	83,028,893	Bos taurus NBAS	Short stature	doi:10.1136/jmg.2009.074815	
	91,108,018				
	104,043,185				
12	23,450,916				
	27,684,536				
	28,205,239				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
12	29,170,799				
	29,191,067				
	29,562,851				
	29,649,126				
	29,681,550				
	30,389,680				
	30,808,992				
	31,272,071				
	33,535,830	Bos taurus ATP8A2	Cerebral atrophy and quadrupedal locomotion	doi:10.1038/ejhg.2012.170	
	80,665,605				
	81,586,853				
13	13,706,672				
	17,064,169				
	18,066,756	Bos taurus ACBD5	Differentiation of megakaryocytes and formation of platelets	GeneCards	
	18,268,908	Bos taurus APBB1IP	Leukocyte adhesion deficiency	GeneCards	
	23,590,320				
	46,203,780				
	49,596,331				X
14	3,484,849				
	11,983,913				
	12,247,110				
	35,663,156				
	51,811,945				
	52,302,089				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
14	53,532,230				
	54,164,119				
	55,219,280				X
	57,145,781				
	59,814,118				
	62,361,079	Bos taurus DPYS	Dihydropyrimidinuria	doi:10.1016/j.bbadis.2010.03.013	
	72,381,743				
	76,043,148	Bos taurus DECR1	Backfat	doi:10.2527/jas.2008-1456	
15	17,631,380				
	36,997,902	Bos taurus SOX6	Bone mineral density	doi:10.1007/s00198-011-1626-x	
	66,456,600	Bos taurus CD44	Cancer cells	doi:10.1158/0008-5472.CAN-13-0087	
	67,816,375				
	67,981,902				
	68,231,379				
	68,988,117				
	69,214,643				
	69,930,274				
	74,137,434				
	79,923,112				
	84,704,791				
16	8,486,467				
	11,064,988				
	11,096,101				
	42,411,339				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
16	47,680,564	Bos taurus NOL9	Phosphoglycerate dehydrogenase deficiency	GeneCards	
	76,423,682				
17	1,970,122				
	33,251,225				
	33,715,935				
	38,001,105	Bos taurus FSTL5	Medulloblastoma	doi:10.1200/JCO.2011.36.2798	
	71,081,308	Bos taurus ASCC2	Initiation of embryogenesis	doi:10.1007/bf00339726	
	72,063,677	Bos taurus SMTN	Gastrointestinal tract smooth muscle neoplasms	doi:10.1097/pas.0b013e3181b76477	
18	6,894,368				
	25,345,775	Bos taurus PLLP	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1007/s00335-001-3035-5	
	26,358,647				
	35,418,613	Bos taurus RANBP10	Modulates noncentrosomal microtubules	doi:10.1074/jbc.M709397200	X
	36,594,231	Bos taurus VPS4A	Submandibular gland cancer	GeneCards	X
	40,502,223				X
	54,311,149	Bos taurus SLC1A5	Cystic fibrosis	doi:10.1038/sj.ejhg.5200726	
	59,662,778				
19	3,071,686				
	3,793,023				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
19	3,816,052				
	8,505,317	Bos taurus MSI2	Acute lymphoblastic leukemia	doi:10.1016/j.leukres.2013.05.012	
	8,770,836				
	19,373,322				
	22,038,801				
	29,890,136				X
	33,450,891	Bos taurus TEKT3	Sperm quality; sperm motility	doi:10.1387/ijdb.072333ag; doi:10.1002/mrd.20957	X
	57,454,104				
20	401,466	Bos taurus SLIT3	Cell migration	doi:10.1038/labinvest.2012.81	
	4,298,545				
	5,730,532				
	6,534,735				
	9,344,675	Bos taurus MAP1B	Neurogenesis	GeneCards	
	13,263,157				
	27,970,417				
	28,957,856				
	34,158,865				
	56,824,862				X
	57,177,369				X
	58,214,328				X
	68,403,701				
	68,713,825				
	69,375,211				
	69,825,743				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
20	70,669,729				
21	21,408,374				X
	25,136,856				X
	26,181,772				X
	29,893,539				
	30,007,996				
	30,224,238				
	39,758,522				X
	42,835,553				X
	43,524,083	Bos taurus AKAP6	Contractility in cardiac myocytes	doi:10.1161/01.res.88.3.291	X
	44,229,968				X
	54,553,298				
	55,375,347	Bos taurus FANCM	DNA interstrand crosslinks	doi:10.1016/j.molcel.2013.09.021	
	59,219,376				
22	24,032,586				X
	27,309,084				X
23	5,931,664				
	7,722,626	Bos taurus ITPR3	Mediates the release of intracellular calcium	doi:10.4161/auto.7.12.17909	
	22,300,959				
	23,909,884				
	33,874,418				
	40,416,708				
	48,791,036				
	49,094,579	Bos taurus FARS2	Mitochondrial phenylalanyl-tRNA synthetase	doi:10.1073/pnas.88.19.8387	

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
23	49,762,070				
	50,388,461	Bos taurus TUBB2B	Microtubules	doi:10.1038/nature03606	
	50,897,089				
24	580,805				
	2,658,119				
	5,696,089				
	33,094,977				X
	52,825,393				
	56,442,291	Bos taurus TXNL1	Ehrlichiosis	GeneCards	
	58,809,468	Bos taurus LMAN1	Cargo receptor for glycoprotein transport	GeneCards	
	62,593,028	Bos taurus SERPINB2	Gingivitis and pre-eclampsia	GeneCards	
25	4,779,974				
	31,625,995				
26	1,065,894				
	11,443,033	Bos taurus KIF20B	Cytokinesis	doi:10.1074/jbc.M304522200	X
	19,344,348	Bos taurus PYROXD2	Trimethylaminuria	GeneCards	XX
	20,668,949				X
	40,519,284				
	42,673,967	Bos taurus HTRA1	Age-related macular degeneration	doi:10.1016/j.exer.2013.09.012	
	49,366,950				
27	8,848,885				

*SNP that fall within more than one ROH on the same chromosome

Table B1. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
27	12,818,675				
	14,173,400				
	14,876,795	Bos taurus SORBS2	Hypotrichosis and Myopathy	GeneCards	
28	7,422,506				
	41,674,187	Bos taurus LDB3	Cardiomyopathy	GeneCards	
29	2,091,741	Bos taurus FAT3	Tissue morphogenesis and planar polarity	doi:10.1242/dev.077461	
	12,581,946				X
	21,244,910				X
	34,618,653	Bos taurus OPCML	Ovarian cancer	doi:10.1158/2159-8290.CD-11-0256	
	39,905,644				
	43,498,073	Bos taurus NRXN2	Vertebrate nervous system	doi:10.1523/jneurosci.15-04-02849.1995	
	45,367,095				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Significant weaning weight (WW) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
1	15,562,295				
	16,119,771				
	31,269,020				
	42,227,217				
	52,953,518				
	53,706,235				
	87,161,990				
	87,941,018	Bos taurus PEX5L	Accessory subunit of HCN channels	doi:10.1016/j.neuron.2009.05.009	
	90,283,892				
	90,689,913				
	94,860,836				
	94,952,782				
	96,677,750	Bos taurus PRKCI	Cell cancer	doi:10.1158/1541-7786.MCR-10-0359	
	97,160,730				
	97,458,910				
	97,906,442				
	99,689,088				
	103,463,199				
	107,384,385	Bos taurus PPM1L	Protein phosphatase	doi:10.1016/j.febslet.2012.06.050	
	114,907,147				X
	122,814,776				X
	143,788,237				X
2	41,592,409				X

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
2	42,424,807	Bos taurus GALNT13	Tricuspid valve insufficiency	doi:10.1164/rccm.201201-0057OC	X
	50,130,815				X
	68,231,252	Bos taurus DPP10	Inflammatory disease	doi:10.1016/j.mrfmmm.2004.06.061	X
	88,925,365				X
	94,702,739				X
	94,865,712				X
	108,529,237				
	110,642,302				
	111,155,237	Bos taurus PAX3	Waardenburg syndrome	doi:10.3109/00016489.2012.744470	
	113,946,668				
	114,710,664				
	115,092,998				
	121,847,018				
	129,882,579				
	135,190,642				
3	709,349	Bos taurus DCAF6	Tumor promoter and tumor suppressor	GeneCards	
	1,267,869	Bos taurus CD247	Rheumatoid arthritis	doi:10.1371/journal.pone.0068295	
	1,582,296				
	1,937,626	Bos taurus MAEL	Loss of spermatogenesis	doi:10.1016/j.devcel.2008.05.015	
	2,449,969				
	4,861,761				
	13,080,516				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
3	49,551,407	Bos taurus ABCA4	Photoreceptor-specific transporter	doi:10.1074/jbc.M405216200	
	53,495,709	Bos taurus LRRC8D	Involved in B cell development	doi:10.1016/S0014-5793(04)00332-1	
	88,456,810				
	111,430,815	Bos taurus SMIM12	Protein coding	GeneCards	
	115,395,556				
	115,659,306				
	117,232,908				
	120,446,774				
	120,573,628				
4	16,393,988				
	33,599,874	Bos taurus KIAA1324L	Embryo development	doi:10.1074/jbc.M110.177907	
	66,830,563	Bos taurus SCRN1	Colorectal cancer; gastric cancer	doi:10.1002/jso.21459; doi:10.1111/j.1349-7006.2006.00194.x	
	67,615,775				X
	73,131,030				
	73,367,338				
	73,597,885	Bos taurus ZNF804B	Gene expression	GeneCards	
	74,460,194				
	84,648,999				
	90,847,252				
	97,185,364				
	110,740,163				
	110,839,255				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
4	114,744,308	Bos taurus WDR86	Gonad development	doi:10.1016/S0925-4773(00)00452-4	
5	4,677,157				
	12,725,994				X
	25,775,985				
	27,869,236				
	28,120,980				
	30,960,699				
	32,310,418	Bos taurus ASB8	Uterine carcinosarcoma	GeneCards	
	33,953,799				
	37,573,018				
	37,804,312				
	55,263,796				
	57,404,217	Bos taurus ANKRD52	Corneal dystrophy	GeneCards	
	64,503,182	Bos taurus UHRF1BP1L	Cell carcinoma	GeneCards	
	72,618,051				
	86,997,963	Bos taurus SOX5	Intellectual disability	doi:10.1016/j.ejmg.2012.11.001	
	101,124,171				
	101,974,400				
	103,821,233				
	104,714,350	Bos taurus VWF	Hypoxia	doi:1161/ATVBAHA.113.301359	
	110,014,606	Bos taurus LGALS1	Luteal phase and early pregnancy	doi:10.1152/physiolgenomics.00251.2010	

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
5	112,686,649	Bos taurus RBX1	Early embryonic death	doi:10.1073/pnas.0812425106	
6	1,040,062				
	3,404,563	Bos taurus BBS7	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1016/j.gde.2005.04.006	
	3,526,170				
	4,890,621				
	7,151,738				
	24,495,145				
	25,713,466				
	37,501,365	Bos taurus HERC3	Gastric and colorectal carcinomas	doi:10.1097/PAT.0b013e32834c7e78	
	48,025,306				
	50,442,769				
	80,915,917				
	87,715,723				
	88,242,415	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	88,442,145	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	90,217,183				
	90,486,780				
	90,989,420				
	92,497,641				
	96,037,952				
	106,158,668				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
7	428,335				
	2,948,577				
	5,903,128	Bos taurus MYO9B	Celiac disease	doi:10.4321/s1130-01082012001100003	
	8,491,850				
	27,732,801	Bos taurus PRRC1	Leukodystrophy	GeneCards	
	40,136,380	Bos taurus MXD3	Perianal hematoma	GeneCards	
	53,989,891				
	59,731,620				
	63,052,639				
	64,109,318				
	73,549,865				
	78,672,889				X
	98,194,828				
	102,564,643				
	108,575,314				
8	712,643				
	10,013,895	Bos taurus FZD3	Schizophrenia	doi:10.1016/j.neulet.2011.10.023	
	22,479,821				
	23,448,920	Bos taurus KIAA1797	Tumor suppressor in gliomas	doi:10.1093/brain/aws045	
	25,133,019	Bos taurus PLIN2	Marbling; embryo viability; milk fat production	doi:10.5483/bmbrep.2009.42.8.529; doi:10.1016/j.anireprosci.2014.01.0101; doi:10.3168/jds.S0022-0302(99)75508-6	

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
8	38,518,604	Bos taurus GLDC	Nonketotic hyperglycinemia	doi:10.1136/jmg.2006.043448	
	54,044,256				
	66,785,437				
	90,480,558				
	96,266,647				
	102,920,161				
	108,772,548				
	111,768,601	Bos taurus CDK5RAP2	Microcephaly	doi:10.1186/1750-1172-8-59	
	113,190,754				
	113,252,230				
9	29,977,009				
	36,440,319				
	76,316,163				
	76,346,736				
10	961,339				
	2,847,964				
	9,558,767				
	26,973,237				
	29,787,321				
	31,162,777				
	31,574,360				
	47,601,270				
	48,225,546				
	57,611,774				
	58,004,357				
	59,761,240				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
10	90,906,002				
	93,019,985				
	93,246,483				
	93,275,196				
	94,425,952				
	96,065,191				
	99,330,554				
	99,731,658				
	100,288,306				
	100,523,095				
11	2,851,698				
	4,110,773				
	7,585,747				
	20,350,454				
	37,876,375	Bos taurus CCDC88A	Metastasis predictor of breast cancer	doi:10.1007/s12032-011-0087-6	
	45,584,828	Bos taurus UXS1	Vulval morphogenesis and embryonic development	doi:10.1073/pnas.172522199	
	48,425,269	Bos taurus REEP1	Spastic paraplegia	doi:10.1007/s10048-008-0163-z	
	78,001,260				
	83,028,893	Bos taurus NBAS	Short stature	doi:10.1136/jmg.2009.074815	
	91,108,018				
12	23,450,916				
	27,684,536				
	28,205,239				
	29,170,799				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
12	29,191,067				
	29,649,126				
	29,681,550				
	30,389,680				
	30,808,992				
	31,272,071				
	33,535,830	Bos taurus ATP8A2	Cerebral atrophy and quadrupedal locomotion	doi:10.1038/ejhg.2012.170	
	80,665,605				
	81,586,853				
13	7,634,910				
	13,706,672				
	17,064,169				
	18,066,756	Bos taurus ACBD5	Differentiation of megakaryocytes and formation of platelets	GeneCards	
	18,268,908	Bos taurus APBB1IP	Leukocyte adhesion deficiency	GeneCards	
	23,590,320				
	46,203,780				
	49,596,331				X
14	3,484,849				
	12,247,110				
	35,663,156				
	51,811,945				
	52,302,089				
	53,532,230				
	54,164,119				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
14	55,219,280				X
	57,145,781				
	59,814,118				
	62,361,079	Bos taurus DPYS	Dihydropyrimidinuria	doi:10.1016/j.bbadis.2010.03.013	
	72,381,743				
	76,043,148	Bos taurus DECR1	Backfat	doi:10.2527/jas.2008-1456	
15	6,335,201	Bos taurus MMP20	Enamel development	doi:10.1177.0022034513506581	
	17,631,380				
	19,059,568				
	36,997,902	Bos taurus SOX6	Bone mineral density	doi:10.1007/s00198-011-1626-x	
	66,456,600	Bos taurus CD44	Cancer cells	doi:10.1158/0008-5472.CAN-13-0087	
	67,816,375				
	67,981,902				
	68,231,379				
	68,988,117				
	69,214,643				
	69,930,274				
	74,137,434				
	79,923,112				
	84,704,791				
16	8,486,467				
	11,064,988				
	11,096,101				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
16	42,411,339				
	47,680,564	Bos taurus NOL9	Phosphoglycerate dehydrogenase deficiency	GeneCards	
17	1,970,122				
	33,251,225				
	33,715,935				
	38,001,105	Bos taurus FSTL5	Medulloblastoma	doi:10.1200/JCO.2011.36.2798	
	71,081,308	Bos taurus ASCC2	Initiation of embryogenesis	doi:10.1007/bf00339726	
	72,063,677	Bos taurus SMTN	Gastrointestinal tract smooth muscle neoplasms	doi:10.1097/pas.0b013e3181b76477	
18	6,894,368				
	25,345,775	Bos taurus PLLP	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1007/s00335-001-3035-5	
	26,358,647				
	35,418,613	Bos taurus RANBP10	Modulates noncentrosomal microtubules	doi:10.1074/jbc.M709397200	X
	36,594,231	Bos taurus VPS4A	Submandibular gland cancer	GeneCards	X
	40,502,223				X
	54,311,149	Bos taurus SLC1A5	Cystic fibrosis	doi:10.1038/sj.ejhg.5200726	
	59,662,778				
19	3,071,686				
	3,793,023				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
19	3,816,052				
	8,505,317	Bos taurus MSI2	Acute lymphoblastic leukemia	doi:10.1016/j.leukres.2013.05.012	
	8,770,836				
	19,373,322				
	22,038,801				
	29,890,136				X
	33,450,891	Bos taurus TEKT3	Sperm quality; sperm motility	doi:10.1387/ijdb.072333ag; doi:10.1002/mrd.20957	X
	57,454,104				
20	401,466	Bos taurus SLIT3	Cell migration	doi:10.1038/labinvest.2012.81	
	4,298,545				
	5,730,532				
	6,534,735				
	9,344,675	Bos taurus MAP1B	Neurogenesis	GeneCards	
	13,263,157				
	27,970,417				
	28,957,856				
	34,158,865				
	47,056,652				
	56,824,862				X
	57,177,369				X
	58,214,328				X
	68,403,701				
	68,713,825				
	69,375,211				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
20	69,825,743				
	70,669,729				
21	21,408,374				X
	25,136,856				X
	26,181,772				X
	29,893,539				
	30,007,996				
	30,224,238				
	39,758,522				X
	42,835,553				X
	44,229,968				X
	54,553,298				
	55,375,347	Bos taurus FANCM	DNA interstrand crosslinks	doi:10.1016/j.molcel.2013.09.021	
	59,219,376				
22	24,032,586				X
	27,309,084				X
23	7,722,626	Bos taurus ITPR3	Mediates the release of intracellular calcium	doi:10.4161/auto.7.12.17909	
	22,300,959				
	23,909,884				
	33,874,418				
	40,416,708				
	48,791,036				
	49,094,579	Bos taurus FARS2	Mitochondrial phenylalanyl-tRNA synthetase	doi:10.1073/pnas.88.19.8387	
	49,762,070				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
23	50,388,461	Bos taurus TUBB2B	Microtubules	doi:10.1038/nature03606	
	50,897,089				
24	580,805				
	2,658,119				
	5,696,089				
	33,094,977				X
	52,825,393				
	56,442,291	Bos taurus TXNL1	Ehrlichiosis	GeneCards	
	58,809,468	Bos taurus LMAN1	Cargo receptor for glycoprotein transport	GeneCards	
	62,593,028	Bos taurus SERPINB2	Gingivitis and pre-eclampsia	GeneCards	
25	4,779,974				
	31,625,995				
26	1,065,894				
	11,443,033	Bos taurus KIF20B	Cytokinesis	doi:10.1074/jbc.M304522200	X
	19,344,348	Bos taurus PYROXD2	Trimethylaminuria	GeneCards	XX
	20,668,949				X
	40,519,284				
	42,673,967	Bos taurus HTRA1	Age-related macular degeneration	doi:10.1016/j.exer.2013.09.012	
	49,366,950				
27	8,848,885				
	12,818,675				

*SNP that fall within more than one ROH on the same chromosome

Table B2. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Function	Reference	ROH Overlap
27	14,173,400				
28	7,422,506				
	41,674,187	Bos taurus LDB3	Cardiomyopathy	GeneCards	
29	12,581,946				X
	21,244,910				X
	34,618,653	Bos taurus OPCML	Ovarian cancer	doi:10.1158/2159-8290.CD-11-0256	
	39,905,644				
	43,498,073	Bos taurus NRXN2	Vertebrate nervous system	doi:10.1523/jneurosci.15-04-02849.1995	
	45,367,095				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Significant yearling weight (YW) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	16,119,771				
	31,269,020				
	42,227,217				
	52,953,518				
	53,706,235				
	87,161,990				
	87,941,018	Bos taurus PEX5L	Accessory subunit of HCN channels	doi:10.1016/j.neuron.2009.05.009	
	90,283,892				
	90,689,913				
	94,860,836				
	94,952,782				
	96,677,750				
	97,160,730				
	97,458,910				
	97,906,442	Bos taurus PRKCI	Cell cancer	doi:10.1158/1541-7786.MCR-10-0359	
	99,597,502				
	99,689,088				
	103,463,199				
	107,384,385	Bos taurus PPM1L	Protein phosphatase	doi:10.1016/j.febslet.2012.06.050	
	114,907,147				X
	122,814,776				X
	143,788,237				X
2	41,592,409				X

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	42,424,807	Bos taurus GALNT13	Tricuspid valve insufficiency	doi:10.1164/rccm.201201-0057OC	X
	50,130,815				X
	68,231,252	Bos taurus DPP10	Inflammatory disease	doi:10.1016/j.mrfmmm.2004.06.061	X
	88,925,365				X
	94,702,739				X
	94,865,712				X
	108,529,237				
	110,642,302				
	113,946,668				
	114,710,664				
	115,092,998				
	121,847,018				
	129,882,579				
	135,190,642				
3	709,349	Bos taurus DCAF6	Tumor promoter and tumor suppressor	GeneCards	
	1,267,869	Bos taurus CD247	Rheumatoid arthritis	doi:10.1371/journal.pone.0068295	
	1,582,296				
	1,937,626	Bos taurus MAEL	Loss of spermatogenesis	doi:10.1016/j.devcel.2008.05.015	
	2,449,969				
	4,861,761				
	13,080,516				
	49,551,407	Bos taurus ABCA4	Photoreceptor-specific transporter	doi:10.1074/jbc.M405216200	

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
3	53,495,709	Bos taurus LRRC8D	Involved in B cell development	doi:10.1016/S0014-5793(04)00332-1	
	88,456,810				
	111,430,815	Bos taurus SMIM12	Protein coding	GeneCards	
	115,395,556				
	115,659,306				
	117,232,908				
	120,446,774				
	120,573,628				
4	16,393,988				
	33,599,874	Bos taurus KIAA1324L	Embryo development	doi:10.1074/jbc.M110.177907	
	66,830,563	Bos taurus SCRN1	Colorectal cancer; gastric cancer	doi:10.1002/jso.21459; doi:10.1111/j.1349-7006.2006.00194.x	
	67,615,775				X
	73,131,030				
	73,367,338				
	73,597,885	Bos taurus ZNF804B	Gene expression	GeneCards	
	74,460,194				
	84,648,999				
	90,847,252				
	97,185,364				
	110,740,163				
	110,839,255				
	114,744,308	Bos taurus WDR86	Gonad development	doi:10.1016/S0925-4773(00)00452-4	

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
5	4,677,157				
	12,725,994				
	25,775,985				
	27,869,236				
	28,120,980				
	30,960,699				
	32,310,418	Bos taurus ASB8	Uterine carcinosarcoma	GeneCards	
	33,953,799				
	37,573,018				
	37,804,312				
	55,263,796				
	57,404,217	Bos taurus ANKRD52	Corneal dystrophy	GeneCards	
	64,503,182	Bos taurus UHRF1BP1L	Cell carcinoma	GeneCards	
	72,618,051				
	76,019,053				
	86,997,963	Bos taurus SOX5	Intellectual disability	doi:10.1016/j.ejmg.2012.11.001	
	101,124,171				
	101,974,400				
	103,821,233				
	104,714,350	Bos taurus VWF	Hypoxia	doi:1161/ATVBAHA.113.301359	
	110,014,606	Bos taurus LGALS1	Luteal phase and early pregnancy	doi:10.1152/physiolgenomics.00251.2010	

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
5	112,686,649	Bos taurus RBX1	Early embryonic death	doi:10.1073/pnas.0812425106	
6	1,040,062				
	3,404,563	Bos taurus BBS7	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1016/j.gde.2005.04.006	
	3,526,170				
	4,890,621				
	7,151,738				
	24,495,145				
	25,713,466				
	37,501,365	Bos taurus HERC3	Gastric and colorectal carcinomas	doi:10.1097/PAT.0b013e32834c7e78	
	48,025,306				
	50,442,769				
	80,915,917				
	87,715,723				
	88,242,415	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	88,442,145	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	88,822,266				
	90,217,183				
	90,486,780				
	90,989,420				
	92,497,641				
	93,039,499				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
6	96,037,952				
	106,158,668				
7	428,335				
	2,948,577				
	5,903,128	Bos taurus MYO9B	Celiac disease	doi:10.4321/s1130-01082012001100003	
	8,491,850				
	40,136,380	Bos taurus MXD3	Perianal hematoma	GeneCards	
	53,989,891				
	59,731,620				
	63,052,639				
	64,109,318				
	73,549,865				
	78,672,889				X
	98,194,828				
	102,564,643				
	102,658,777				
	108,575,314				
8	10,013,895	Bos taurus FZD3	Schizophrenia	doi:10.1016/j.neulet.2011.10.023	
	23,448,920	Bos taurus KIAA1797	Tumor suppressor in gliomas	doi:10.1093/brain/aws045	
	25,133,019	Bos taurus PLIN2	Marbling; embryo viability; milk fat production	doi:10.5483/bmbrep.2009.42.8.529; doi:10.1016/j.anireprosci.2014.01.010; doi:10.3168/jds.S0022-0302(99)75508-6	
	38,518,604	Bos taurus GLDC	Nonketotic hyperglycinemia	doi:10.1136/jmg.2006.043448	

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
8	54,044,256				
	66,785,437				
	90,480,558				
	96,266,647				
	102,920,161				
	108,772,548				
	111,768,601	Bos taurus CDK5RAP2	Microcephaly	doi:10.1186/1750-1172-8-59	
	112,571,608				
	113,190,754				
	113,252,230				
9	29,977,009				
	36,440,319				
	76,316,163				
	76,346,736				
10	961,339				
	2,847,964				
	9,558,767				
	26,973,237				
	29,787,321				
	31,162,777				
	31,574,360				
	47,601,270				
	48,225,546				
	57,611,774				
	58,004,357				
	59,761,240				
	90,906,002				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
10	93,019,985				
	93,246,483				
	93,275,196				
	94,425,952				
	96,065,191				
	99,330,554				
	99,731,658				
	100,288,306				
	100,523,095				
11	2,851,698				
	4,110,773				
	7,585,747				
	31,519,537				
	37,876,375	Bos taurus CCDC88A	Metastasis predictor of breast cancer	doi:10.1007/s12032-011-0087-6	
	38,512,409				
	45,584,828	Bos taurus UXS1	Vulval morphogenesis and embryonic development	doi:10.1073/pnas.172522199	
	48,425,269	Bos taurus REEP1	Spastic paraplegia	doi:10.1007/s10048-008-0163-z	
	78,001,260				
	83,028,893	Bos taurus NBAS	Short stature	doi:10.1136/jmg.2009.074815	
	91,108,018				
	104,043,185				
12	23,450,916				
	27,684,536				
	28,205,239				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
12	29,170,799				
	29,191,067				
	29,562,851				
	29,649,126				
	29,681,550				
	30,389,680				
	30,808,992				
	31,272,071				
	33,535,830	Bos taurus ATP8A2	Cerebral atrophy and quadrupedal locomotion	doi:10.1038/ejhg.2012.170	
	80,665,605				
	81,586,853				
13	13,706,672				
	17,064,169				
	18,066,756	Bos taurus ACBD5	Differentiation of megakaryocytes and formation of platelets	GeneCards	
	18,268,908	Bos taurus APBB1IP	Leukocyte adhesion deficiency	GeneCards	
	23,590,320				
	46,203,780				
	49,596,331				X
14	3,484,849				
	11,983,913				
	12,247,110				
	35,663,156				
	51,811,945				
	52,302,089				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
14	53,532,230				
	54,164,119				
	55,219,280				X
	57,145,781				
	59,814,118				
	62,361,079	Bos taurus DPYS	Dihydropyrimidinuria	doi:10.1016/j.bbadis.2010.03.013	
	72,381,743				
	76,043,148	Bos taurus DECR1	Backfat	doi:10.2527/jas.2008-1456	
15	17,631,380				
	36,997,902	Bos taurus SOX6	Bone mineral density	doi:10.1007/s00198-011-1626-x	
	66,456,600	Bos taurus CD44	Cancer cells	doi:10.1158/0008-5472.CAN-13-0087	
	67,816,375				
	67,981,902				
	68,231,379				
	68,988,117				
	69,214,643				
	69,930,274				
	74,137,434				
	79,923,112				
	84,704,791				
16	8,486,467				
	11,064,988				
	11,096,101				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
16	42,411,339				
	47,680,564	Bos taurus NOL9	Phosphoglycerate dehydrogenase deficiency	GeneCards	
	76,423,682				
17	1,970,122				
	33,251,225				
	33,715,935				
	38,001,105	Bos taurus FSTL5	Medulloblastoma	doi:10.1200/JCO.2011.36.2798	
	71,081,308	Bos taurus ASCC2	Initiation of embryogenesis	doi:10.1007/bf00339726	
	72,063,677	Bos taurus SMTN	Gastrointestinal tract smooth muscle neoplasms	doi:10.1097/pas.0b013e3181b76477	
18	6,894,368				
	25,345,775	Bos taurus PLLP	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1007/s00335-001-3035-5	
	26,358,647				
	35,418,613	Bos taurus RANBP10	Modulates noncentrosomal microtubules	doi:10.1074/jbc.M709397200	X
	36,594,231	Bos taurus VPS4A	Submandibular gland cancer	GeneCards	X
	40,502,223				X
	54,311,149	Bos taurus SLC1A5	Cystic fibrosis	doi:10.1038/sj.ejhg.5200726	
	59,662,778				
19	3,071,686				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
19	3,793,023				
	3,816,052				
	8,505,317	Bos taurus MSI2	Acute lymphoblastic leukemia	doi:10.1016/j.leukres.2013.05.012	
	8,770,836				
	19,373,322				
	22,038,801				
	29,890,136				X
	33,450,891	Bos taurus TEKT3	Sperm quality; sperm motility	doi:10.1387/ijdb.072333ag; doi:10.1002/mrd.20957	X
	57,454,104				
20	401,466	Bos taurus SLIT3	Cell migration	doi:10.1038/labinvest.2012.81	
	4,298,545				
	5,730,532				
	6,534,735				
	9,344,675	Bos taurus MAP1B	Neurogenesis	GeneCards	
	13,263,157				
	27,970,417				
	28,957,856				
	34,158,865				
	56,824,862				X
	57,177,369				X
	58,214,328				X
	68,403,701				
	68,713,825				
	69,375,211				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
20	69,825,743				
	70,669,729				
21	21,408,374				X
	25,136,856				X
	26,181,772				X
	29,893,539				
	30,007,996				
	30,224,238				
	39,758,522				X
	42,835,553				X
	43,524,083	Bos taurus AKAP6	Contractility in cardiac myocytes	doi:10.1161/01.res.88.3.291	X
	44,229,968				X
	54,553,298				
	55,375,347	Bos taurus FANCM	DNA interstrand crosslinks	doi:10.1016/j.molcel.2013.09.021	
	59,219,376				
22	24,032,586				X
	27,309,084				X
23	5,931,664				
	7,722,626	Bos taurus ITPR3	Mediates the release of intracellular calcium	doi:10.4161/auto.7.12.17909	
	22,300,959				
	23,909,884				
	33,874,418				
	40,416,708				
	48,791,036				

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
23	49,094,579	Bos taurus FARS2	Mitochondrial phenylalanyl-tRNA synthetase	doi:10.1073/pnas.88.19.8387	
	49,762,070				
	50,388,461	Bos taurus TUBB2B	Microtubules	doi:10.1038/nature03606	
	50,897,089				
24	580,805				
	2,658,119				
	5,696,089				
	33,094,977				X
	52,825,393				
	56,442,291	Bos taurus TXNL1	Ehrlichiosis	GeneCards	
	58,809,468	Bos taurus LMAN1	Cargo receptor for glycoprotein transport	GeneCards	
	62,593,028	Bos taurus SERPINB2	Gingivitis and pre-eclampsia	GeneCards	
25	4,779,974				
	31,625,995				
26	1,065,894				
	11,443,033	Bos taurus KIF20B	Cytokinesis	doi:10.1074/jbc.M304522200	X
	19,344,348	Bos taurus PYROXD2	Trimethylaminuria	GeneCards	XX
	20,668,949				X
	40,519,284				
	42,673,967	Bos taurus HTRA1	Age-related macular degeneration	doi:10.1016/j.exer.2013.09.012	

*SNP that fall within more than one ROH on the same chromosome

Table B3. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
26	49,366,950				
27	8,848,885				
	12,818,675				
	14,173,400				
	14,876,795	Bos taurus SORBS2	Hypotrichosis and Myopathy	GeneCards	
28	7,422,506				
	41,674,187	Bos taurus LDB3	Cardiomyopathy	GeneCards	
29	2,091,741	Bos taurus FAT3	Tissue morphogenesis and planar polarity	doi:10.1242/dev.077461	
	12,581,946				X
	21,244,910				X
	34,618,653	Bos taurus OPCML	Ovarian cancer	doi:10.1158/2159-8290.CD-11-0256	
	39,905,644				
	43,498,073	Bos taurus NRXN2	Vertebrate nervous system	doi:10.1523/jneurosci.15-04-02849.1995	
	45,367,095				

*SNP that fall within more than one ROH on the same chromosome

Table B4. Significant calving ease (CE) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	15,562,295				
	16,119,771				
	31,269,020				
	42,227,217				
	53,706,235				
	87,161,990				
	87,941,018	Bos taurus PEX5L	Accessory subunit of HCN channels	doi:10.1016/j.neuron.2009.05.009	
	90,283,892				
	90,689,913				
	94,860,836				
	94,952,782				
	96,677,750	Bos taurus PRKCI	Cell cancer	doi:10.1158/1541-7786.MCR-10-0359	
	97,458,910				
	97,906,442				
	99,597,502				
	99,689,088				
	107,384,385	Bos taurus PPM1L	Protein phosphatase	doi:10.1016/j.febslet.2012.06.050	
	114,907,147				X
	122,814,776				X
	143,788,237				X
	146,919,708				X
2	42,424,807	Bos taurus GALNT13	Tricuspid valve insufficiency	doi:10.1164/rccm.201201-0057OC	X

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
2	68,231,252	Bos taurus DPP10	Inflammatory disease	doi:10.1016/j.mrfmmm.2004.06.061	X
	88,925,365				X
	94,702,739				X
	94,865,712				X
	103,491,995				X
	108,529,237				
	115,092,998				
	121,847,018				
	129,882,579				
	135,190,642				
3	1,267,869	Bos taurus CD247	Rheumatoid arthritis	doi:10.1371/journal.pone.0068295	
	1,937,626	Bos taurus MAEL	Loss of spermatogenesis	doi:10.1016/j.devcel.2008.05.015	
	2,188,546				
	4,861,761				
	13,080,516				
	49,551,407	Bos taurus ABCA4	Photoreceptor-specific transporter	doi:10.1074/jbc.M405216200	
	52,834,458				
	53,495,709	Bos taurus LRRC8D	Involved in B cell development	doi:10.1016/S0014-5793(04)00332-1	
	77,446,808	Bos taurus WLS	Focal dermal hypoplasia	GeneCards	
	88,456,810				
	111,430,815	Bos taurus SMIM12	Protein coding	GeneCards	

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
3	115,395,556				
	115,659,306				
	117,232,908				
	120,446,774				
	120,573,628				
4	16,393,988	Bos taurus KIAA1324L	Embryo development	doi:10.1074/jbc.M110.177907	
	33,599,874	Bos taurus SCRN1	Colorectal cancer; gastric cancer	doi:10.1002/jso.21459; doi:10.1111/j.1349-7006.2006.00194.x	
	51,655,250	Bos taurus ST7	Cancer	doi:10.1007/s00432-010-0863-2	
	66,830,563				
	67,615,775				X
	72,920,828				
	73,367,338				
	73,597,885	Bos taurus ZNF804B	Gene expression	GeneCards	
	74,460,194				
	74,672,227				
	90,847,252				
	93,489,894				
	97,185,364				
	110,740,163				
	110,839,255				
	114,744,308	Bos taurus WDR86	Gonad development	doi:10.1016/S0925-4773(00)00452-4	
5	4,677,157				
	12,725,994				X
	25,775,985				

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
5	27,869,236				
	28,120,980				
	30,960,699				
	32,310,418	Bos taurus ASB8	Uterine carcinosarcoma	GeneCards	
	33,953,799				
	37,573,018				
	37,804,312				
	55,263,796				
	57,383,719	Bos taurus CS	Citrate synthesis	doi:10.1038/srep00785	
	57,404,217	Bos taurus ANKRD52	Corneal dystrophy	GeneCards	
	64,503,182	Bos taurus UHRF1BP1L	Cell carcinoma	GeneCards	
	72,618,051				
	86,997,963	Bos taurus SOX5	Intellectual disability	doi:10.1016/j.ejmg.2012.11.001	
	101,124,171				
	101,974,400				
	103,821,233				
	104,714,350	Bos taurus VWF	Hypoxia	doi:1161/ATVBAHA.113.301359	
	110,014,606	Bos taurus LGALS1	Luteal phase and early pregnancy	doi:10.1152/physiolgenomics.00251.2010	
6	1,040,062				
	3,316,210				

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
6	3,404,563	Bos taurus BBS7	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1016/j.gde.2005.04.006	
	17,456,425				
	24,495,145				
	38,133,743				
	39,837,065				
	48,025,306				
	50,442,769				
	80,915,917				
	88,242,415	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	88,442,145	Bos taurus SLC4A4	Proximal renal tubular acidosis	doi:10.1097/MNH.ob013e328363ff43	
	88,822,266				
	90,217,183				
	90,486,780				
	90,989,420				
	93,039,499				
	96,037,952				
	106,158,668				
7	428,335				
	2,948,577				
	8,491,850				
	40,136,380	Bos taurus MXD3	Perianal hematoma	GeneCards	
	53,989,891				

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
7	59,731,620				
	63,052,639				
	64,109,318				
	73,549,865				
	78,672,889				X
	98,194,828				
	98,566,391	Bos taurus CAST	Carcass and meat quality traits	doi:10.2527/2006.842291x	
	102,564,643				
	102,658,777				
	108,575,314				
8	10,013,895	Bos taurus FZD3	Schizophrenia	doi:10.1016/j.neulet.2011.10.023	
	25,133,019	Bos taurus PLIN2	Marbling; embryo viability; milk fat production	doi:10.5483/bmbrep.2009.42.8.529; doi:10.1016/j.anireprosci.2014.01.0101; doi:10.3168/jds.S0022-0302(99)75508-6	
	37,109,268				
	37,508,875				
	38,518,604	Bos taurus GLDC	Nonketotic hyperglycinemia	doi:10.1136/jmg.2006.043448	
	43,465,813				
	66,785,437				
	90,480,558				
	94,708,244				
	102,920,161				
	113,190,754				
	113,252,230				
9	36,440,319				

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
9	76,316,163				
	76,346,736				
10	961,339				
	9,558,767				
	26,973,237				
	31,574,360				
	47,601,270				
	48,225,546				
	54,829,993				
	57,611,774				
	58,004,357				
	59,761,240				
	87,848,389				
	90,906,002				
	93,246,483				
	93,275,196				
	94,425,952				
	96,065,191				
	99,330,554				
	99,731,658				
	100,288,306				
	100,523,095				
11	2,851,698				
	4,110,773				
	6,794,673				
	7,585,747				
	37,876,375	Bos taurus CCDC88A	Metastasis predictor of breast cancer	doi:10.1007/s12032-011-0087-6	

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
11	45,584,828	Bos taurus UXS1	Vulval morphogenesis and embryonic development	doi:10.1073/pnas.172522199	
	48,425,269	Bos taurus REEP1	Spastic paraplegia	doi:10.1007/s10048-008-0163-z	
	78,001,260				
	89,589,073				
	89,627,301				
	104,043,185				
12	860,453				
	23,450,916				
	27,684,536				
	28,205,239				
	29,170,799				
	29,649,126				
	29,681,550				
	30,808,992				
	31,272,071				
	33,535,830	Bos taurus ATP8A2	Cerebral atrophy and quadrupedal locomotion	doi:10.1038/ejhg.2012.170	
	87,150,059	Bos taurus FAM155A	Psychiatric disorders	doi:10.1016/S0140-6736(12)62129-1	
13	4,851,794				
	7,634,910				
	13,706,672				
	18,066,756	Bos taurus ACBD5	Differentiation of megakaryocytes and formation of platelets	GeneCards	

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
13	18,268,908	Bos taurus APBB1IP	Leukocyte adhesion deficiency	GeneCards	
	23,590,320				
	46,203,780				
	82,336,468				
14	3,484,849				
	11,983,913				
	12,247,110				
	35,663,156				
	51,811,945				
	52,302,089				
	54,164,119				
	55,219,280				X
	56,645,668				
	57,145,781				
	59,814,118				
	62,361,079	Bos taurus DPYS	Dihydropyrimidinuria	doi:10.1016/j.bbadis.2010.03.013	
	72,381,743				
	76,043,148	Bos taurus DECR1	Backfat	doi:10.2527/jas.2008-1456	
15	6,335,201	Bos taurus MMP20	Enamel development	doi:10.1177.0022034513506581	
	17,631,380				
	67,981,902				
	68,231,379				
	68,988,117				
	69,214,643				

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
15	69,930,274				
	74,137,434				
	84,704,791				
16	8,486,467				
	11,064,988				
	11,096,101				
	15,689,319				
	17,070,345				
	42,411,339				
	47,680,564	Bos taurus NOL9	Phosphoglycerate dehydrogenase deficiency	GeneCards	
	76,423,682				
17	1,970,122				
	33,251,225				
	33,715,935				
	38,001,105	Bos taurus FSTL5	Medulloblastoma	doi:10.1200/JCO.2011.36.2798	
18	25,345,775	Bos taurus PLLP	Bardet-Biedl syndrome – obesity, retinal degeneration, polydactyly, and nephropathy	doi:10.1007/s00335-001-3035-5	
	25,533,545	Bos taurus COQ9	Neonatal-onset primary coenzyme Q10 deficiency	doi:10.1016/j.ajhg.2009.03.018	
	25,709,879	Bos taurus ADGRG1	Cerebral cortical patterning	doi:10.1126/science.1244392	
	26,232,914				
	26,358,647				
	35,418,613	Bos taurus RANBP10	Modulates noncentrosomal microtubules	doi:10.1074/jbc.M709397200	X

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
18	36,594,231	Bos taurus VPS4A	Submandibular gland cancer	GeneCards	X
	40,502,223				X
	40,738,568	Bos taurus URI1	Ubiquitination and transcription	GeneCards	X
	59,662,778				
	62,250,437				
19	3,071,686				
	3,793,023				
	3,816,052				
	8,505,317	Bos taurus MSI2	Acute lymphoblastic leukemia	doi:10.1016/j.leukres.2013.05.012	
	8,770,836				
	19,373,322				
	22,038,801				
	29,890,136				X
	33,450,891	Bos taurus TEKT3	Sperm quality; sperm motility	doi:10.1387/ijdb.072333ag; doi:10.1002/mrd.20957	X
20	401,466	Bos taurus SLIT3	Cell migration	doi:10.1038/labinvest.2012.81	
	4,298,545				
	5,730,532				
	6,534,735				
	13,263,157				
	27,970,417				
	28,957,856				
	33,048,635	Bos taurus PLCXD3	Creutzfeldt-Jakob disease	doi:10.1186/1471-2350-14-91	

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
20	56,824,862				X
	57,177,369				X
	57,845,716				X
	58,214,328				X
	59,016,802				X
	68,403,701				
	68,681,680				
	68,713,825				
	69,825,743				
	70,669,729				
21	26,181,772				X
	30,007,996				
	44,229,968				X
	54,553,298				
	55,375,347	Bos taurus FANCM	DNA interstrand crosslinks	doi:10.1016/j.molcel.2013.09.021	
	59,219,376				
	65,776,237				
22	27,309,084				X
23	5,931,664				
	7,722,626	Bos taurus ITPR3	Mediates the release of intracellular calcium	doi:10.4161/auto.7.12.17909	
	22,300,959				
	23,909,884				
	33,874,418				
	48,791,036				
	49,094,579	Bos taurus FARS2	Mitochondrial phenylalanyl-tRNA synthetase	doi:10.1073/pnas.88.19.8387	

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
23	49,762,070				
	50,897,089				
24	580,805				
	2,658,119				
	5,696,089				
	29,553,275				XX
	52,825,393				
	56,442,291	Bos taurus TXNL1	Ehrlichiosis	GeneCards	
	62,593,028	Bos taurus SERPINB2	Gingivitis and pre-eclampsia	GeneCards	
25	4,779,974				
	31,625,995				
26	1,065,894				
	10,020,259	Bos taurus RNLS	Kidney disease	doi:10.1097/HJH.0b013e32834f0bb7	X
	11,443,033	Bos taurus KIF20B	Cytokinesis	doi:10.1074/jbc.M304522200	X
	19,344,348	Bos taurus PYROXD2	Trimethylaminuria	GeneCards	XX
	20,668,949				X
	40,519,284				
	49,366,950				
27	480,387				
	1,580,498				
	8,848,885				
	12,818,675				
	14,173,400				

*SNP that fall within more than one ROH on the same chromosome

Table B4. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
27	14,876,795	Bos taurus SORBS2	Hypotrichosis and Myopathy	GeneCards	
28	37,591,354	Bos taurus NRG3	Schizophrenia and bipolar disorder	doi:10.1017/S1461145712000697	
	41,674,187	Bos taurus LDB3	Cardiomyopathy	GeneCards	
29	2,091,741	Bos taurus FAT3	Tissue morphogenesis and planar polarity	doi:10.1242/dev.077461	
	12,581,946				X
	21,244,910				X
	34,618,653	Bos taurus OPCML	Ovarian cancer	doi:10.1158/2159-8290.CD-11-0256	
	43,498,073	Bos taurus NRXN2	Vertebrate nervous system	doi:10.1523/jneurosci.15-04-02849.1995	
	45,367,095				
	49,009,465				

*SNP that fall within more than one ROH on the same chromosome

Table B5. Significant age at first calving (AFC) single nucleotide polymorphism (SNP; $p < 0.005$), previously identified genes and their functions, and runs of homozygosity (ROH) overlap.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
1	23,489,264				
	57,752,344	Bos taurus ATG3	Cell autophagy	doi:10.1038/nature12606	
	66,344,261	Bos taurus STXBP5L	Neurotransmitter	doi:10.1016/s0896-6273(00)80472-9	
	103,463,199				
	105,355,814				
	123,372,013	Bos taurus PLOD2	Collagen fibrillogenesis	doi:10.1359/JBMR.041026	X
3	13,217,260				
	77,446,808	Bos taurus WLS	Focal dermal hypoplasia	GeneCards	
	80,517,326	Bos taurus AK4	Regulate adenine and guanine nucleotide compositions within a cell	GeneCards	
	81,047,780				
	105,467,351				
4	57,375,930				
	116,083,500				
	116,355,356				
5	968,910				
	1,087,211	Bos taurus LGR5	Intestinal stem cell population	doi:10.1016/j.stem.2013.01.003	
	86,997,963	Bos taurus SOX5	Intellectual disability	doi:10.1016/j.ejmg.2012.11.001	
	97,593,586				
6	17,378,057				
	20,297,397				
	39,257,620				
	61,182,251	Bos taurus RBM47	Head development	doi:10.1002/dvdy.24039	
	92,497,641				
	103,683,720				
7	35,071,656				

Table B5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
7	72,732,120	Bos taurus EBF1	Early adipogenesis	doi:10.1074/jbc.M113.491936	
9	20,937,396				X
10	20,550,545				
	26,973,237				
	28,996,491				
11	34,068,419				
	50,467,910				
12	27,684,536				
	31,639,399				
13	81,701,980				
14	60,682,230				
	73,979,692				
16	10,859,069				
	56,340,812				X
18	8,410,770				
	9,118,293				
19	50,696,008				X
	53,871,632	Bos taurus RBFOX3	Neural tissue development and regulation of adult brain function	GeneCards	X
	57,832,194				
20	21,967,184				
	52,271,324				X
	69,375,211				
	69,459,313				
21	27,296,213				X
	37,233,645	Bos taurus NOVA1	Breast cancer	GeneCards	
	37,522,232				
	59,875,525				

Table B5. Continued.

Chromosome	Base Pair Position	Previously Identified Genes	Gene Associated Trait	Reference	ROH Overlap
23	4,811,920	Bos taurus HMGCLL1	Breast cancer	GeneCards	
	33,874,418				
26	45,909,407	Bos taurus ADAM12	Modulation of proteolytic processing, cell adhesion, cell function, and signaling	doi:10.1080/10495390802212445	
27	20,757,482				
	23,144,459				
	31,625,207				
28	12,683,164	Bos taurus CHRM3	Muscarinic acetylcholine	doi:10.1016/s1499-3872(12)60201-x	
	15,300,456				
29	16,907,482				X
	43,498,073	Bos taurus NRXN2	Vertebrate nervous system	doi:10.1523/jneurosci.15-04-02849.1995	

APPENDIX C

AMERICAN SIMMENTAL ASSOCIATION CARCASS MERIT PROGRAM SINGLE-LOCUS MODEL SUPPLEMENTARY TABLES AND FIGURES

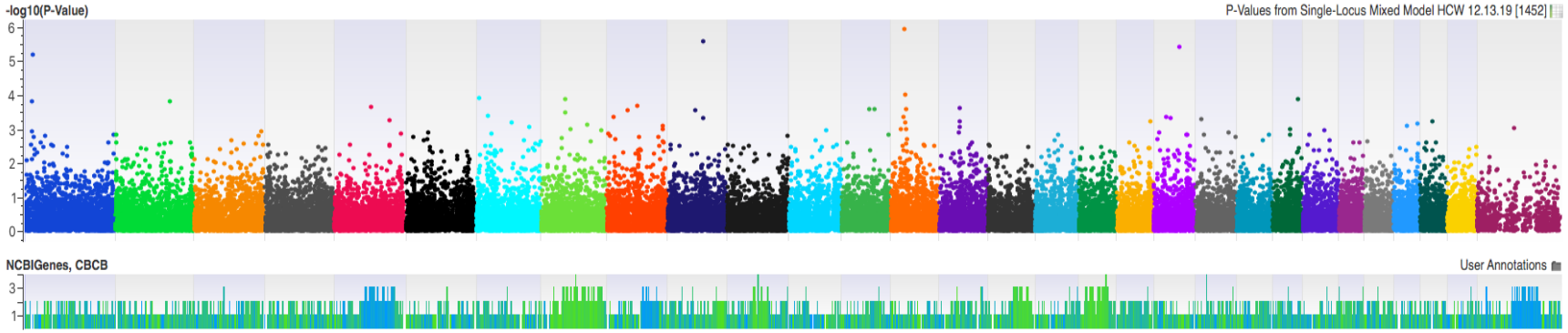


Figure C1. Manhattan plot for single-locus model hot carcass weight (HCW). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

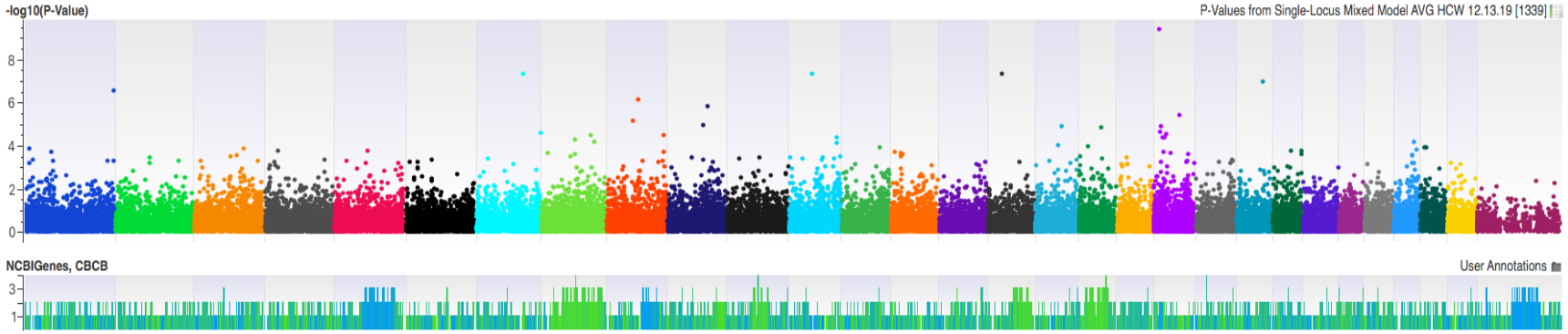


Figure C2. Manhattan plot for single-locus model average hot carcass weight (HCW). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

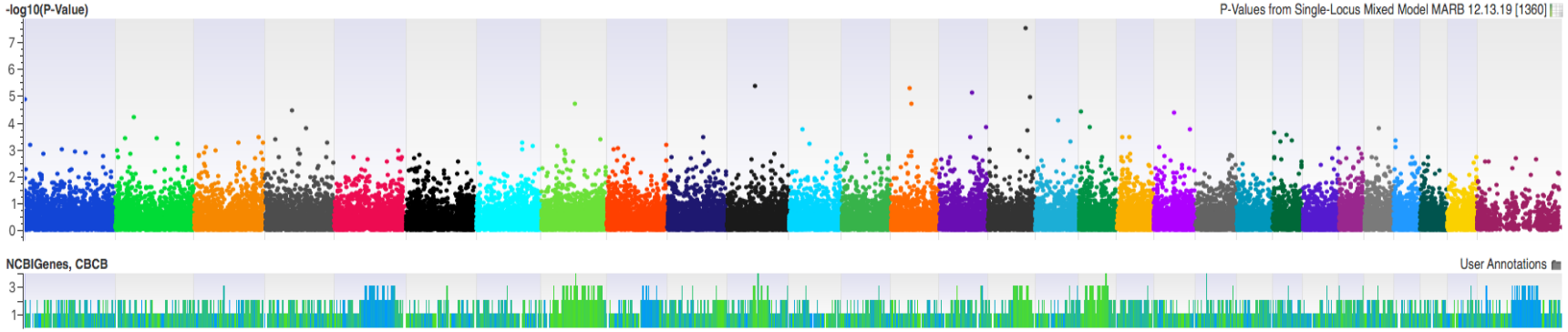


Figure C3. Manhattan plot for single-locus model marbling (MARB). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

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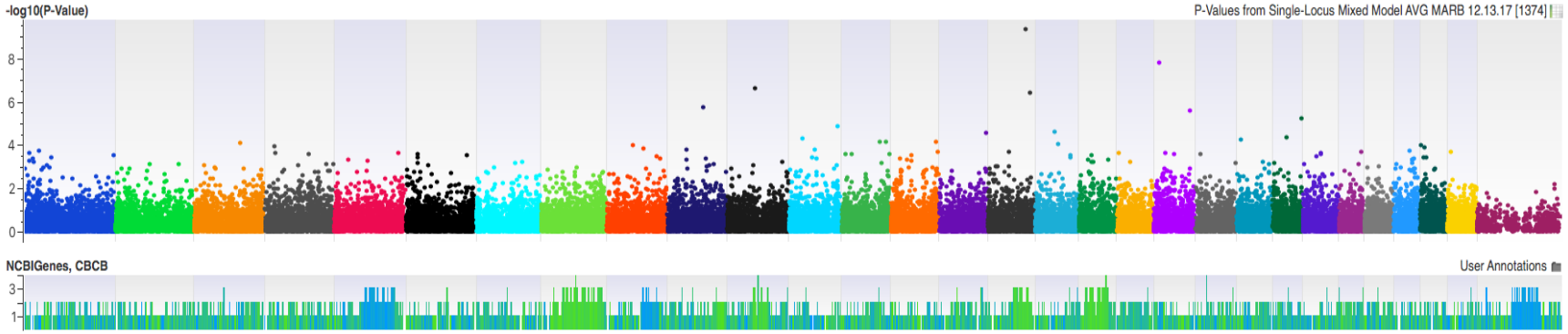


Figure C4. Manhattan plot for single-locus model average marbling (MARB). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

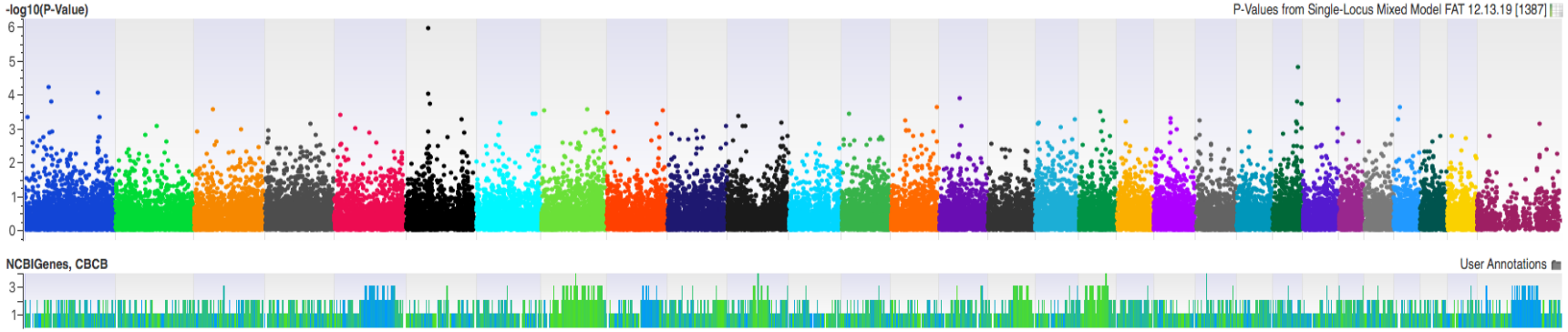


Figure C5. Manhattan plot for single-locus model 12th rib fat (BF). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

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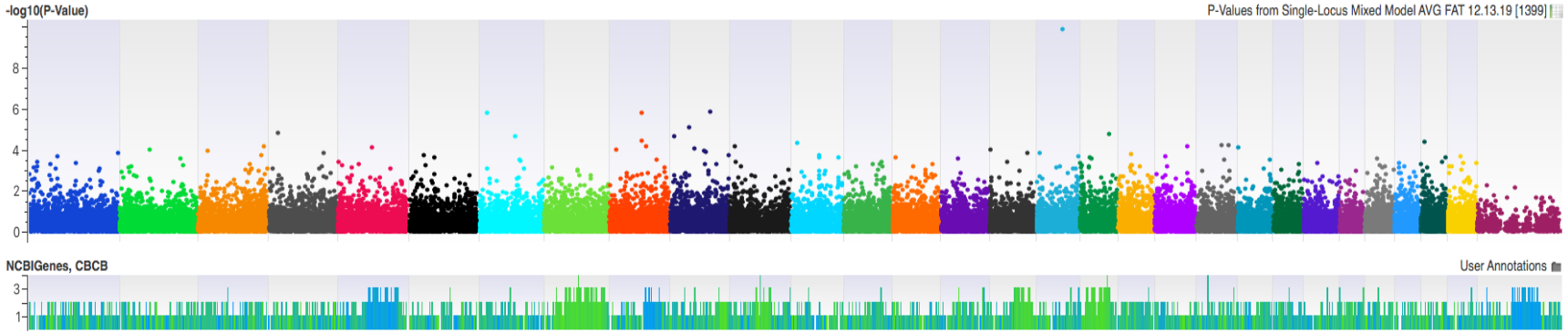


Figure C6. Manhattan plot for single-locus model average 12th rib fat (BF). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

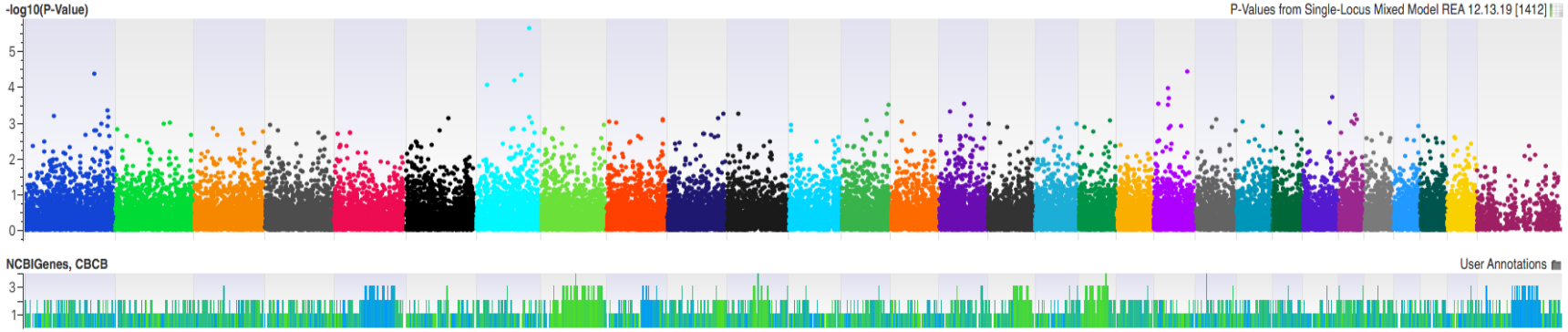


Figure C7. Manhattan plot for single-locus model rib eye area (REA). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

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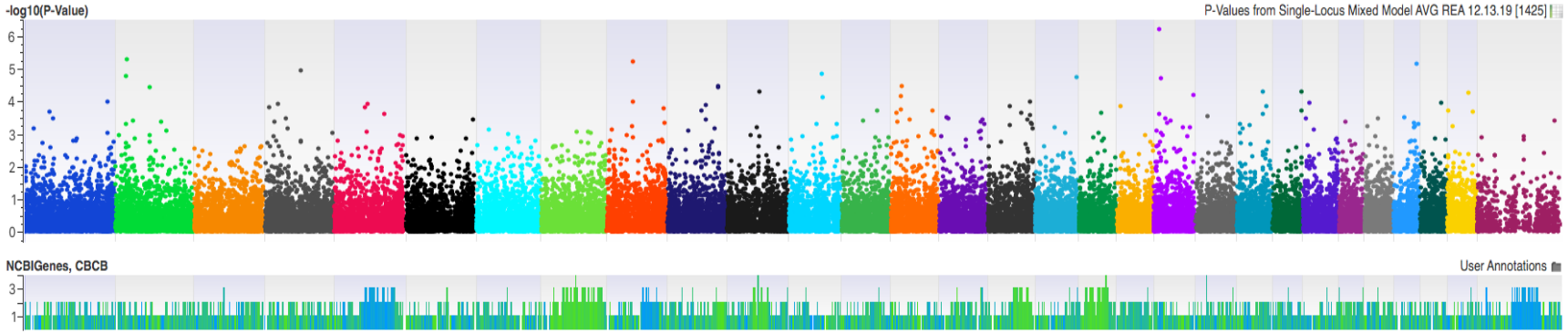


Figure C8. Manhattan plot for single-locus model average rib eye area (REA). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

Table C1. Significant single-locus model hot carcass weight (HCW) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	147,955,914-148,009,894	Beginning of Bos taurus S100B			
	156,254,566-156,294,225	Bos taurus TBC1D5			
2	21,389,327-21,448,855		QTL 20354	Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
	96,021,111-96,049,233				
	133,258,339-133,349,015	Bos taurus PLA2G2A, Bos taurus LOC 100123947			
4	5,463,939-5,549,277	End of Bos taurus IKZF1			
	105,738,302-105,794,912	End of Bos taurus AGK			
5	97,490,658-97,530,532	End of Bos taurus DDX47, Bos taurus APOLD1			
	97,530,532-97,593,586	Bos taurus CDKN1B			
6	42,057,261-42,120,804				
	61,640,981-61,733,479	Bos taurus APBB2	QTL 10779	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	89,104,201-89,133,819				
	107,086,553-107,095,193	Bos taurus NSG1			

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Table C1. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
6	108,372,085-108,404,861				
7	6,134,663-6,206,251	Beginning of Bos taurus NWD1			
	20,423,138-20,500,709	Bos taurus UHRF1, Bos taurus ARRDC5			
	26,309,154-26,360,833	End of Bos taurus SLC27A6			
9	56,406,855-56,490,122				
10	91,330,836-91,357,108				
11	252,264-317,337				
14	18,811,289-18,832,428		QTL 1733	Waygu	10.2527/2004.8212415x
15	36,755,580-36,817,688	Bos taurus SOX6			
	61,893,000-61,927,861				
16	2,813,940-2,841,879	End of Bos taurus DSTYK, Beginning of Bos taurus TMCC2	QTL 11009	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
17	41,013,290-41,089,654	End of Bos taurus C17H4orf45			
	41,089,654-41,178,453				
19	57,098,859-57,128,225	End of Bos taurus OTOP3, Bos taurus OTOP2, Bos taurus USH1G			

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Table C1. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
19	57,128,225-57,149,037	Beginning of Bos taurus FADS6			
20	25,255,282-25,296,510		QTL 11107	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	44,892,168-44,916,116				
	58,292,591-58,329,179				
	64,169,690-64,185,456				
25	24,625,971-24,661,275		QTL 11210	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
27	40,951,386-41,049,981	Beginning of Bos taurus MCM4			
	41,191,284-41,226,347				
28	27,564,486-27,618,750	End of Bos taurus UNC5B, Beginning of Bos taurus SLC29A3			
	38,961,890-39,061,596				

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Table C2. Significant single-locus model average hot carcass weight (HCW) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	156,254,566-156,294,225	Bos taurus TBC1D5			
2	59,644,564-59,690,093		QTL 10665	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
			QTL 13187 **PRKAG3**	Aberdeen Angus sired steers	10.1016.j.meatsci.2010.08.005
3	88,923,355-88,950,716				
4	93,398,396-93,462,288	End of Bos taurus IMPDH1, Beginning of Bos taurus HILPDA			
5	117,795,427-117,823,521				
6	20,430,846-20,475,948		QTL 1369	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
			QTL 10425, 10426, 10428, 10429	Japanese Black	10.1186.1471-2156-10-43
			QTL 24619	Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, Shorthorn, Maine, Simmental	10.1186/1471-2164-15-442

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Table C2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
6	44,305,092-44,337,791				
7	106,398,519-106,422,549				
8	58,505,244-58,594,366				
9	5,188,669-5,288,398				
	26,228,944-26,262,054				
	31,043,707-31,067,189		QTL 37238, 37240, 37250, 37255, 37259, 37264, 37267, 37275	Holstein	10.1186/1471-2164-15-837
10	66,659,307-66,687,859		QTL 10881	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	73,855,126-73,884,120	Bos taurus PRKCH			
	88,605,589-88,630,762				
12	51,403,603-51,461,607				
	88,703,946-88,759,054				
13	57,524,735-57,570,093				
14	18,811,289-18,832428		QTL 1733	Waygu	10.2527/2004.8212415x

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Table C2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
15	71,342,153-71,375213				
	73,739,991-73,762207				
17	34,564,610-34,591,064		QTL 11048	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	41,066,514-41,089,654	End of Bos taurus C17H4orf45			
	72,710,280-72,790,867	End of Bos taurus SLC5A1, Bos taurus SLC5A4			
	73,206,420-73,257,794	Bos taurus CHCHD10, Bos taurus SMARCB1, Bos taurus DERL3, Beginning of Bos taurus SLC2A11			
20	23,052,519-23,085,736	Bos taurus ANKRD55	QTL 11107	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	58,264,762-58,292,591				

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Table C2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
21	42,051,380-42,089,249	End of Bos taurus STRN3, Beginning of Bos taurus AP4S1			
	61,310,103-61,370,773	Bos taurus LOC784932, Bos taurus KRTCAP2			
25	19,901,965-19,975,551		QTL 11210	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
26	6,620,890-6,692,455				
27	24,231,664-24,273,840				
	31,216,225-31,261689				
	39,916,848-39,994,067	End of Bos taurus NGLY1			
29	24,228,574-24,259532		QTL 1316	Brahman x Angus cross	10.2527/2003.8181933x
			QTL 1344	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
			QTL 11292	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

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Table C3. Significant single-locus model marbling (MARB) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
2	30,899,389-30,992,555	Beginning of Bos taurus SCN2A			
3	105,173,273-105,209,697				
	119,559,145-119,584,154				
	121,310,309-121,374,825				
4	100,436,744-100,497,231				
5	118,475,383-118,501,191				
6	20,350,438-20,430,846				
	23,700,430-23,738,304	Bos taurus NFKB1			
	35,577,199-35,611,267	Bos taurus CCSER1	QTL 10770	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	66,509,207-66,572,393	Beginning of Bos taurus GABRA2			
8	41,096,123-41,147,533				
	76,530,816-76,582,220	End of Bos taurus AQP3, Bos taurus NOL6, Beginning of Bos taurus UBE2R2			

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Table C3. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
9	105,074,182-105,168,826	End of Bos taurus C9H6orf120, Bos taurus PHF10, Bos taurus TCTE3, Bos taurus ERMARD			
10	73,855,126-73,884,120	Bos taurus PRKCH			
13	43,009,513-43,054,682	End of Bos taurus APMAP, Bos taurus ENTPD6, Beginning of Bos taurus ACSS1	QTL 10947	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	70,171,253-70,195,187				
	82,443,688-82,455,320				
15	65,967,835-65,990,096				
	76,930,018-76,960,713	Bos taurus PHF21A			
	84,540,041-84,575,987	End of Bos taurus MS4A7, Bos taurus MS4A14			
17	49,702,881-49,743,917				

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Table C3. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
19	10,305,065-10,367,765	End of Bos taurus TRIM37, Bos taurus SKA2, Bos taurus MIR454, Bos taurus MIR301A, Beginning of Bos taurus PRR11	QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	10,617,246-10,694,269		QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	19,718,709-19,789,422	Bos taurus LGALS9, Beginning of Bos taurus NOS2	QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	22,864,442-22,963,249	Beginning of Bos taurus RPH3AL			
	23,732,618-23,798,617	Bos taurus SMG6			
20	9,627,990-9,651,103				
	18,719,808-18,743,927				
21	59,853,238-59,875,525				
	63,930,679-63,955,841				
26	20,813,204-20,903,573	Bos taurus CPN1, Beginning of Bos taurus LOC511498			
	26,234,033-26,296,169	Bos taurus SORCS3	QTL 11238	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

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Table C3. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
27	32,129,484-32,157,142		QTL 1372	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	41,552,379-41,613,442				
29	51,438,462-51,502,868				

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Table C4. Significant single-locus model average marbling (MARB) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	16,196,001-16,245,203		QTL 10636	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
2	21,290,918-21,389,327		QTL 20298, 20299, 20317, 20398, 20399, 20400		
	85,427,167-85,452,055				
3	17,195,924-17,280,333	Bos taurus LOR			
	116,990,141-117,023,378				
4	93,828,702-93,872,285				
5	118,430,785-118,475,383				
6	2,217,430-2,296,875		QTL 10756	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	15,391,410-15,484,522	Bos taurus MIR2444			
	18,653,222-18,750,621	Beginning of Bos Taurus PAPSS1			
	20,297,397-20,350,438				
	20,350,438-20,430,846				
	20,430,846-20,475,948		QTL 10498	Hanwoo	10.1007/s00335-011-9331-9

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Table C4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
7	5,352,670-5,400,415	End of Bos taurus MAP1S			
	31,601,869-31,655,835				
8	58,505,244-58,594,366				
	58,986,469-59,085,873				
	108,772,548-108,819,340				
10	34,316,340-34,407,598		QTL 10874	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	34,407,598-34,438,367		QTL 10874	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	68,162,634-68,231,955				
	69,379,251-69,474,936	Bos taurus OTX2			
	81,648,739-81,695,290				
11	6,724,678-6,758,495	Bos taurus IL1R2			
	106,708,013-106,741,315	End of Bos taurus OLFM1			
12	84,817,834-84,882,391				
	85,428,753-85,453,952				

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Table C4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
13	17,146,206-17,232,510	End of Bos taurus PRKCQ	QTL 10941	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	43,319,313-43,367,995	End of Bos taurus GDI2	QTL 10947	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	67,810,247-67,888,763	Bos taurus BPI, End of Bos taurus LBP			
14	18,263,091-18,331,919	End of Bos taurus TBC1D31, Beginning of Bos taurus DERL1	QTL 1334	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	18,331,919-18,408,275	End of Bos taurus DERL1, Bos taurus ZHX2	QTL 1334	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	19,441,969-19,531,288		QTL 1334	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x

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Table C4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
14	38,044,172-38,095,683	Bos taurus KCNB2	QTL 1334	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
			QTL 18980	Hanwoo	10.1007/s00335-011-9331-9
			QTL 20867-20869	Crossbred	10.1111/j.1365-2052.2011.02307.x
	58,589,050-58,687,826	Bos taurus RSPO2			
	81,269,892-81,309,300				
	84,505,345-84,594,318				
15	35,333,265-35,364,770	End of Bos taurus MYOD1	QTL 10999	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	54,939,673-54,995,188	End of Bos taurus XRRA1			
16	2,685,332-2,775,425	Bos taurus TMEM81, Bos taurus RBBP5, Beginning of Bos taurus DSTYK			
	36,744,747-36,817,218				

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Table C4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
17	41,178,453-41,272,672	Bos taurus PPID, Beginning of Bos taurus ETFDH			
18	2,630,430-2,716,884	Beginning of Bos taurus CFDP1			
	21,993,542-22,064,133				
	22,574,534-22,610,574				
	25,981,472-26,045,554	Bos taurus USB1, Bos taurus MMP15			
	38,296,121-38,394,166				
	40,502,223-40,587,048	Bos taurus CCNE1			
19	8,622,586-8,648,705	Bos taurus MSI2	QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	15,107,270-15,137581	End of Bos taurus SLFN14	QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
20	6,534,735-6,605,865	Beginning of Bos taurus FAM169A			
	16,120,614-16,166,220				
	22,093,001-22,165,165	End of Bos taurus GPBP1			
21	9,741,507-9,784,549				

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Table C4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
22	7,623,264-7,691,228	Beginning of Bos taurus FBXL2	QTL 11138	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	20,397,580-20,451,252		QTL 7104	Charolais x Holstein crosses	10.2527/jas.2008-0922
	56,603,472-56,675,252				
23	3,167,662-3,239,987	Bos taurus MIR2375, Bos taurus MIR2285J-2			
	3,544,538-3,626,219				
	3,626,219-3,664,434				
	40,203,865-40,258,672				
24	24,904,038-24,961,929				
25	39,468,067-39,518,953	Beginning of Bos taurus SLC29A4			
26	26,234,033-26,267,018	Bos taurus SORCS3	QTL 11238	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
27	8,589,473-8,689,042		QTL 1342	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	12,330,184-12,355,411		QTL 11253	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

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Table C4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
27	20,791,916-20,863,121		QTL 1342	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	31,216,225-31,261,689		QTL 1372	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	36,935,085-37,004,165	Beginning of Bos taurus SLC20A2			
	41,613,442-41,649,895				
28	717,380-811,398				
	2,092,581-2,181,928	Beginning of Bos taurus RHOU	QTL 20328, 20409	Crosses of Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
	7,068,698-7,138,132	Bos taurus SLC35F3			
	8,080,087-8,105,051	Bos taurus ARID4B	QTL 11270	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

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Table C5. Significant single-locus model 12th rib fat (BF) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	14,853,644-14,909,272				
	47,123,160-47,177,862				
	76,505,437-76,534,601				
	81,160,609-81,239,683	End of Bos taurus FETUB, Bos taurus AHSG, Beginning of Bos taurus DNAJB11	QTL 10649	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	127,998,001-128,031,876	End of Bos taurus TFDP2			
	128,864,268-128,938,068	End of Bos taurus SPSB4			
	131,642,361-131,684,053				
3	81,428,130-81,472,159		QTL 10701	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
4	5,639,667-5,712,778				
	62,549,908-62,606,492	Bos taurus NPSR1			
	73,861,517-73,894,130	Bos taurus ZNF804F			
	74,076,693-74,148,361				

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Table C5. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
4	80,350,223-80,407,501				
5	118,307,910-118,392,147	End of Bos taurus TBC1D22A, Bos taurus MIR2285O-5, Bos taurus MIR2284H			
6	41,123,393-41,178,449				
	41,178,449-41,253,845	Beginning of Bos taurus SLIT2			
	41,253,845-41,343,408	Bos taurus SLIT2			
7	38,997,984-39,060,855	Bos taurus COMMD10			
8	91,086,691-91,125,290	Beginning of Bos taurus NXNL2			
	104,829,510-104,862,806				
9	92,242,453-92,250,839				
10	17,867,003-17,955,497	End of Bos taurus LRRC49			
	102,849,006-102,935,702	Bos taurus PSMC1, Beginning of Bos taurus NRDE2			
11	91,995,272-92,059,274				

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Table C5. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
11	95,501,827-95,516,698	Beginning of Bos taurus NR5A1			
	98,407,974-98,482,863	Bos taurus TTC16, Bos taurus TOR2A, Bos taurus SH2D3C, Bos taurus CDK9			
13	48,594,834-48,622,655	Beginning of Bos taurus FERMT1			
	65,761,897-65,855,988				
14	27,271,835-27,321,716		QTL 10965	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	27,669,598-27,751,888	End of Bos taurus CA8	QTL 10965	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	43,499,031-43,526,891		QTL 10973	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
			QTL 20854-20861	Crossbred	10.1111/j.1365-2052.2011.02307.x
	48,184,967-48,256,343	End of Bos taurus SAMD12			
	75,517,287-75,571,250	End of Bos taurus SLC26A7			
15	34,294,990-34,342,385	End of Bos taurus CLMP			
16	66,609,042-66,676,299	End of Bos taurus TSEN15			

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Table C5. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
17	5,590,969-5,663,467				
	7,756,498-7,794,593				
18	22,574,534-22,610,574				
19	16,578,349-16,598,801				
20	28,850,177-28,887,439		QTL 15736	Angus x Brahman	10.3389/fgene.2011.00044
			QTL 20540, 20542	Brangus	10.4238/2011.December.19.3
22	60,105,535-60,130,492	Bos taurus EEFSEC			
23	41,901,234-41,965,164				
	43,925,150-43,950,048				
	52,038,120-52,128,894	Bos taurus IRF4			
24	61,885,106-61,931,908	Beginning of Bos taurus BCL2			
25	17,860,710-17,891,876				
28	6,499,231-6,547,497	Bos taurus KCNK1			
	21,014,194-21,066,992		QTL 20273	Crosses of Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x

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Table C5. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
29	7,276,898-7,355,188				

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Table C6. Significant single-locus model average 12th rib fat (BF) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	1,288,510-1,359,951	End of Bos taurus GART, Beginning of Bos taurus TMEM50B	QTL 1317 **IFNAR1**	Brahman, Angus	10.2527/2003.8181933x
	14,853,644-14,909,272				
	37,289,127-37,355,979		QTL 4854	Wagyu x Limousin	10.1111/j.1365.2052.2007.01643.x
	50,252,331-50,320,575				
	55,359,042-55,386,945				
	73,106,447-73,140,918				
	100,513,127-100,605,192	End of Bos taurus SERPINI1, Bos taurus PDCD10	QTL 10653	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
2	16,157,387-16,238,330		QTL 1322	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	111,103,057-111,181,420	Beginning of Bos taurus PAX3, Bos taurus MIR2284Y-5			

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Table C6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
3	17,241,980-17,280,333	Bos taurus LOR	QTL 1325	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	112,922,761-112,955,526				
	115,730,569-115,790,125				
	116,968,644-117,023,378				
4	21,937,293-21,973,829		QTL 20280, 20285, 20368, 20446	Crosses of Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
	37,440,961-37,489,913				
	96,258,114-96,282,870				
5	6,976,839-7,053,234		QTL 20001 **MYF5**	Jiaxian Red, Qinchuan, Luxi, Nanyang, Xianan	10.4238/2011.December.12.6
	21,922,004-21,947,260		QLT 20265, 20281-20283, 20369, 20370,	Crosses of Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
			QTL 20546, 20550, 20551, 20554 **STAT6**	Brangus	10.4238/2011.December.19.3

Table C6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
6	20,276,795-20,297,397		QTL 24647	Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, Shorthorn, Maine, Simmental	10.1186/1471-2164-15-442
	44,305,092-44,337,791				
	107,016,833-107,095,193	Bos taurus NSG1			
7	12,833,745-12,889,689	End of Bos taurus DCAF15, Beginning of Bos taurus CC2D1A			
	66,156,674-66,212,415				
8	8,647,926-8,507,614	Beginning of Bos taurus MSRA	QTL 2546, 2548	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	81,573,118-81,638,162				
	81,638,162-81,715,421				
	112,323,763-112,345,659	End of Bos taurus C5			
9	31,043,707-31,067,189				
	46,583,336-46,662,943				
	59,972,449-59,995,189				

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Table C6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
9	74,223,999-74,293,236	End of Bos taurus MYB			
	97,872,904-97,929,407				
10	20,498,087-20,550,545	Bos taurus TBC1D21			
	66,659,307-66,687,859				
	80,546,262-80,567,844	Bos taurus RAD51B			
	81,648,739-81,695,290				
	102,887,596-102,935,702	Bos taurus PSMC1, Beginning of Bos taurus NRDE2			
11	8,763,389-8,836,373				
	8,836,373-8,904,074				
	103,799,585-103,830,982				
12	48,909,344-49,006,756	Bos taurus KLF12			
	48,984,802-49,057,460	Bos taurus KLF12			
	49,006,756-49,095,991	Bos taurus KLF12			

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Table C6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
12	82,765,192-82,812,721				
	89,095,085-89,154,911				
14	4,468,478-4,563,129	Bos taurus TRAPPC9	QLT 10957	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	33,580,690-33,604,665		QTL 10971	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	58,589,050-58,687,826	Bos taurus RSPO2			
15	41,707,747-41,757,348	Bos taurus GALNT18			
	80,003,887-80,097,824				
	81,488,498-81,540,854				
16	31,382,509-31,462,716	Bos taurus H3F3C, Beginning of Bos taurus CNST			
17	4,868,261-4,926,550	End of Bos taurus ARFIP1			
	34,409,623-34,429,947				
	41,178,453-41,272,672	Bos taurus PPID, Beginning of Bos taurus ETFDH	QTL 11052	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	63,855,514-63,939,534				

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Table C6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
17	70,699,234-70,776,835	End of Bos taurus EWSR1, Bos taurus GAS2L1, Bos taurus RASL10A, Beginning of Bos taurus AP1B1			
	72,710,280-72,790,867	End of Bos taurus SLC5A1, Bos taurus SLC5A4			
18	3,146,088-3,177,824		QTL 11058	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
19	5,057,128-5,083,994				
	22,749,859-22,771,407	Bos taurus VPS53			
	30,674,477-30,723,576				
	58,551,913-58,591,027				
20	4,395,656-4,425,557		QTL 24655	Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, Shorthorn, Maine, Simmental	10.1186/1471-2164-15-442
	18,631,431-18,719,808	End of Bos taurus DEPDC1B			

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Table C6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
20	18,719,808-18,743,927				
	21,938,158-21,967,184				
	22,093,001-22,165,165	End of Bos taurus GPBP1	QTL 20540, 20542	Brangus	10.4238/2011.December.19.3
	57,373,160-57,403,850				
21	58,944,572-58,966,585	Bos taurus PRIMA1			
22	499,356-574,301	Bos taurus VOPP1			
	58,397,411-58,429,229				
23	45,048,666-45,106,522	Beginning of Bos taurus ELOVL2			
25	17,860,710-17,891,876				
26	22,557,427-22,648,915	Beginning of Bos taurus HPS6			
27	8,589,473-8,689,042				
	11,657,439-11,715,052				
28	6,499,231-6,547,497	Bos taurus KCNK1			
29	24,228,574-24,259,532				

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Table C7. Significant single-locus model rib eye area (REA) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	122,789,893-122,814,776				
	143,741,734-143,831,554	End of Bos taurus ZBTB21			
	145,643,805-145,710,047				
3	82,187,624-82,250,730	Beginning of Bos taurus PGM1			
7	16,588,162-16,611,621	End of Bos taurus YIPF2, Bos taurus TIMM29			
	60,436,313-60,475,602	Beginning of Bos taurus STK32A			
	78,762,342-78,822,792				
	84,925,417-84,991,860				
8	19,811,075-19,863,242				
	37,136,374-37,158,190				
9	99,334,002-99,354,827	Bos taurus PRKN			
10	32,409,981-32,422,588	Bos taurus C10H15orf41			
	88,563,925-88,605,589				
11	20,202,555-20,271,885				
	22,688,045-22,716,948	Bos taurus SLC8A1			
12	4,324,502-4,397,035				
	86,938,949-86,961,976	Bos taurus FAM155A			
13	79,914,560-79,991,041				
14	20,323,857-20,347,849				
	27,575,294-27,669,598	Beginning of Bos taurus CA8			
15	34,763,290-34,852,656	Bos taurus SCN3B			
	37,237,274-37,309,941				
	55,206,099-55,254,553				
	56,571,496-56,663,853	End of Bos taurus THAP12, Beginning of Bos taurus EMSY			
16	38,807,074-38,830,470				
17	13,941,499-13,984,972				
	41,089,654-41,178,453				
20	25,255,282-25,296,510				

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Table C7. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
21	43,579,015-43,649,910	End of Bos taurus AKAP6			
23	46,334,617-46,401,353				
	52,038,120-52,128,894	Bos taurus IRF4			
25	28,974,015-29,065,778	Bos taurus CALN1			
26	37,733,926-37,797,893	Beginning of Bos taurus VAX1			

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Table C8. Significant single-locus model average rib eye area (REA) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	151,835,916-151,858,713				
	156,254,566-156,294,225	Bos taurus TBC1D5			
2	9,810,493-9,867,063	Beginning of Bos taurus ZC3H15			
	15,250,050-15,303,929				
	18,164,650-18,233,729				
	29,369,336-29,405,628				
	59,644,564-59,690,093				
3	62,458,422-62,509,283				
4	15,468,000-15,537,254				
	93,462,288-93,489,894	End of Bos taurus HILPDA, Bos taurus FAM71F2			
5	12,338,455-12,408,591				
	42,166,749-42,188,101				
	117,738,204-117,795,427	End of Bos taurus GTSE1, Bos taurus TRMU			
	119,949,553-120,016,258	Bos taurus SHANK3, Bos taurus ADM2, Bos taurus MIOX			
7	2,323,494-2,346,546				
	3,488,080-3,570,752				
	5,6055,399-56,152,302	Bos taurus ARHGAP26			
8	81,612,097-81,638,162				
	102,664,941-102,694,365				
9	5,188,669-5,288,398				
	14,794,389-14,817,532				
	90,423,605-90,521,235				
	98,566,722-98,648,213	Bos taurus PRKN			
10	61,684,704-61,769,231				
	68,089,016-68,162,634	End of Bos taurus ATG14			
	68,162,634-68,231,955				

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Table C8. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
10	72,023,342-72,060,561	End of Bos taurus JKAMP, Beginning of Bos taurus CCDC175			
	88,563,925-88,630,762				
	90,543,010-90,589,157				
11	54,855,548-54,887,301	Bos taurus CTNNA2			
	71,811,673-71,875,910	End of Bos taurus BABAM2, Beginning of Bos taurus RBKS			
13	2,342,625-2,372,577	Bos taurus PLCB4			
	37,675,851-37,757,395				
	57,524,735-57,570,093				
	59,963,672-60,002,265	Bos taurus FAM209A, Beginning of Bos taurus RTF2			
14	2,194,228-2,239,085	Beginning of Bos taurus MAPK15			
	18,811,289-18,832,428				
	19,132,330-19,172,385				
	28,818,196-28,911,839	End of Bos taurus ASPH			
15	73,739,991-73,762,207				
16	933,282-950,232	End of Bos taurus FMOD			
	3,206,597-3,287,341	Bos taurus ELK4			
17	19,184,418-19,207,100				
	49,702,881-49,791,728				
18	40,690,801-40,738,568	Bos taurus URI1			
20	13,048,063-13,130,283				
	39,950,657-40,004,925	Bos taurus ADAMTS12			
	53,635,068-53,674,655	Bos taurus CDH18			
	69,430,215-69,459,313				
21	55,059,767-55,096,333				
22	6,450,949-6,485,383				
	51,214,861-51,245,935				
	51,452,218-51,484,825	Bos taurus LAMB2, Beginning of Bos taurus QARS1			

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Table C8. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
23	32,682,177-32,757,561	Bos taurus RIPOR2			
	51,621,297-51,719,827				
24	11,851,627-11,916,234				
	60,745,394-60,842,899				
25	40,282,215-40,341,603				
26	9,669,992-9,725,747				
27	37,283,994-37,357,125	Bos taurus HOOK3			
	37,357,125-37,389,551	End of Bos taurus HOOK3			

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Table C9. Significant single-locus model internal fat (KPH) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	883,895-950,841	Bos taurus ATP5O, Bos taurus MIR12045			
	16,145,053-16,196,001				
	142,401,535-142,446,153				
2	30,262,141-30,307,800				
6	3,093,621-3,149,732				
	27,158,687-27,183,822		QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
	30,782,962-30,832,561	Beginning of Bos taurus BMPR1B	QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
	41,343,408-41,443,081	Bos taurus SLIT2	QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
	42,155,077-42,239,393		QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
8	40,775,647-40,800,617				
	51,330,787-51,369,892				
	73,881,694-73,907,982				
	101,044,054-101,135,756	Bos taurus PALM2			
	101,135,756-101,167,884	Bos taurus PALM2			

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Table C9. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
9	55,740,550-55,802,932				
10	6,076,725-6,096,967				
	47,114,150-47,197,199				
	92,952,608-92,984,267				
11	15,919,622-15,945,389	Bos taurus LTBP1			
13	49,963,611-50,004,272				
	62,881,877-62,909,025	End of Bos taurus BPIFB6, Beginning of Bos taurus BPIFB3			
14	59,112,331-59,139,878	Beginning of Bos taurus ANGPT1			
16	37,479,436-37,505,165		QTL 1354	(Brahman x Angus) x Hereford, Angus, MARC III	10.1046/j.1365-2052.2003.01067.x
17	64,189,856-64,225,341				
19	37,670,702-37,699,961	End of Bos taurus NXPH3			
22	37,615,930-37,652,444				
24	56,487,933-56,564,480	Bos taurus WDR7			

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Table C9. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
25	40,022,986-40,060,928				
	41813,524-41,849,369	Bos taurus ELFN1			
26	6,051,502-6,092,833				
	23,048,759-23,129,849	Bos taurus SUFU			
27	10,697,257-10,764,825				
	30,025,162-30,089,811				
29	41,778,946-41,854,768	End of Bos taurus POLR2G, Bos taurus TAF6L, Bos taurus TMEM179B, Bos taurus TMEM223, Bos taurus NXF1, Bos taurus STX5, Bos taurus WDR74			
	42,620,218-42,696,595	End of Bos taurus ATL3, Beginning of Bos taurus RTN3			
	42,985,739-43,043,207	Bos taurus MACROD1, Beginning of Bos taurus NAA40			

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APPENDIX D

AMERICAN SIMMENTAL ASSOCIATION CARCASS MERIT PROGRAM MULTI-LOCUS MODEL SUPPLEMENTARY TABLES AND FIGURES

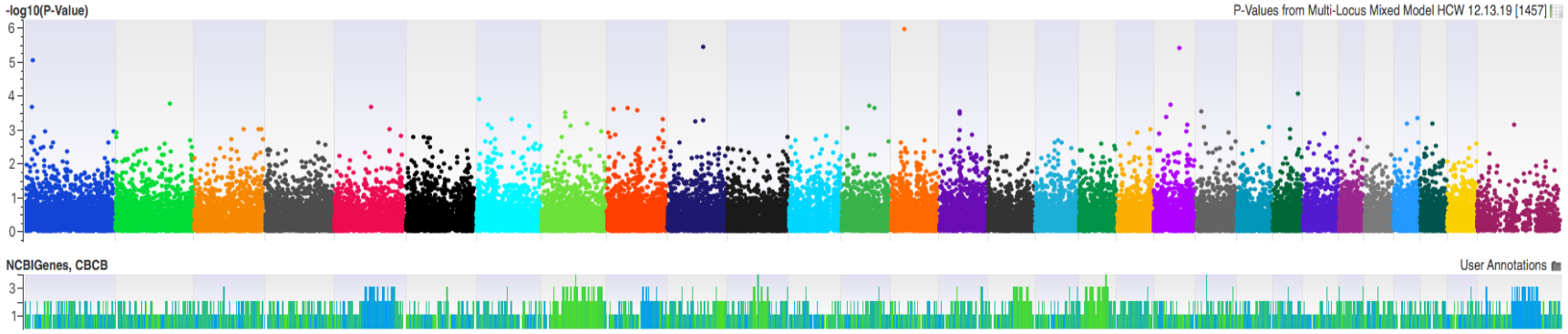


Figure D1. Manhattan plot for multi-locus model hot carcass weight (HCW). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

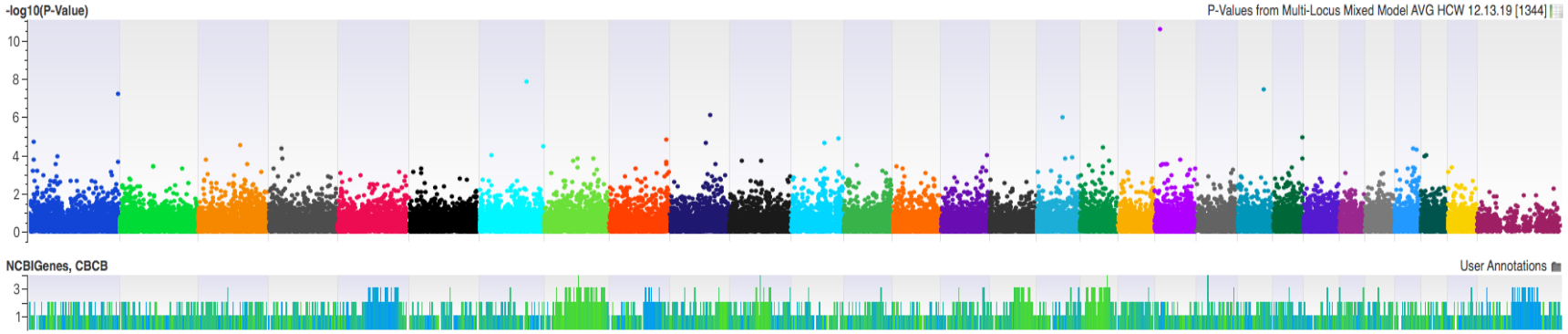


Figure D2. Manhattan plot for multi-locus model average hot carcass weight (HCW). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

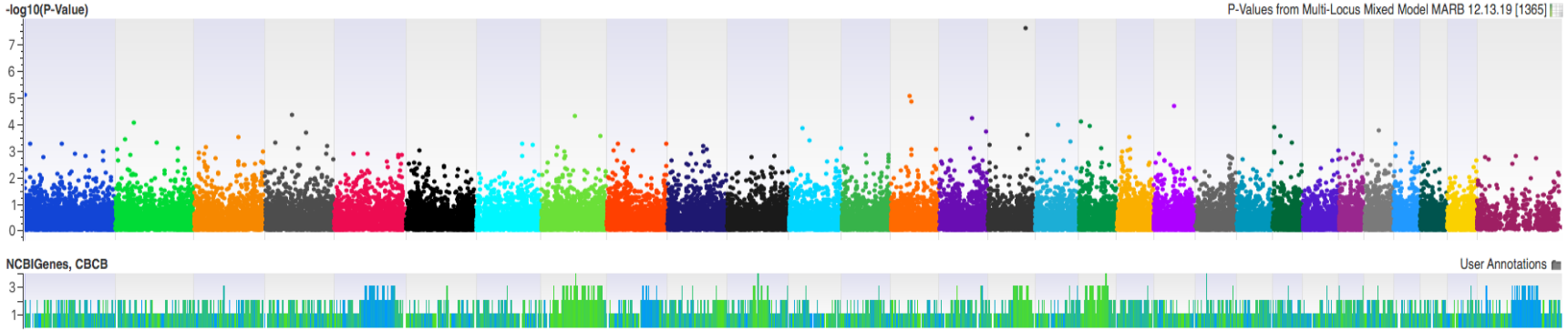


Figure D3. Manhattan plot for multi-locus model marbling (MARB). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

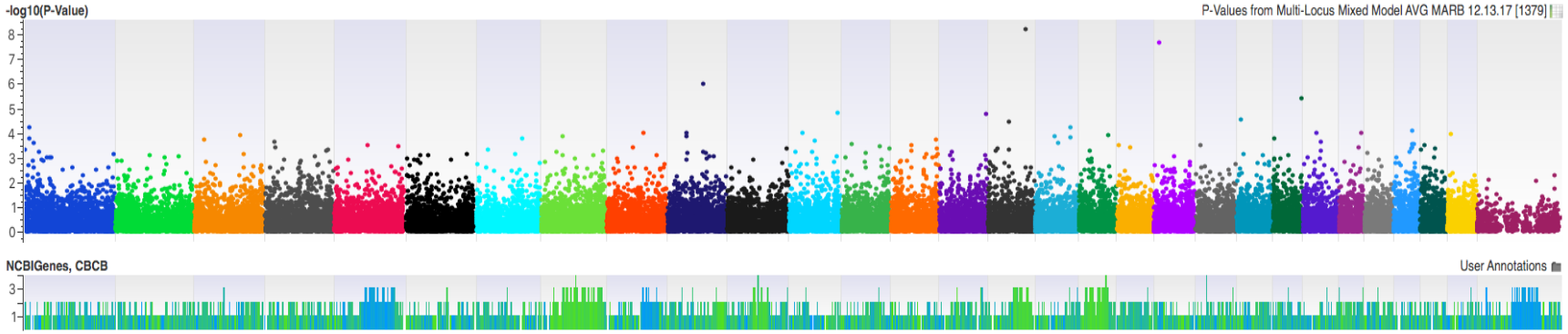


Figure D4. Manhattan plot for multi-locus model average marbling (MARB). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

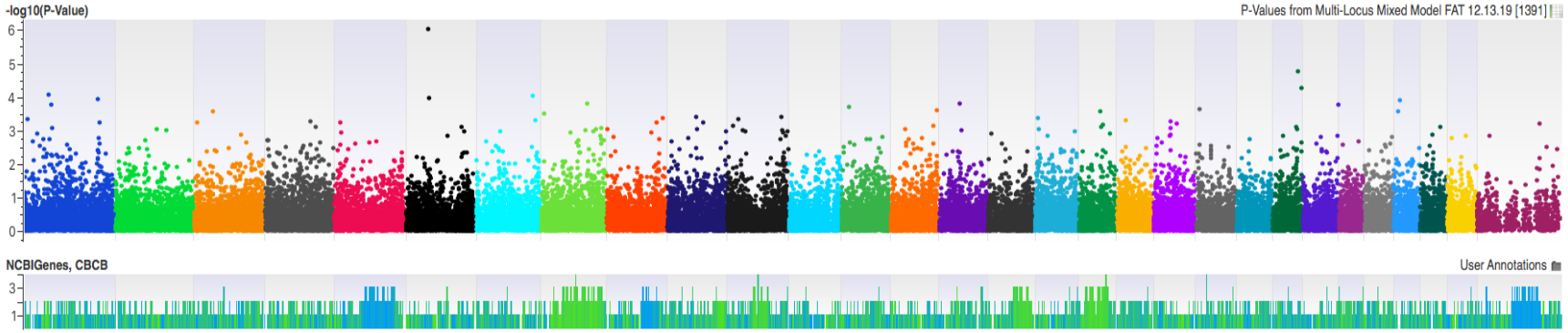


Figure D5. Manhattan plot for multi-locus model 12th rib fat (BF). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

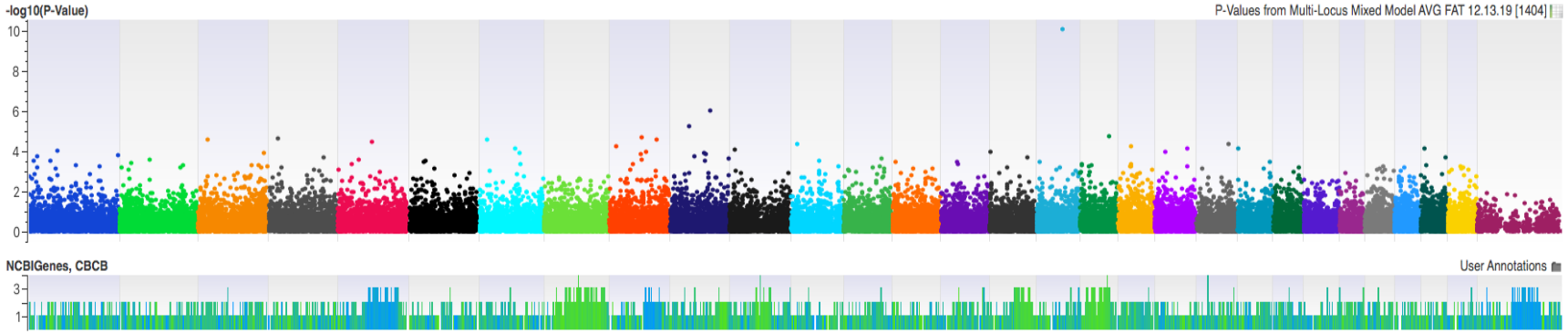


Figure D6. Manhattan plot for multi-locus model average 12th rib fat (BF). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

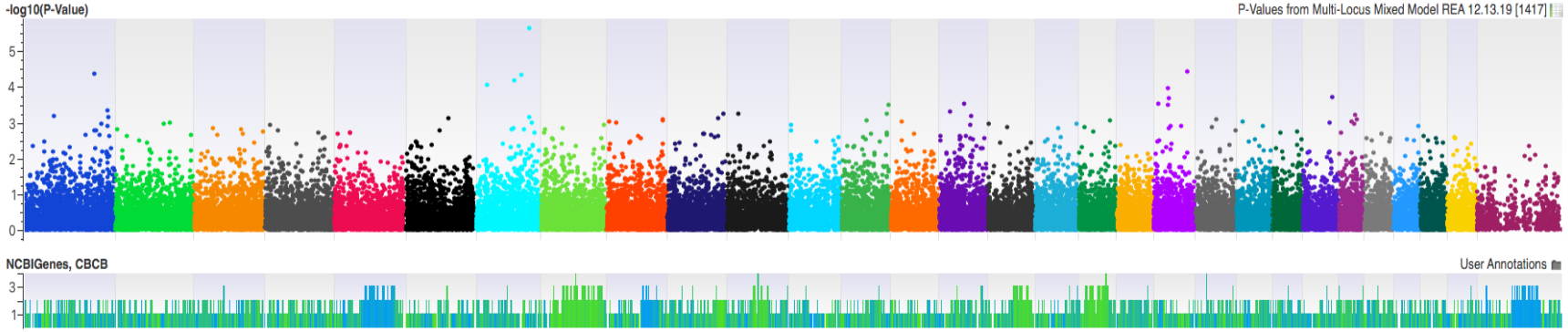


Figure D7. Manhattan plot for multi-locus model rib eye area (REA). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

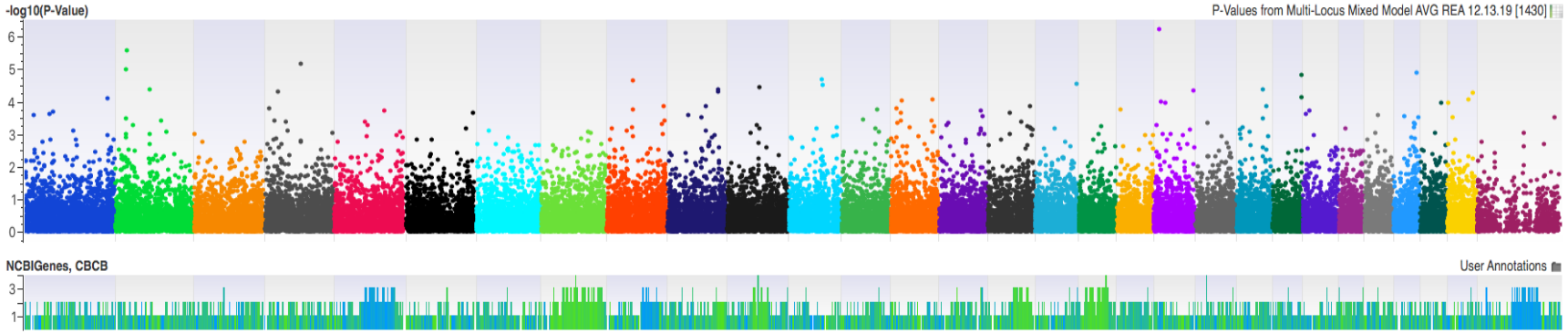


Figure D8. Manhattan plot for multi-locus model average rib eye area (REA). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

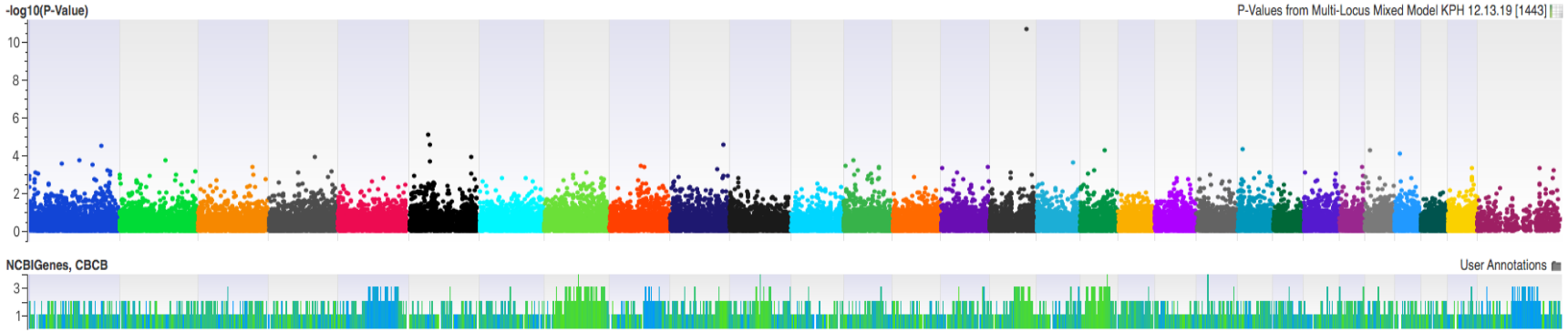


Figure D9. Manhattan plot for multi-locus model internal fat (KPH). Markers above -log10(*p*-value) of 5 x 10^{-8} are genome-wide association significant markers. Vertical clusters of markers are also of interest as they are indicating suggestive QTL in those regions.

Table D1. Significant multi-locus model hot carcass weight (HCW) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	34,450,639-34,492,226				
	156,254,566-156,294,225	Bos taurus TBC1D5			
2	21,389,327-21,448,855		QTL 20354	Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
	37,729,012-37,813,654				
	133,258,339-133,349,015	Bos taurus PLA2G2A, Bos taurus LOC100125947			
6	42,057,261-42,120,804				
	89,104,201-89,133,819				
7	6,134,663-6,206,051	Beginning of Bos taurus NWD1			
	20,423,138-20,500,709	Bos taurus UHRF1, Bos taurus ARRDC5			
	26,309,154-26,360,833	End of Bos taurus SLC27A6			
	83,621,039-83,648,346	Bos taurus ACOT12			
9	56,406,855-56,490,122				
10	12,659,662-12,707,435	Bos taurus MIR2290, Beginning of Bos taurus RAB11A			

Table D1. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
10	60,168,183-60,267,486	Bos taurus GABPB1, Beginning of Bos taurus SLC27A2	QTL 10876	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	91,330,836-91,357,108				
11	252,264-317,337				
14	18,296,407-18,331,919	Beginning of Bos taurus DERL1	QTL 1733	Waygu	10.2527/2004.8212415x
15	36,755,580-36,817,688	Bos taurus SOX6			
	61,893,000-61,927,861				
16	2,813,940-2,841,879	End of Bos taurus DSTYK, Beginning of Bos taurus TMCC2	QTL 11009	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
17	41,013,290-41,089,654	End of Bos taurus C17H4orf45			
	41,089,654-41,178,453				
19	57,098,859-57,128,225	End of Bos taurus OTOP3, Bos taurus OTOP2, Bos taurus USH1G			
	57,128,225-57,149,037	Beginning of Bos taurus FADS6			
20	25,255,282-25,296,510		QTL 11107	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	44,892,168-44,916,116				

Table D1. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
20	58,292,591-58,329,179				
	64,169,690-64,185,456				
22	56,603,472-56,675,252				
25	40,022,986-40,060,928				
27	40,951,386-41,049,981	Beginning of Bos taurus MCM4			
	41,191,284-41,226,347				
28	38,961,890-39,061,596				

Table D2. Significant multi-locus model average hot carcass weight (HCW) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	8,347,160-8,377,141				
	14,853,644-14,909,272				
	50,252,331-50,320,575				
	118,694,108-118,777,869				
	138,528,244-138,612,242				
	156,254,566-156,294,225	Bos taurus TBC1D5			
2	59,644,564-59,690,093		QTL 10665	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
			QTL 13187 **PRKAG3**	Aberdeen Angus sired steers	10.1016.j.meatsci.2010.08.005
3	65,445,867-65,467,544		QTL 10699	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	88,923,355-88,950,716				
	116,968,644-117,023,378				
4	93,398,396-93,462,288	End of Bos taurus IMPDH1, Beginning of Bos taurus HILPDA			
5	5,923,591-6,001,881				

Table D2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
5	117,795,427-117,823,521				
6	14,094,866-14,120,051		QTL 10425, 10426, 10428, 10429	Japanese Black	10.1186.1471-2156-10-43
	20,350,438-20,430,846		QTL 1369	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
			QTL 10425, 10426, 10428, 10429	Japanese Black	10.1186.1471-2156-10-43
	20,430,846-20,475,948		QTL 1369	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
			QTL 10425, 10426, 10428, 10429	Japanese Black	10.1186.1471-2156-10-43
			QTL 24619	Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, Shorthorn, Maine, Simmental	10.1186/1471-2164-15-442
7	6,097,996-6,166,179	End of Bos taurus F2RL3, Beginning of Bos taurus NWD1			
	16,588,162-16,611621	End of Bos taurus YIPF2, Bos taurus TIMM29	QTL 10784	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

Table D2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
7	62,508,803-62,599,314	Bos taurus ABLIM3	QTL 10809	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	65,497,498-65,520,210				
	106,398,519-106,422,549				
8	64,438,267-64,476,783	Bos taurus COL15A1			
	88,181,529-88,237,379				
9	26,228,944-26,262,054				
	28,337,856-28,400,169				
	31,043,707-31,116,835		QTL 37238, 37240, 37250, 37255, 37259, 37264, 37267, 37275	Holstein	10.1186/1471-2164-15-837
	100,827,855-100,892,769				
	102,007,389-102,027,971				
10	66,659,307-66,687,859		QTL 10881	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	68,089,016-68,162,634	End of Bos taurus ATG14	QTL 151847	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	73,855,126-73,884,120	Bos taurus PRKCH			

Table D2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
10	77,206,128-77,234,231				
	88,562,925-88,630,762				
11	54,855,548-54,887,301	Bos taurus CTNNA2			
12	30,967,371-30,992,759		QTL 37280, 37281 – 37284	Holstein	10.1186/1471-2164-15-837
	51,403,603-51,461,607				
	57,769,768-57,840,455				
	90,483,656-90,536,166	Bos taurus F7, Bos taurus F10			
13	8,347,568-8,386,291	Bos taurus MAROD2	QTL 10938	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	10,368,225-10,400,443		QTL 10938	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	23,478,182-23,529,663				
	53,167,293-53,266,833	Beginning of Bos taurus TGM3			
	75,192,838-75,240,419				
14	18,811,289-18,832,428		QTL 1733	Waygu	10.2527/2004.8212415x
	58,589,050-58,687,826	Bos taurus RSPO2			

Table D2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
15	71,342,153-71,375,213				
	73,739,991-73,762,207				
	81,540,854-81,595,546				
16	69,167,269-69,202,739				
17	4,306,870-4,347,226	Beginning of Bos taurus TRIM2	QTL 11040	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	41,013,290-41,089,654	End of Bos taurus C17H4orf45			
	41,089,654-41,178,453				
	41,178,453-41,272,672	Bos taurus PPID, Beginning of Bos taurus ETFDH			
	73,206,420-73,257,794	End of Bos taurus CHCHD10, Bos taurus SMARCB1, Bos taurus DERL3, Beginning of Bos taurus SLC2A11			
18	9,891,406-9,948,949	Bos taurus CDH13	QTL 1336	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x

Table D2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
18	22,574,534-22,610,574				
	40,502,223-40,587,048	Bos taurus CCNE1			
	40,690,801-40,738,568	Bos taurus URI1			
19	8,622,586-8,648,705	Bos taurus MSI2			
	58,551,913-58,591,027				
	60,165,029-60,247,211				
20	23,052,519-23,085,736	Bos taurus ANKRD55	QTL 11107	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	58,240,835-58,264,762				
	58,264,762-58,362,004				
21	42,051,380-42,089,249	End of Bos taurus STRN3, Beginning of Bos taurus AP4S1			
23	7,240,128-7,297,256	End of Bos taurus BOLA-DOA, End of Bos taurus BRD2, Beginning of Bos taurus COL11A2	QTL 11168	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	28,792,687-28,819,118	End of Bos taurus GABBR1			

Table D2. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
23	35,606,289-35,642,738				
	36,112,949-36,139,914				
24	46,606,824-46,688,139				
25	21,808,238-21,843,463	Bos taurus PRKCB	QTL 11210	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
26	6,620,890-6,692,455				
27	31,216,225-31,261,689				
	36,959,262-37,004,165	Bos taurus SLC20A2			
	39,916,848-39,994,067	End of Bos taurus NGLY1			
29	24,228,574-24,259,532		QTL 1316 **PRNP**	Brahman x Angus cross	10.2527/2003.8181933x
			QTL 1344	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
			QTL 11292	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

Table D3. Significant multi-locus model marbling (MARB) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
3	8,196,046-8,250,205	End of Bos taurus SDHC, Bos taurus MPZ, Beginning of Bos taurus PCP4L	QTL 10060-10066 **RORC**	Angus, Shorthorn, other taurine	10.1534/genetics.106.064535
			QTL 11592 **RORC**	Angus, Hereford, Brahman	10.2527/jas.2009-2178
	17,195,924-17,280,333	Bos taurus LOR			
	77,666,001-77,734,314		QTL 10700	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	105,173,273-105,209,697				
	119,550,145-119,584,154				
	121,251,149-121,310,309	Bos taurus PDCD1			
	121,310,309-121,374,825				
4	100,436,744-100,497,231				
5	118,475,383-118,501,191				
6	14,094,866-14,120,051				
	23,700,430-23,738,304	Bos taurus NFKB1			
	35,577,199-35,611,267	Bos taurus CCSER1	QTL 10770	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

Table D3. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
6	66,509,207-66,572,393	Beginning of Bos taurus GABRA2			
8	41,096,123-41,147,533				
	76,530,816-76,582,220	End of Bos taurus AQP3, Bos taurus NOL6, Beginning of Bos taurus UBE2R2			
9	10,765,698-10,838,261	Bos taurus MIR30A	QTL 4507	Japanese Black	10.1080/10495390601090992
			QTL 10850	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	34,943,071-35,002,290	Bos taurus NT5DC1, Bos taurus COL10A1	QTL 4906	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	35,368,035-35,396,173		QTL 4906	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	105,074,182-105,168,826	End of Bos taurus C9H6orf120, Bos taurus PHF10, Bos taurus TCTE3, Bos taurus ERMARD			

Table D3. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
10	73,855,126-73,884,120	Bos taurus PRKCH			
11	78,755,260-78,831,137		QTL 10909	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
13	43,009,513-43,054,682	End of Bos taurus APMAP, Bos taurus ENTPD6, Beginning of Bos taurus ACSS1	QTL 10947	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	70,171,253-70,195,187				
	82,443,688-82,455,320				
14	49,385,228-49,450,613				
15	55,185,032-55,254,553	End of Bos taurus SLCO2B1			
	65,967,835-65,990,096				
	76,930,018-76,960,713	Bos taurus PHF21A			
16	2,246,201-2,329,194				
17	9,558,819-9,624,970		QTL 1371	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	13,386,146-13,455,790	End of Bos taurus ANAPC10	QTL 1371	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	49,702,881-49,743,917				

Table D3. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
19	10,305,065-10,367,765	End of Bos taurus TRIM37, Bos taurus SKA2, Bos taurus MIR454, Bos taurus MIR301A, Beginning of Bos taurus PRR11	QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	10,617,246-10,694,269		QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	19,637,405-19,718,709		QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	19,718,709-19,789,422	Bos taurus LGALS9, Beginning of Bos taurus NOS2	QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	23,732,618-23,798,617	Bos taurus SMG6			
20	6,605,865-6,638,385	Bos taurus FAM169A			
	18,631,431-18,719,808	End of Bos taurus DEPDC1B			
	18,719,808-18,743,927				
21	59,853,238-59,875,525				
	63,930,679-63,955,841				
23	51,097,849-51,118,713	Beginning of Bos taurus GMDS			
24	62,130,639-62,169,295	Bos taurus KDSR			

Table D3. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
26	20,813,204-20,903,573	Bos taurus CPN1, Beginning of Bos taurus LOC511498			
	26,234,033-26,296,160	Bos taurus SORCS3	QTL 11238	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
27	32,129,484-32,157,142		QTL 1372	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	36,959,262-37,004,165	Bos taurus SLC20A2			
	41,552,379-41,613,442				
29	51,438,462-51,502,868				

Table D4. Significant multi-locus model average marbling (MARB) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	16,196,001-16,245,203		QTL 10636	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
2	21,290,918-21,389,327		QTL 20298, 20299, 20317, 20398, 20399, 20400	Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
	21,389,327-21,448,855		QTL 20298, 20299, 20317, 20398, 20399, 20400	Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
	85,427,167-85,452,055				
3	17,195,924-17,280,333	Bos taurus LOR			
	116,781,408-116,801,749				
	116,943,803-116,968,664				
	116,968,664-116,990,141				
	116,990,141-117,023,378				
4	96,282,870-96,308,638		QTL 24661	Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, Shorthorn, Maine, Simmental	10.1186/1471-2164-15-442
5	118,430,785-118,475,383				
6	2,217,430-2,296,875		QTL 10756	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

Table D4. Continued

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
6	20,350,438-20,430,846				
	20,430,846-20,475,948		QTL 10498	Hanwoo	10.1007/bf02717893
7	5,352,670-5,400,415	End of Bos taurus MPA1S			
8	58,505,244-58,594,366				
	58,986,469-59,085,873				
	106,245,419-106,291,686				
	108,652,993-108,732,464				
	108,732,464-108,772,548				
	108,772,548-108,819,340				
9	36,556,225-36,645,234	Bos taurus HS3ST5	QTL 4906	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
10	34,316,340-34,407,598		QTL 10874	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	34,407,598-34,438,367		QTL 10874	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
11	6,724,678-6,758,495	Bos taurus IL1R2			

Table D4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
11	106,708,013-106,741,315	End of Bos taurus OLFM1			
12	85,428,753-85,453,952				
13	17,146,206-17,232,510	End of Bos taurus PRKCQ	QTL 10941	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	43,319,313-43,367,995	End of Bos taurus GDI2	QTL 10947	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	67,810,247-67,888,763	Bos taurus BPI, Beginning of Bos taurus LBP			
14	18,263,091-18,331,919	End of Bos taurus TBC1D31, Beginning of Bos taurus DERL1	QTL 1334	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	18,331,919-18,408,275	End of Bos taurus DERL1, Bos taurus ZHX2	QTL 1334	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	19,441,969-19,531,288		QTL 1334	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	58,342,794-58,408,381	Beginning of Bos taurus EIF3E			

Table D4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
14	58,589,050-58,687,826	Bos taurus RSPO2			
	81,197,368-81,269,892				
	81,269,892-81,309,300				
	84,505,345-84,594,318				
15	35,333,265-35,364,770	End of Bos taurus MYOD1	QTL 10999	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	54,939,673-54,995,188	End of Bos taurus XRRA1			
	82,558,282-82,655,879				
	82,655,879-82,689,485				
16	13,656,858-13,733,378		QTL 1353	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	36,744,747-36,768,083				
	36,768,083-36,817,218				
17	41,178,453-41,272,672	Bos taurus PPID, Beginning of Bos taurus ETFDH			
18	22,574,534-22,610,574				
19	8,622,586-8,648,705	Bos taurus MSI2	QTL 11077	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

Table D4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
20	15,454,163-15,528,205				
21	9,741,507-9,784,549				
22	56,603,472-56,675,252				
23	3,626,219-3,664,434				
24	24,904,038-24,961,929				
26	26,234,033-26,267,018	Bos taurus SORCS3	QTL 11238	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
27	1,271,954-1,312,576				
	8,589,473-8,689,042		QTL 1342	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	20,791,916-20,863,121		QTL 1342	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	30,479,059-30,510,177	Bos taurus UNC5D	QTL 11258	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
			QTL 1372	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x

Table D4. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
27	31,216,225-31,261,689		QTL 1372	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	32,129,484-32,157,142		QTL 1372	Belgian Blue x MARC III, Piedmontese x Angus	10.2527/2000.783560x
	36,935,085-36,959,262	Beginning of Bos taurus SLC20A2			
	41,613,442-41,649,895				
28	8,080,087-8,105,051	Bos taurus ARID4B	QTL 11270	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	16,097,749-16,097,772		QTL 11270	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

Table D5. Significant multi-locus model 12th rib fat (BF) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	34,450,639-34,492,226		QTL 4854	Waygu x Limousin	10.1111/j.1365.2052.2007.01643.x
	47,123,160-47,177,862	Bos taurus MIR2285DK			
	76,505,437-76,534,601				
	81,160,609-81,239,683	End of Bos taurus FETUB, Bos taurus AHSG, Beginning of Bos taurus DNAJB11	QTL 10649	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	127,998,001-128,031,876	End of Bos taurus TFDP2			
	128,864,268-128,938,068	End of Bos taurus SPSB4			
	131,642,361-131,684,053				
3	81,428,130-81,472,159		QTL 10701	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
4	5,639,667-5,712,778				
	62,549,908-62,606,492	Bos taurus NPSR1			
	74,076,693-74,148,361				
	80,350,223-80,407,501				
5	12,174,285-12,213,478				

Table D5. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
5	118,307,910-118,392,147	End of Bos taurus TBC1D22A, Bos taurus MIR2285O-5, Bos taurus MIR284H			
7	38,997,984-39,060,855	Bos taurus COMMD10			
8	91,086,691-91,125,290	Beginning of Bos taurus NXNL2			
	104,829,510-104,862,806				
9	92,242,453-92,250,839				
	98,306,160-98,349,764	Bos taurus AGPAT4			
10	102,849,006-102,935,702	Bos taurus PSMC1, Beginning of Bos taurus NRDE2			
11	91,995,272-92,059,274				
	95,501,827-95,516,698	Beginning of Bos taurus NR5A1			
	98,407,974-98,482,863	Bos taurus TTC16, Bos taurus TOR2A, Bos taurus SH2D3C, Bos taurus CDK9			
12	60,040,871-60,134,810				
13	48,594,834-48,622,655	Beginning of Bos taurus FERMT1			

Table D5. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
13	65,761,897-65,855,988				
14	27,271,835-27,321,716		QTL 10965	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	27,669,598-27,751,888	End of Bos taurus CA8	QTL 10965	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	48,184,967-48,256,343	End of Bos taurus SAMD12			
	70,250,637-70,314,452	End of Bos taurus PTDSS1, Beginning of Bos taurus MTERF3			
	75,517,287-75,571,250	End of Bos taurus SLC267			
15	34,294,990-34,342,385	End of Bos taurus CLMP			
16	66,609,042-66,676,299	End of Bos taurus TSEN15			
17	5,590,969-5,663,467				
	7,756,498-7,794,593				
19	16,578,349-16,598,801				
20	28,850,177-28,887,439		QTL 15736	Angus x Brahman	10.3389/fgene.2011.00044
			QTL 20540, 20542	Brangus	10.4238/2011.December.19.3

Table D5. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
21	27,927,781-27,956,825	End of Bos taurus FAN1, Beginning of Bos taurus MTMR10	QTL 11125	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	27,956,825-28,055,227	End of Bos taurus MTMR10, Bos taurus MIR211	QTL 11125	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
22	60,105,535-60,130,492	Bos taurus EEFSEC			
23	41,901,234-41,965,164				
	52,038,120-52,068,611	Bos taurus IRF4			
	52,068,611-52,128,894				
24	61,885,106-61,931,908	Beginning of Bos taurus BCL2			
27	32,541,258-32,561,963				
28	6,499,231-6,547,497	Bos taurus KCNK1			
	21,014,194-21,066,992		QTL 20273	Crosses of Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x

Table D6. Significant multi-locus model average 12th rib fat (BF) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	1,288,510-1,359,951	End of Bos taurus GART, Beginning of Bos taurus TMEM50B	QTL 1317 **IFNAR1**	Brahman x Angus cross	10.2527/2003.8181933x
	14,853,644-14,909,272				
	50,252,331-50,320,575				
	100,513,127-100,605,192	End of Bos taurus SERPINI1, Bos taurus PDCD10	QTL 10653	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
2	16,157,387-16,238,330		QTL 1322	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x
	111,103,057-111,181,420	Beginning of Bos taurus PAX3, Bos taurus MIR2284Y-5			
3	10,956,984-11,040,167				
	17,241,980-17,280,333	Bos taurus LOR	QTL 1325	Sires: Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, Saler Dam: Hereford, Angus	10.2527/2003/81122976x

Table D6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
3	82,037,605-82,113,195		QLT 10701	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	89,579,376-89,675,602				
	112,922,761-112,955,526				
	115,730,569-115,790,125				
	116,968,644-117,023,378				
4	21,937,293-21,973,829		QTL 20280, 20285, 20368, 20446	Crosses of Angus, Charolais, University of Alberta hybrid bulls	10.1111/j.1439-0388.2011.00954.x
	96,258,114-96,282,870				
5	6,976,839-7,053,234		QTL 20001 **MYF5**	Jiaxian Red, Qinchuan, Luxi, Nanyang, Xianan	10.4238/2011.December.12.6
	97,884,594-97,972,722	End of Bos taurus BORCS5, Bos taurus MANSC1			
6	20,276,795-20,297,397		QTL 24647	Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, Shorthorn, Maine, Simmental	10.1186/1471-2164-15-442
	44,305,092-44,337,791				
	107,016,833-107,095,193	Bos taurus NSG1			

Table D6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
7	12,833,745-12,889,689	End of Bos taurus DCAF15, Beginning of Bos taurus CC2D1A			
	66,156,674-66,212,415				
	66,212,415-66,254,499				
8	37,081,128-37,158,190				
	81,573,118-81,612,097				
	112,323,763-112,345,659	End of Bos taurus C5			
9	31,043,707-31,067,189				
	74,223,999-74,293,236	End of Bos taurus MYB			
	81,166,662-81,216,232	Bos taurus MIR2284AA-4			
10	66,659,307-66,687,859				
	101,953,883-101,984,056	Bos taurus FOXN3			
	102,887,596-102,935,702	Bos taurus PSMC1, End of Bos taurus NRDE2			
11	103,799,585-103,830,982				
12	48,909,344-48,984,802	Bos taurus KLF12			

Table D6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
12	48,984,802-49,006,756	Bos taurus KLF12			
	49,006,756-49,057,460	Bos taurus KLF12			
	49,057,460-49,095,991	Bos taurus KLF12			
	82,765,192-82,812,721				
14	33,580,690-33,604,665		QTL 10971	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
	58,589,050-58,687,826	Bos taurus RSPO2			
15	41,707,747-41,757,348	Bos taurus GALNT18			
	80,003,887-80,097,824				
16	1,199,397-1,296,954	Beginning of Bos taurus ARP2B4			
	31,382,509-31,462,716	Bos taurus H3F3C, Beginning of Bos taurus CNST			
17	4,868,261-4,926,550	End of Bos taurus ARFIP1			
	34,409,623-34,429,947				
	41,178,453-41,272,672	Bos taurus PPID, Beginning of Bos taurus ETFDH	QTL 11052	Commercial Angus	10.1111/j.1365-2052.2010.02063.x

Table D6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
17	49,702,881-49,791,728				
	70,699,234-70,776,835	End of Bos taurus EWSR1, Bos taurus GAS2L1, Bos taurus RASL10A, Beginning of Bos taurus AP1B1			
	72,710,280-72,790,867	Beginning of Bos taurus SLC5A1, Bos taurus SLC5A4			
18	3,146,088-3,177,824		QTL 11058	Commercial Angus	10.1111/j.1365-2052.2010.02063.x
19	5,057,128-5,083,994				
	22,749,859-22,771,407	Bos taurus VPS53			
	22,771,407-22,864,442	End of Bos taurus VPS53, Bos taurus MIR2336			
	33,862,979-33,895,220	Beginning of Bos taurus PIGL			
	58,551,913-58,591,027				
20	18,631,431-18,719,808	End of Bos taurus DEPDC1B			
	18,719,808-18,743,927				
	22,093,001-22,165,165	End of Bos taurus GPBP1	QTL 20540, 20542	Brangus	10.4238/2011.December.19.3

Table D6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
20	57,373,160-57,403,850				
21	58,994,572-58,996,585	Bos taurus PRIMA1			
22	499,356-574,301	Bos taurus VOPP1			
	56,765,689-56,833,606	Beginning of Bos taurus H1FOO			
	56,833,606-56,916,823	End of Bos taurus H1FOO, Bos taurus RHO, Beginning of Bos taurus IFT122			
	58,397,411-58,429,229				
23	45,048,666-45,106,522	Beginning of Bos taurus ELOVL2			
24	1,529,327-1,582,182				
	62,104,076-62,130,639	End of Bos taurus BCL2, Beginning of Bos taurus KDSR			
	62,104,076-62,130,639	End of Bos taurus BCL2, Beginning of Bos taurus KDSR			
25	17,860,710-17,891,876				
26	22,557,427-22,628,269	Beginning of Bos taurus HPS6			

Table D6. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
27	8,589,473-8,649,727				
	8,649,727-8,689,042				
	11,657,439-11,715,052				
28	6,499,231-6,547,497	Bos taurus KCNK1			
	7,001,292-7,068,698	Bos taurus SCL35F3			
	7,068,698-7,138,132	Bos taurus SCL35F3			

Table D7. Significant multi-locus model rib eye area (REA) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	122,789,893-122,814,776				
	143,741,734-143,831,554	End of Bos taurus ZBTB21			
	145,643,805-145,682,206				
	145,682,206-145,710,047				
3	82,187,624-82,250,730	Beginning of Bos taurus PGM1			
7	16,588,162-16,611,621	End of Bos taurus YIPF2, Bos taurus TIMM29			
	60,436,313-60,475,602	Beginning of Bos taurus STK32A			
	78,762,342-78,822,792				
	84,925,417-84,991,860				
8	19,811,075-19,863,242				
	37,136,374-37,158,190				
9	99,334,002-99,354,827	Bos taurus PRKN			
10	32,409,981-32,433,588	Bos taurus C10H15orf41			
	88,563,925-88,605,589				

Table D7. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
11	20,202,555-20,271,885				
	22,688,045-22,716,948	Bos taurus SLC8A1			
	75,586,338-75,662,200	End of Bos taurus KLHL29			
12	4,324,502-4,397,035				
	86,938,949-86,961,976	Bos taurus FAM155A			
13	79,914,560-79,991,041				
14	20,323,857-20,347,849				
	27,575,294-27,669,598	Beginning of Bos taurus CA8			
15	34,763,290-34,852,656	Bos taurus SCN3B			
	37,237,274-37,309,941				
	55,206,099-55,254,553				
	56,571,496-56,663,853	End of Bos taurus THAP12, Beginning of Bos taurus EMSY			
16	38,807,074-38,830,470				
17	13,941,499-13,984,972				
	41,089,654-41,178,453				

Table D7. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
20	25,255,282-25,296,510				
	43,579,015-43,649,910				
23	46,334,617-46,401,353				
	52,038,120-52,128,894	Bos taurus IRF4			
25	28,974,015-29,065,778	Bos taurus CALN1			
26	37,733,926-37,797,893	Beginning of Bos taurus VAX1			

Table D8. Significant multi-locus model average rib eye area (REA) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	48,726,549-48,802,718				
	114,085,424-114,180,799				
	151,835,916-151,858,713				
2	9,810,493-9,867,063	Beginning of Bos taurus ZC3H15			
	15,250,050-15,303,929				
	18,164,650-18,233,729				
	29,369,336-29,405,628				
	59,644,564-59,690,093				
3	62,458,422-62,509,283				
4	15,468,000-15,537,254				
	28,350,426-28,413,603				
5	109,134,816-109,167,093				
	117,738,204-117,795,427	End of Bos taurus GTSE1, Bos taurus TRMU			
	119,949,553-120,016,258	Bos taurus SHANK3, Bos taurus ADM2, Bos taurus MIOX			
7	2,323,494-2,346,546				
	3,488,080-3,570,752				
	56,055,399-56,152,302	Bos taurus ARHGAP26			
	78,762,342-78,822,792				
	78,822,792-78,877,775				
	80,229,987-80,307,024				
8	81,612,097-81,638,162				
9	14,794,389-14,817,532				
	98,566,722-98,648,213	Bos taurus PRKN			
10	61,648,704-61,769,231				
	68,089,016-68,162,634	End of Bos taurus ATG14			
	68,162,634-68,231,955				
	72,023,342-72,060,561	End of Bos taurus JKAMP, Beginning of Bos taurus CCDC175			

Table D8. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
10	88,563,925-88,630,762				
	90,543,010-90,589,157				
11	41,114,000-41,204,355				
	54,855,548-54,887,301	Bos taurus CTNNA2			
	55,229,674-55,264,686	Bos taurus CTNNA2			
	71,811,673-71,875,673	End of Bos taurus BABAM2, Beginning of Bos taurus RBKS			
12	77,964,481-78,014,490				
13	2,342,625-2,372,577	Bos taurus PLCB4			
	4,634,576-4,733,016				
	37,675,851-37,725,131				
	37,725,131-37,757,395				
	57,524,735-57,570,093				
	59,963,672-60,002,265	Bos taurus FAM209A, Beginning of Bos taurus RTF2			
14	2,194,228-2,239,085	Beginning of Bos taurus MAPK15			
	18,811,289-18,832,428				
	19,132,330-19,172,385				
15	73,739,991-73,762,207				
16	933,282-950,232	End of Bos taurus FMOD			
	61,668,331-61,716,582	Bos taurus RALGPS2, End of Bos taurus ANGPTL1			
17	49,702,881-49,791,728				
	63,885,514-63,939,534				
20	53,635,068-53,674,655	Bos taurus CDH18			
	69,430,215-69,459,313				
22	6,450,949-6,485,383				
	51,214,861-51,245,935				
	51,452,218-51,484,825	Bos taurus LAMB2, Beginning of Bos taurus QARS1			
23	32,682,177-32,757,561	Bos taurus RIPOR2			

Table D8. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
23	51,621,297-51,719,827				
	52,068,611-52,091,670				
24	60,745,394-60,842,899				
25	40,282,215-40,341,603				
26	9,669,992-9,725,747				
27	37,283,994-37,357,125	Bos taurus HOOK3			
	37,357,125-37,389,551	End of Bos taurus HOOK3			
	37,389,551-37,430,965	Bos taurus FNTA, Beginning of Bos taurus POMK			
	39,916,848-39,994,067	End of Bos taurus NGLY1			
29	21,987,120-22,019,432				

Table D9. Significant multi-locus model internal fat (KPH) markers that are within 100,000 base pairs and previously reported QTL and genes for those locations.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
1	883,895-950,841	Bos taurus ATP5PO, Bos taurus MIR12045			
	10,404,023-10,468,415				
	16,145,053-16,169,001				
	118,694,108-118,714,300				
	142,401,535-142,446,153				
2	30,262,141-30,307,800				
4	53,316,893-53,400,639				
	117,292,302-117,339,600	Bos taurus DPP6			
6	3,093,621-3,149,732				
	27,158,687-27,183,822		QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
	30,782,962-30,832,561	Beginning of Bos taurus BMPR1B	QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
	41,343,408-41,443,081	Bos taurus SLIT2	QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
	42,155,077-42,239,393		QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
	44,622,597-44,649,549		QTL 12153	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x

Table D9. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
6	66,509,207-66,572,393	Beginning of Bos taurus GABRA2			
8	40,775,647-40,800,617				
	51,330,787-51,369,892				
	73,881,694-73,907,982				
	101,044,054-101,135,756	Bos taurus PALM2			
	101,135,756-101,167,884	Bos taurus PALM2			
9	55,740,550-55,802,932				
10	92,952,608-92,984,267				
11	15,919,622-15,945,389	Bos taurus LTBP1			
12	45,919,459-45,952,853				
13	49,963,611-50,004,272				
	62,881,877-62,909,025	End of Bos taurus BPIPB6, Beginning of Bos taurus BPIFB3			
14	59,112,331-59,139,878	Beginning of Bos taurus ANGPT1			

Table D9. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
16	37,479,436-37,505,165		QTL 1354	(Brahman x Angus) x Hereford, Angus, MARC III	10.1046/j.1365-2052.2003.01067.x
17	1,180,289-1,261,843				
	64,189,856-64,225,341				
	68,952,931-69,030,893				
20	26,330,033-26,397,183		QTL 12157	Jersey x Limousin	10.1111/j.1365-2052.2010.02058.x
21	7,283,843-7,311,519	Bos taurus LYSMD4			
	57,819,236-57,848,290				
22	37,615,930-37,652,444				
24	56,487,933-56,564,480	Bos taurus WDR7			
25	40,022,986-40,060,928				
26	6,051,502-6,092,833				
27	30,025,162-30,089,811				

Table D9. Continued.

Chromosome	Base Pair Position	Positional Candidate Gene	Previously Identified QTL/Genes	Breed	DOI
29	41,778,946-41,854,768	End of Bos taurus POLR2G, Bos taurus TAF6L, Bos taurus TMEM179B, Bos taurus TMEM223, Bos taurus NXF1, Bos taurus STX5, Bos taurus WDR74			
	42,620,218-42,696,595	End of Bos taurus ATL3, Beginning of Bos taurus RTN3			
	42,985,739-43,043,207	Bos taurus MACROD1, Beginning of Bos taurus NAA40			