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REVIEW

Genetic basis of improving the palatability of beef cattle: current insights

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ABSTRACT

Beef palatability is a complex concept and could be described through an array of features such as tenderness, juiciness and flavor traits. Improving the eating experience when consuming beef and the ability to accurately inform the consumers of the expected eating quality when the product is purchased are critical challenges. In this review, we discuss the current knowledge of quantitative and molecular genetic aspects of palatability and discuss implications of genetic manipulation for the cattle industry.

KEYWORDS

Beef; genomics; meat quality; genetic improvement

1. Introduction

Beef palatability is a complex concept and includes an array of intrinsic features such as tenderness, juiciness, and flavor (Calkins and Hodgen 2007; Hocquette et al. 2014; Mateescu 2015) which are perceived by a consumer and have a direct impact on consumer satisfaction. The need to assess the palatability of beef was recognized very early by the beef industry. The USDA Beef Quality grading system specifications were published in June 1923 (USDA 2016), and they were designed to separate beef carcasses into groups with uniform quality. In the absence of any other system to predict eating quality, the beef industry is using the USDA grading system based on marbling and maturity as an indicator of palatability of the meat from a beef carcass. Improving eating experience when consuming beef and the ability to accurately inform the consumers of the expected eating quality when the product is purchased are critical challenges. Meeting these challenges would increase consumers' confidence in the quality of the product and allow the industry to more accurately align the value with the quality of the product for marketing purposes.

All the components defining beef palatability are quantitative traits, controlled by many genes and impacted by environmental factors. Most of these component traits are difficult and expensive to measure and not available to

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measure until late in life or after the animal has been harvested. Such traits are impractical to improve through traditional phenotypic selection, but are ideal candidates for genomic selection if genetic markers that account for a worthwhile proportion of variation can be identified. Warner–Bratzler Shear Force (WBSF) and marbling were identified from an extensive set of carcass and meat composition traits to be the best predictors of eating quality (Mateescu et al. 2016). DNA tests that can accurately identify cattle with superior genetics for WBSF and marbling would be helpful tools.

In this review, we discuss the current knowledge of quantitative and molecular genetic aspects of palatability and discuss implications of genetic manipulation for the cattle industry. Over the last decade, research of genetic contributions to beef palatability and meat quality, in general, has transitioned from candidate gene approaches for traits with extensive phenotypic and pedigree information to large-scale approaches of genome analysis including nucleotide sequence, gene analysis and expression, proteomics, metabolomics, and biochemical modeling. A number of genetic markers have been identified, and their effects on different palatability traits have been evaluated in different breeds. New genetic and genomic techniques are allowing detailed dissection of the genetic architecture underlying various palatability traits and may help discover functional candidate genes or gene networks involved in the regulation of these traits. Knowledge of gene pathways and networks contributing to variation in these traits is essential for our ability to select animals with desired palatability profiles without negatively affecting other traits. The ability to mine the underlying gene networks would allow pinpointing genes that do not contribute to common networks and allow divergent selection for the respective traits.

2. Phenotypic measures describing palatability of beef

Beef palatability cannot be assessed directly through a single measurement. Therefore, an array of phenotypes could be used to describe beef palatability and these include tenderness, juiciness, and flavor. Complex relationships exist between these traits and many extrinsic factors influence them, with marbling having the largest impact. Marbling explains about 5% of the variation in beef palatability across carcasses; however, higher marbling has been associated with better performance in tenderness, juiciness, and flavor, and marbling is also able to promote structural disorganization of intramuscular connective tissue (Riley et al. 2009; Corbin et al. 2015; Nishimura, Hattori, & Takahashi, 1999). The assessment of each individual component contributing to the palatability phenotype is very difficult and a complete differentiation between these component traits is probably impossible. The sensory panel has a moderate to high consistency and reproducibility and was identified as the best way to assess the complex parameters involved in the eating experience (Gill et al. 2010; Legako

et al. 2015). A brief description of the main component traits describing beef palatability and different ways of effectively measuring them is presented below.

2.1. *Tenderness*

Out of all the palatability attributes, tenderness and texture have been identified as the most important to the consumer and appear to be preferred over flavor or color and when tenderness is satisfactory, flavor and juiciness are associated with overall acceptability (Feuz et al. 2004; Hunt et al. 2014; Lawrie and Ledward 2006). The overall impression of tenderness perceived by the consumer or trained participant in a sensory panel consists of three aspects: the initial ease of penetration of the meat by the teeth, the ease with which the meat breaks into fragments during mastication, and the amount of residue remaining after chewing (Weir 1960).

Meat tenderness is determined by the amount and solubility of the connective tissue, the amount of marbling, and by the extent of the proteolysis of cytoskeletal, cytoskeletal-associated proteins, and extracellular matrix-associated proteins postmortem (Cho et al. 2016; Koohmaraie and Geesink 2006; Legako et al. 2015). The postmortem proteolysis that occurs during the tenderization process and results in the disruption of key structural sarcomere proteins is accomplished through the action of endogenous enzymes. The main proteolytic system involved in meat tenderization is the μ-calpain-calpastatin system. The activation rate of μ-calpain has been linked to the degradation of structural proteins such as desmin and talin during aging (Bee et al. 2007; Monsón, Sañudo, and Sierra 2005). Several enzymes could be implicated in the disruption of connective tissue-related proteins; however, the solubility of connective tissue is highly dependent on cooking (Bouhrara et al. 2011, 2012; Christensen, Purslow, and Larsen 2000; Palka 1999).

Meat tenderness can be assessed during a sensory panel where participants are asked to rate beef samples for tenderness on an 8-point scale, or using a WBSF test which is an objective measure of the force required shearing the cooked steak. A negative and moderate genetic correlation was identified between the panel tenderness and WBSF (Mateescu et al. 2015), suggesting that the two methods are capturing similar but not identical information relative to tenderness. When evaluating several carcass and meat quality traits to identify a subset with the highest predictive accuracy for eating quality, Mateescu et al. (2016) found WBSF and intramuscular fat content to be the best predictors of eating quality in Angus cattle.

2.2. *Juiciness*

The most reliable and consistent measure of juiciness is obtained through sensory methods. Juiciness experienced initially during chewing depends

mainly on water content or wetness, whereas juiciness experienced later during chewing is determined by a combination of water, marbling and saliva production (Aaslyng et al. 2003). Water content can be defined as the final amount of water that is retained in the meat after any technological procedure with a possible major effect on juiciness, such as aging or cooking (Farouk et al. 2012; Huff-Lonergan and Lonergan 2005). Marbling has a major effect on the perceived juiciness and this is reflected in the high correlation between tenderness and juiciness (Serra et al. 2004), where steaks with high marbling score have superior juiciness and overall liking (Killinger et al. 2004; Legako et al. 2015; Okumura et al. 2007). Marbling has a lubrication effect and stimulates salivation, which results in the perception of increased juiciness whilst chewing the meat (Thompson 2004).

2.3. *Flavor*

Flavor is another sensory panel-related trait most highly correlated with overall acceptability ratings in beef (Corbin et al. 2015; Crownover et al. 2017; Hunt et al. 2014; Killinger et al. 2004). It is a complex sensation, because flavor involves odor, taste, texture, temperature, and pH. Nevertheless, the odor is the most important feature, and in the absence of odor, the other four primary taste sensations are predominant: bitter, sweet, sour or saline (Sato and Lee 2003). Flavor is associated with the development of volatile elements, especially sulfur-compounds, during the cooking process by a complex series of reactions that occur between components of lean and fat tissues (Mottram 1998). The development of specific volatile compounds is muscle dependent, and *longissimus lumborum* muscle has been identified as having a limited flavor development capacity, regardless of quality grade (Legako et al. 2015).

3. Genetic effects on beef palatability

Breed composition has a large effect on beef palatability traits, mostly due to differences in marbling, in the amount and solubility of the connective tissue, and in proteolysis of myofibrillar proteins (Chung and Davis 2011; Marino et al. 2013). Differences in the genetic background are a result of the phenotypic selection humans have performed after the domestication of cattle and during the breed formation process. The genetic divergence achieved through this selection process could be detected through "signatures of selection", genomic regions where allelic frequencies of favorable genetic markers and their neighboring polymorphisms are increased or completely fixed (Gobena, Elzo, and Mateescu 2018; Qanbari et al. 2014; Utsunomiya et al. 2013; Zhao et al. 2015). Several pathways associated with meat quality traits and feeding efficiency were enriched when the Angus genome was compared to the Hanwoo and Jersey cattle genomes (Taye et al. 2018). In

addition, specific genes controlling different traits from meat quality, stature, and body size to feed efficiency and fertility were detected to be under a positive selection in Angus cattle (Taye et al. 2018).

The effect of selection for beef palatability traits can be realized through changes in the muscle morphology, composition, and biochemistry. McGilchrist et al. (2016) compared the *longissimus thoracis* muscle from Angus steers selected for high and low muscling. High muscling steers had 8.6% less type IIX myofibres, 4.9% lower lactate dehydrogenase activity, 10.2% and 12.3% higher citrate synthase and isocitrate dehydrogenase activity, respectively. Hocquette et al. (2012b) assessed the effect of selection on muscle growth potential in the *semitendinosus* muscle from Charolais young bulls. Bulls with a high muscle growth potential had 27% higher muscle mass and 24% less fat content, 32% less intramuscular lipids and 40% less triglyceride content. Additionally, animals with higher muscle growth had lower citrate synthase, H-FABP, and cytochrome-c oxidase activity. Based on these and previous studies, it is hypothesized that selection for high muscling in Charolais and Angus is associated with an increase in glycolytic muscles (Delp and Dyan 1996; Werner, Natter, and Wicke 2010). Differences in muscle biochemistry were detected between *Bos taurus* and *Bos indicus* cattle, with *Bos indicus* animals having a higher basal concentration of heat shock proteins HSP27, HSP70 and crystallin alpha polypeptide 2 Cryab (Mullins et al. 2016). The *HSP27* and *HSP70* genes encode molecular chaperones that are involved in stress resistance, actin organization, phosphorylation and axonal transport of neurofilament proteins. Cryab is reported to be selectively expressed in slow-twitch oxidative muscle fibers and has a chaperone-like activity related to cytoskeletal network maintenance. Glycolytic rates have been reported to be higher in tender meat, even in the live animal, possibly due to higher levels of glycolytic enzymes, which translates into a lower pH two days after slaughter (D'Alessandro and Zolla 2013).

Numerous other breed differences have been reported related to the muscle morphology, composition, and biochemistry. Some of these differences are reviewed in the Supplementary Table 1 and include changes in muscular collagen content, collagen solubility, chemical compositional, extension of proteolysis, enzymatic activity, fatness, and muscle structural characteristics (Marino et al. 2013; Monsón, Sañudo, and Sierra 2004; Muchenje et al. 2008; Sañudo et al. 1998; Strydom et al. 2000; Wheeler et al. 1990). Angus has been reported as having higher collagen content and solubility at 48 hours postmortem, higher cooking loss and lower juiciness than Limousin, and lower dressing percentage and WBSF than Angus-Brahman crossbreds (Chambaz et al. 2003; Elzo et al. 2012; Leal-Gutiérrez et al., 2018). Brahman has been identified as a breed with less fat over ribeye and smaller ribeye than Angus-Brahman crossbreds, and lower marbling than Angus (Elzo et al. 2012).

3.1. *Heritability and genetic correlations*

Knowledge of heritability estimates for palatability is important for producers to be able to assess the potential challenges and benefits of designing selection schemes for improved palatability. In Angus, medium-high heritability has been reported for fat over ribeye (0.35; 0.67), ribeye area (0.27; 0.39), tenderness (0.33), juiciness (0.22), marbling (0.4), WBSF (0.38), MUFA (0.39), PUFA (0.28) and SFA (0.56), and low heritability for cooking loss (0.05), overall liking (0.16) (Gill et al. 2010; Arthur et al., 2001; Mateescu, Garrick, and Reecy, 2017) (Supplementary Table 2). Medium to high heritability for fat-related traits confirms that these meat quality traits are the easiest to target for phenotypic improvement in Angus cattle using traditional selection.

Phenotypic correlations among traits exist for a variety of reasons and even strong correlations do not imply causation, which is why reported correlations should be treated with caution. Unlike phenotypic correlations, genetic correlations are more difficult to estimate because larger data sets with a known pedigree structure are required. In Angus cattle, strong and favorable genetic correlations between marbling and juiciness, WBSF, panel tenderness, or connective tissue were found, indicating that similar genes and gene networks control these traits (Mateescu et al. 2015). These strong correlations among sensory panel traits are not surprising given the interdependency among these traits (Corbin et al. 2015; Crownover et al. 2017; Hunt et al. 2014), where the score for one trait is likely to influence the score for the other traits (i.e., steaks with at least one negative attribute being likely to be scored lower for the other traits and vice versa). The genetic correlations between WBSF and marbling score were – 0.50 and – 0.47, respectively, which indicated that a lower WBSF (more tender steaks) is genetically correlated with higher marbling (Mateescu et al. 2015). Two other reports on genetic correlations between intramuscular fat and tenderness reported similar moderate and favorable estimates (Reverter et al. 2003; Wheeler et al. 1990). In contrast, moderate and positive genetic correlations (i.e., more fat, higher shear force) estimated by Riley et al. (2003) for Brahman cattle suggest a unique fat-tenderness relationship for this breed, which is supported by the residual correlations between WBSF and marbling estimated by Dikeman and Pollak (2005).

Reports on the relationship between important minerals, micronutrients and other bioactive compounds in meat and palatability traits are scarce. A recent report in Angus cattle identified a few genetic correlations between minerals and all were positive and favorable (Mateescu et al. 2013). A moderate positive genetic correlation was identified between iron and zinc (0.49). More importantly, high heritability for iron and moderate heritability for zinc estimated in this study suggest genetic improvement of beef

content for these two nutritionally important minerals would be feasible with practically no negative impact on beef palatability traits. Similarly, other compounds including carnitine, creatine, creatinine, carnosine, and anserine have been reported to potentially have protective effects on human health. Several genetic correlations were identified between these compounds, but no significant associations with beef palatability traits in *longissimus dorsi* of beef cattle were detected (Mateescu et al. 2013).

3.2. *Genes associated with beef palatability*

The assessment of meat quality attributes by consumer panels or even physical measures is difficult and costly, which hampers the efforts to develop and implement a traditional selection program to improve these types of traits. Identification of biological components related to sensory attributes is necessary for developing easy and inexpensive ways to measure palatability traits for management and selection programs (Dekkers 2004; Renand et al. 2001). The genes and pathways controlling palatability can be classified in two broad categories: those influencing the amount and solubility of marbling and connective tissue, and genes and pathways related to the postmortem proteolysis of cytoskeletal and cytoskeletal-associated proteins (Cho et al. 2016; Koohmaraie and Geesink 2006; Legako et al. 2015). However, it is very likely that only a few genes and pathways will be common across subspecies, breeds and even populations, given the known differences in allele frequencies and linkage disequilibrium across breeds (Ramayo-Caldas et al. 2016). A recent study found out of 79 genomic regions associated with WBSF, only 42 were in common in three of the five breeds, and only eight in all five *Bos taurus* breeds (McClure et al. 2012). An even greater challenge is the ability to find these genes given the complex genetic architecture of each palatability trait, with thousands of very small effect genes explaining only a fraction of the genetic variation.

A brief summary and description of several genes and pathways identified as controlling different palatability traits is presented below.

3.2.1. *Genomic regions associated with solubility and amount of connective tissue*

In an Angus–Brahman multibreed population (Leal-Gutiérrez et al. 2019), a number of genes including CCR4-NOT Transcription Complex Subunit 3 (CNOT3), Osteoclast Associated, Immunoglobulin-Like Receptor (OSCAR), and NLR Family Pyrin Domain Containing *5* (*NLRP5*) were associated with the connective tissue score in a sensory panel. The *CNOT3* gene is part of the CCR4-NOT complex, a major mRNA deadenylases complex with a vital role in several cellular processes related to transcription regulation (www.genecards.org). Dysregulation of *CNOT3* has been associated with changes in Pyruvate

Dehydrogenase Kinase 4 (PDK4) and Insulin-Like Growth Factor Binding Protein 1 (IGFBP1) activity and decreased visceral and subcutaneous fat deposition in mice (Morita et al. 2011). Additionally, PIBF1, a cytoskeletal pericentriolar protein co-localized with γ-tubulin and involved in organization maintenance (Lachmann et al. 2004) and ITGB3, a gene encoding a transmembrane protein related to cell-adhesion, were associated with palatability-related traits (Leal-Gutiérrez et al. 2019). Expression of both genes was associated with cell migration and cell invasion suggesting a possible modulation of the extracellular matrix degradation and metalloproteinases activity (Balassa et al. 2018; Ni, Huang, and Wang 2015; Sun et al. 2015; Ye et al. 2014).

Several polymorphisms in connective tissue-related genes have been reported (Ramayo-Caldas et al. 2016; Tizioto et al. 2013) including an association of *Collagen type XI alpha 1* (*COL11A1*) across Limousine, Charolaise and Blonde d'Aquitaine cattle breeds, and enrichment of *COL1A1, COL24A1, COL28A, COL2A1, COL4A3*, and *COL6A3* in an association with WBSF.

3.2.2. *Genomic regions associated with marbling deposition*

In recent years, important associations have been identified for a number of candidate genes and beef quality traits. Leptin, one of the most important adipose-derived hormones, plays an important role in the regulation of energy intake and expenditure, appetite and body composition (Houseknecht et al. 1998). The leptin gene is located on bovine chromosome 4, and significant associations have been identified between the leptin genotypes and carcass fat (Buchanan and Fitzsimmons 2002; Lusk 2007), body weight (Lusk 2007), feed intake (Lagonigro et al. 2003), meat quality (Gill et al. 2009) and growth rate (Nkrumah et al. 2005) in beef cattle, as well as fertility and milk production traits in dairy cattle. However, other studies failed to identify an association between the leptin SNPs and cattle marbling and fatness traits (Barendse, Bunch, and Harrison 2005) or backfat thickness and total lipids (Fortes et al. 2009; Pannier et al. 2009).

The *diacylglycerol acyltransferase 1* (*DGAT1*) gene was mapped to chromosome 14, in a region where the thyroglobulin gene and the DNA marbling score marker CSSM66 are located (Barendse et al. 1997). The *DGAT1* gene encodes acyl CoA:diacylglycerol acyltransferase, a key enzyme in triacylglycerol synthesis (Cases et al. 1998). A dinucleotide substitution (AA/GC) in exon 8 of *DGAT1* resulting in a nonconservative lysine to alanine substitution is suspected to have a direct impact on the enzyme activity (Grisart et al. 2004). An association with sirloin weight and fat depth around the sirloin has been identified in Aberdeen Angus-sired cattle (Gill et al. 2009), but no other associations have been confirmed in other *Bos taurus* cattle (Pannier et al. 2010) and no associations with carcass fat traits have been identified in Brahman cattle (Casas et al. 2005) or a number of *Bos indicus*-influenced cattle (Fortes et al. 2009).

Several other genes including fatty acid binding protein 4 (FABP4), stearoyl-coA desaturase (SCD), fatty acid synthase (FASN) and sterol regulatory

element-binding protein 1 (SREBP1), fatty acid desaturase 1 (FADS1) and lipin 3 (LPIN3) have been associated with fat composition and quality in *Bos indicus* and *Bos taurus* populations (Bolormaa et al. 2014; Ramayo-Caldas et al. 2016). The *FABP4* gene is located on bovine chromosome 14 in a QTL region for meat production traits fat thickness, yield grade, and marbling and encodes a lipid transport protein expressed in adipocytes which can bind long-chain fatty acids and retinoic acid (Casas et al. 2003). Two SNPs in this gene were found to have a significant effect on marbling score and subcutaneous fat depth (Barendse et al. 2009; Lee et al. 2010; Michal et al. 2006); however, a number of studies failed to identify an association between markers in *the FABP1* gene and intramuscular fat levels and marbling scores (Pannier et al. 2009; Tizioto et al. 2012).

The enzyme that catalyzes the desaturation of saturated to unsaturated fatty acids is encoded by *SCD* gene, which has been reported to play a key role primarily in the conversion of stearic (C18:0) and palmitic acid (C16:0) to oleic acid (C18:1) (Bené, Lasky, and Ntambi 2001). In Wagyu cattle, a SNP replacing valine with alanine in the *SCD* gene was associated with monounsaturated fatty acid content and melting point of intramuscular fat (Taniguchi et al. 2004). Analysis of 3 other SNPs in the 3′-untranslated region of the *SCD* gene revealed a positive correlation with marbling score, amount of monounsaturated fatty acids and conjugated linoleic acid content, but negative correlation with the amount of saturated fatty acids (Jiang et al. 2008).

The expression of the *SCD* gene is regulated by *SREBP* (Bené, Lasky, and Ntambi 2001). A *SREBP1* polymorphism has been related to carcass weight (Ohsaki et al. 2009), but no significant effects on meat yield traits were identified in Japanese Black cattle (Matsuhashi et al. 2011). An 84 bp insertion/deletion in intron 5 of the *SREBP1* gene has been suggested to affect monounsaturated fatty acid content through regulation of *SCD* gene expression (Hoashi et al. 2007) with favorable *SREBP1* and *SCD* genotypes showing 1.3% and 2.1% higher monounsaturated fatty acid content, respectively, and 1.6°C and 2.5°C lower melting point, respectively.

Fatty acid synthase (FASN) is a multifunctional enzyme catalyzing the *de novo* synthesis of long-chain saturated fatty acids in cells. Polymorphisms in *the FASN* gene were associated with the fatty acid composition of back fat, intermuscular and intramuscular fat in Japanese Black and Limousin cattle (Abe et al. 2008; Matsuhashi et al. 2011). Amino acid substitutions in the thioesterase domain of the *FASN* gene were associated with fatty acid composition in Angus cattle (Zhang et al. 2008), while five SNPs were associated with increased monounsaturated fatty acids, marbling score, and decreased saturated fatty acids in Korean cattle (Oh et al. 2012).

3.2.3. *Genomic regions associated with proteolysis of cytoskeletal and cytoskeletal-associated proteins*

3.2.3.1. *Calpain-calpastatin system.* Calpain activity is modulated by calcium and it has been implicated in several fundamental physiological processes, including cytoskeletal remodeling, cellular signaling, apoptosis and cell survival (Juszczuk-Kubiak et al. 2008; Storr et al. 2011). Postmortem proteolysis is largely inhibited in μ-calpain knockout mice, even when m-calpain is active (Geesink et al. 2006). This proteolytic degradation is the result of autolysis of μ-calpain and its activity decreases more rapidly and consistently than does its endogenous inhibitor, calpastatin (Boehm et al. 1988). This suggested that μ-calpain was largely responsible for postmortem proteolysis, excluding a major role for any of the other members of the calpain family or any other proteolytic system in tenderization (Geesink 2005; Geesink et al. 2006). Calpastatin is the specific inhibitor of μ-calpain and it is involved in cell viability and proliferation. Calpastatin is assumed to explain genetic differences in meat tenderness based on findings that the over-expression of calpastatin significantly inhibited calpain activity in muscle, heart and neuronal tissue (Li et al. 2009; Liang et al. 2010; Van Ba, Reddy, and Hwang 2015). The μ-calpain/calpastatin enzyme/inhibitor ratio was proposed as the major determinant of meat tenderness (Ouali 1992). However, Wright et al. (2018) using an Angus–Brahman multibreed population showed that the activation rate of μ-calpain could be an important element in the tenderization process. In this population, animals with higher Brahman proportion had slower μ-calpain activation and lower palatability performance.

McClure et al. (2012) estimated that 1.02% and 1.85% of the phenotypic variation in WBSF in five *Bos taurus* breeds could be explained by variation in calpastatin and μ-calpain genes, respectively. A comparable effect of 0.46% of the additive genetic variance in tenderness could be explained by variation in calpastatin in a Nellore cattle population (Magalhães et al. 2016).

The expression of calpastatin gene is highly regulated through several different mechanisms. Calpastatin gene has highly conserved intron–exon boundaries, several putative translational start sites (within exons 1xa, 1xb, 2 and 14t), and is lacking TATA boxes associated to predicted promoter sequences for transcript types I–III. The specific roles of each calpastatin isoform remain unclear, but one hypothesis is that individual calpastatin domains have different affinities for heterodimeric "tissue-specific" calpains (Hanna, Garcia-Diaz, and Davies 2007) therefore serving different purposes. The four inhibitor domains of calpastatin protein have a different affinity for calpain.

The calpain-calpastatin proteolytic system has been reported as associated with palatability-related traits in beef cattle (Bolormaa et al. 2014; Leal-Guti érrez, et al., 2018; McClure et al. 2012), and the most important polymorphisms associated with tenderness are summarized below.

3.2.3.1.1. *Capn4751.* This C/T polymorphism is located in intron 18 of *calpain* (*CAPN*) gene. In a Nellore population, Capn4751 was associated

with tenderness at 7-, 14- and 21-day postmortem (Pinto et al. 2010). The C allele was favorable, and the estimated effect of the CC-TT contrasts was −0.30, −0.27 and −0.34 kg of WBSF at 7, 14 and 21 days, respectively. A dominance effect was also identified across all aging periods, with the CC and CT genotypes being more tender than TT (Pinto et al. 2010).

3.2.3.1.2. *Capn316.* Capn316 is a missense G/C SNP in exon 9 (Allais et al. 2011). Pinto et al. (2010) found that the contrast CG-GG was associated with values of −0.71, −1.1, and −0.69 kg of shear force at 7, 14 and 21-day postmortem, respectively. Multiple reports are available in *Bos indicus* and *Bos taurus* populations, where the GG genotype has an unfavorable effect on tenderness (Casas et al. 2005; Costello et al. 2007; Curi et al. 2010; Morris et al. 2006; Papaleo et al. 2010). The G allele was estimated to have a negative effect on WBSF in Charolais (1.60 ± 0.61 N/cm^2) and Limousin (0.90 ± 0.37 N/cm^2) (Allais et al. 2011). Corva et al. (2007) reported that WBSF from Angus, Hereford, and Limousin crossbred steers with CC genotype was 11% lower than for CG and 17% lower than GG genotypes. Capn316 was confirmed useful in populations with high *Bos taurus* background where the C allele is favorable and associated with lower WBSF values (White et al. 2005). In this report, when Capn316 and Capn4751 were considered simultaneously in the analysis, Capn316 showed no significant effect once Capn4751 was fit in the model, suggesting these two markers may explain the same variation in WBSF. It is also important to highlight that the C allele has a very low frequency in several breeds, especially *Bos indicus* cattle (Parra et al. 2015).

3.2.3.1.3. *Capn530.* Capn530 is a missense G/A polymorphism in exon 14 resulting in a V/I substitution at the protein level (Allais et al. 2011). An association with shear force at 14 days was reported with a difference of 0.26 kg between the A and the G allele (Page et al. 2002). A similar result was reported in crossbred Angus, Hereford and Limousin cattle where meat from steers with the GG genotype showed an 11.5% higher shear force compared to the GA genotype (Corva et al. 2007). However, in Brahman populations, the G allele was uninformative or close to being fixed (Casas et al. 2005; White et al. 2005). A lack of association with tenderness was also reported in Nellore and Irish cattle (Costello et al. 2007; Pinto et al. 2010).

3.2.3.1.4. *UoG-Cast and WsuCast.* The UoG-Cast marker is a G/C SNP in intron 5 of *calpastatin* (*CAST*) (Van Eenennaam et al. 2007). Pinto et al. (2010) observed an additive effect of this marker across different aging periods, and a significant dominance effect of the unfavorable allele G over C at 7 and 21 days of aging. Animals with the CC genotype had more tender meat than CG or GG. The contrast CC-GG for WBSF showed −0.17, −0.21 and −0.25 kg of additive effect for 7, 14 and 21 days of aging, respectively. Multiple studies reported an association of this marker with tenderness in different cattle populations (Allais et al. 2011; Calvo et al. 2014; Schenkel et al. 2006; Van Eenennaam et al. 2007). However, there are also several reports which failed to identify an association (Curi et al. 2010; Reardon et al.

2010). WsuCast is a G/A substitution reported in high linkage disequilibrium with UoGCast (Pinto et al. 2010). An epistatic relationship exists between WsuCast and Capn4751, where the additive effect of WsuCast is observed only when the Capn4751 genotype is different from TT.

3.2.3.1.5. *Cast2959.* Cast2959 is a A/G SNP located in the 3′UTR of the calpastatin mRNA (Casas et al. 2006) and was associated with WBSF and tenderness, where CC and CT animals produced tougher meat when compared with TT animals (Casas et al. 2006; Li et al. 2010). Cast2959 was reported to be associated with water-holding capacity in raw meat and myofibrillar fragmentation (Curi et al. 2009; Leal-Gutiérrez et al. 2015). Leal-Gutiérrez et al. (2018) reported an association of Cast2959 with WBSF in an Angus–Brahman crossbred population and the C allele was predicted to change the mRNA molecular folding, producing long single-stranded regions and theoretically slower transcription, less calpastatin protein, and less μ-calpain postmortem inhibition.

3.2.3.1.6. *Cast2832.* Another A/G SNP located in the 3′UTR of the CAST mRNA, Cast2832 was associated with shear force in *longissimus* muscle from cattle with high *Bos indicus* influence (Cafe et al. 2010; Leal-Guti érrez, et al., 2018). The favorable A allele has been shown to produce a more energetically unstable mRNA (Leal-Gutiérrez, et al., 2018). This is substantiated by reports of Brahman animals with the AA genotype having approximately 14% lower mRNA expression than the GG genotype (Nattrass et al. 2014), suggesting less calpastatin protein being produced and therefore less postmortem μ-calpain inhibition.

3.2.3.2. *Desmin and αβ-crystallin.* Desmin interacts with other proteins to form a continuous cytoskeletal network that maintains a spatial relationship between the contractile apparatus and other structural elements of the cell, thus maintaining cellular integrity, force transmission, and mechano-chemical signaling (Spaendonck-Zwarts van et al. 2011). A possible effect on meat quality traits is suggested by the fact that the accumulation of desmin is caused by a resistance of the mutant protein to the regular turnover catalyzed by the calpain-calpastatin enzymatic machinery (Goldfarb et al. 2004). On the other hand, αβ-crystallin serves as a chaperone in the muscle, preventing desmin aggregations under various forms of stress, and an afunctional protein may cause a similar phenotype to that resulting from desmin mutations (Goldfarb et al. 2004).

3.2.3.3. *Transmembrane anchoring proteins.* The process of meat tenderization involves proteolysis of key myofibrillar and associated proteins. These proteins are involved in maintaining the structural integrity of myofibrils. Desmin and vinculin are involved in the inter-myofibril linkages; titin, nebulin and possibly troponin-T are important for intra-myofibril linkages; while

vinculin and dystrophin are essential in linking myofibrils to the sarcolemma by costameres and the attachment of the cell to the basal lamina (Koohmaraie 1996). Pathways like "Endoplasmic reticulum membrane", "Endoplasmic system", "Golgi apparatus" and "Cell adhesion" containing several transmembranes were enriched in association studies for meat quality traits (Castro et al. 2017; Leal-Gutiérrez et al. 2019; Mudadu et al. 2016; Tizioto et al. 2013). Additionally, other transmembrane anchoring genes have been identified as associated with beef palatability-related traits (Fig. 1) in an Angus–Brahman multibreed population (Leal-Gutiérrez et al. 2019). Although many of these transmembrane anchoring proteins represent minor proteolytic substrates during the aging process, they could be very important in the overall tenderization.

3.2.4. *Other mechanisms*

3.2.4.1. *PRKAG3 and RYR1.* The Protein Kinase AMP-Activated Non-Catalytic Subunit gamma 3 (PRKAG3) and Beta 1 (PRKAB1) proteins are regulatory subunits of the AMP-activated protein kinase (AMPK), a glycolytic protein complex that regulates transcription of genes involved in lipid (*Lpl, Cd36* and *Cpt1*) and glucose metabolism (*Gys* and *Ldh2*) (Long et al. 2005). Several polymorphisms in the swine *PRKAG3* gene (RN-, rn+ and rn*) have large effects on meat quality traits through changes in pH decline during aging (Lindahl et al. 2004). The association of *PRKAG3* with cooking loss and tenderness was also demonstrated in cattle (Reardon et al. 2010). Similarly, *PRKAB1* was found to be associated with water-holding capacity in Nellore cattle (Tizioto et al. 2013), while the RYR1-11195 SNP in the bovine *Ryanodine Receptor 1* (*RYR1*) was associated with cooking loss in a *Bos indicus* influenced population (Leal-Guti érrez et al. 2015).

3.2.4.2. *Transcription factors and epigenetic-related genes.* In a study of epigenetic-related genes, Several transcription factors including *VDR, GLI2, LHX9, PLAG1* and *ZEB1* and polymorphisms in DNA methyltransferases genes *DNMT1, DNMT3a, DNMT3b* were associated with meat quality traits (Liu et al. 2015; Magalhães et al. 2016; Mudadu et al. 2016). This is in agreement with other multi-trait analysis reports which reported enrichment for "Negative regulation of transcription from RNA polymerase II promoter" and "Positive regulation of transcription from RNA polymerase II promoter" terms (Bolormaa et al. 2014; Leal-Gutiérrez et al. 2019; Tizioto et al. 2013).

4. Conclusion

Genomic resources and tools have been developed for improving meat palatability, in particular, tenderness. Biological markers that can be used to predict meat quality have been identified using transcriptomics and

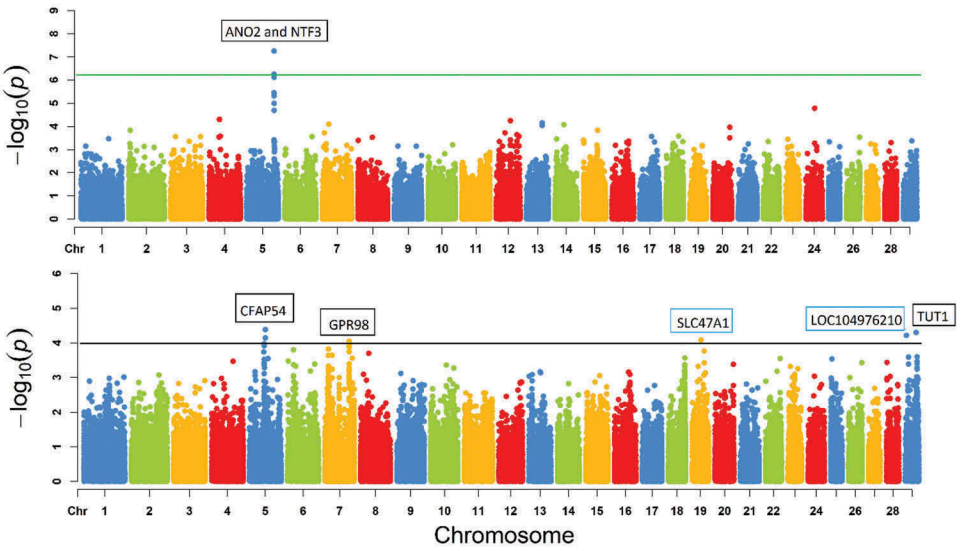

Figure 1. Genome-wide association plots of the significance (−log*P* on the y-axis) of each SNP in genome order (x-axis) for cooking loss (a) and tenderness (b) in *longissimus dorsi* in an Angus–Brahman multibreed population. The black horizontal line represents a 10^{-4} *P*-value and the green line represents the adjusted 6×10^{-7} *P*-value. The black box around a gene indicates the significant SNP were located in the gene, a blue box indicates the SNP was in an intergenic region.

proteomics approaches. This includes markers in genes not suspected to play a role in these traits (Bendixen, Hedegaard, and Horn 2005; Cassar-Malek et al. 2008; Hocquette et al., 2012a). Functional genomics offers new opportunities to identify biological and molecular indicators for desirable quality attributes in live animals. This can be especially useful in managing each animal to meet its potential. As reviewed in this article, the effect of every gene and genetic marker on meat quality traits varies considerably with the environment or other factors (sex, breed, production system, etc.). Therefore, the validation of these tools is important before large-scale adoption and implementation. Recent advances in biotechnology such as high-density genotyping panels, and whole-genome sequencing provides new opportunities for progress toward the goal of identifying the genes and gene networks controlling the variation in meat palatability traits.

Disclosure statement

The author reports no conflicts of interest in this work.

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