Genetic markers associated with beef quality: A review

Jakeline Vieira Romero [a,*], José Luis Olleta [a], Virginia Celia Resconi [a], Pilar Santolaria [b], María del Mar Campo [a]

[a] *Dep. Animal Husbandry and Food Science, Instituto Agroalimentario IA2, University of Zaragoza-CITA, 50013, Zaragoza, Spain*
[b] *Dep. Animal Husbandry and Food Science, Environmental Sciences Institute (IUCA), University of Zaragoza, 22071, Huesca, Spain*

HIGHLIGHTS

- There are at least 27 genes and >60 traits related to meat quality.
- MSTN, LEP, CAST, FASN, SCD and CAPN are the main genes associated to beef quality.
- New traits and QTLs are constantly updated and are available in online databases.

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ABSTRACT

Classic animal breeding focuses on changes in genetic composition of populations through selection and breeding systems designed to increase the frequency of favorable alleles incrementing production by improving traits of commercial interest. Meat quality involves traits that have received considerable attention in genetic breeding programs in recent years. The genomic selection using single nucleotides polymorphisms (SNPs) markers is a strong tool to obtain desired phenotypes for economically important traits, including those which are perceived by consumers. Trait such as back and intramuscular fat contribute to the juiciness, flavor and tenderness of beef, all of which directly influences consumer choice. Over the years, many studies have been conducted resulting in multiple quantitative trait locus (QTLs) candidates for carcass and meat quality traits, and an extensive database has been created. Traits such as marbling score, intramuscular fat and subcutaneous fat thickness (which includes back fat and rump fat thickness), have been associated with 2448, 192 and 1044 QTLs, respectively. Although genetic analyses are costly and laborious, the use of molecular markers help to increase favorable genes in the population. Their advance is becoming more concrete and acceptable as a measure of economic importance.

1. Introduction

Meat quality is one of the most important economic aspects in farm animals and, in some countries, is critical for determination of quality grades of meat products in the commercial beef industry (Choi et al., 2015). Visual appearance of fat (firmness and color), meat color (MC), flavor, tenderness, juiciness, and shelf life are the main intrinsic quality attributes perceived by consumers (Reardon et al., 2010; Henchion et al., 2017), which are taken into account when selecting beef products at the time of purchase by customers. However, ideal meat quality standards will vary depending on individual consumer preferences, as well as regional, cultural, and processing factors. Furthermore, there is a tendency to value the nutritional composition, especially linked to the fatty acid (FA) composition (Poli et al., 2019), as they are related to

human health (Michas et al., 2014). That is why meat quality traits have increasingly gained more attention in breeding programs.

Since the discovery of the DNA structure in the 1950′s by Watson and Crick (1953), the science has made progress in identifying the genes and their function, which has made possible to detect genetic differences (polymorphisms) for traits among individual animals, thus allowing the selection of the most desired traits within a population. Identifying the candidate genes responsible for phenotypic variation has been a challenge, mainly because of the quantitative nature of these variables, since they are controlled by many genes and are affected by the environment (Blecha et al., 2015).

Many studies attempt to find significant associations between QTLs and SNPs markers and have focused on finding genetic variants related to production traits in beef cattle. As a result, several candidate genes

have been identified and associated with meat quality traits, among others *MSTN* (Allais et al., 2010; Bennett et al., 2019), *LEP* (Melucci et al., 2012; Kawaguchi et al., 2017), *FASN* (Oh et al., 2012a; Kim et al., 2017), *SCD* (Reardon et al., 2010; Wu et al., 2012) or *CAST* and *CAPN* (Leal-Gutiérrez et al., 2018; Abo-Ismail et al., 2018; Lee et al., 2019) (Table 1). Information on quantitative traits related to a particular gene can be found in public databases which are valuable resources for indirect use in breeding programs or for academic research, focusing on achieving better rates of genetic progress for economically important traits. Given the number of genes associated so far with production traits, in this review we will focus on presenting the main candidate genes and some of their respective QTLs detected related to meat quality, which stand out as the most promising and well-described genes associated especially with traits selected for meat quality, particularly those most relevant to the consumer. Additionally, other aspects related to carcass quality will also be considered.

2. Genomic selection and use of markers in livestock breeding

In 2003, the sequencing of the bovine genome was set in motion with samples provided by Hereford breed specimens. Subsequently, sequencing was carried out with a lower degree of precision in other breeds such as Holstein, Angus, Jersey, Limousin, Norwegian Red and Brahman. At the end of 2004, the availability of the first draft of the bovine genome in public databases was announced (Bovine HapMap Consortium et al., 2009). The cattle genome contains a minimum of 22, 000 genes (Bovine Genome Sequencing and Analysis Consortium, 2009). SNPs occur approximately every 700 base pairs (bp) in taurine and every 300 bp in indicine, which means that there is more genetic variation in *Bos indicus* cattle.

When genome sequencing in domestic animals was available, a large number of SNPs were identified and associated with quantitative traits. Once new genetic associations are identified, researchers can use the information to develop better strategies to increase, improve or even to avoid these traits in the target population (National Human Genome Research Institute, 2019). That is why the genomic selection by using SNPs is a strong tool to obtain desired phenotypes for economically important traits in beef cattle breeds, including those which are perceived by consumers.

Over the years much research has been carried out and numerous QTLs candidates for quality traits in beef cattle have been found, and an extensive database has been created and is available, such as: NCBI Genome data viewer (2023), UCSC Genome Browser Gateway (n.d.), Cattle QTL Database (n.d.) Hu et al. (2022) and Ensembl genome browser (n.d.). These databases are continuously updated. The current release of the Cattle QTL database (August 2024) contains >192,000 QTLs for public access. These data were selected from >1170 publications and represent 680 different cattle traits and 344 cattle genes. Data are also submitted to the other databases mentioned above and the next release will be in late December 2024.

Species of zootechnical interest, such as domesticated cattle (*Bos taurus* and *Bos taurus indicus*), are known to possess millions of SNPs in their genomes. Initially, estimates suggested around 4 million SNPs for these species (Bovine HapMap Consortium et al., 2009; Seidel, 2010). However, advancements in sequencing technologies and the expansion of genomic analysis have provided a more comprehensive view of genetic diversity. The 1000 Bull Genomes Project, which sequenced the entire genomes from >2700 individuals, identified at least 84 million SNPs (Hayes and Daetwyler, 2019). This substantial increase in SNP estimates highlights not only the progress in genomic technologies but also the broader and more detailed genetic sampling achieved in recent studies. The discrepancy between previous and current estimates underlines the rapid evolution of genetic research methodologies and the increasing ability to capture a more comprehensive view of genetic variation. Furthermore, hundreds of SNPs have been detected and many of them associated to several economically relevant traits in beef cattle,

such as QTLs related to meat quality, as shown in Table 1.

3. Genetic markers related to meat quality

Consumer perception of beef quality is determined by intrinsic (convenience, safety, technological, appearance, sensory and nutritional) and extrinsic attributes (related to other factors such as the animal husbandry system, image, price, marketing strategy, etc.). Intramuscular and subcutaneous fat deposition exerts a direct or indirect influence on the quality, with marbling - determined by the intramuscular fat content (IMF) - being the main factor influencing the sensory attributes such as tenderness, juiciness, flavor and colour. These traits play a crucial role in shaping consumer preferences and, in some countries, directly affect the final price of the product (Henchion et al., 2017; Choi et al., 2019; Santos et al., 2021; Hocquette, 2023). A large variation of genes associated with meat quality has been identified (Table 1). However, complex traits such as tenderness or fat deposition are controlled by several genes (Wang et al., 2020).

Up to August 2024, 83 genes were associated with marbling score, 16 with IMF and 84 with to subcutaneous fat thickness (SF), which includes back fat thickness (BFT) and rump fat thickness (RFT), and, respectively 2436, 185 and 1033 QTLs, were found for these traits. Genes such as *ADIPOQ, MSTN, RORC, CAST, CAPN, POMC, TG, DGAT1, FABP4* and *FASN* substantially influence IMF, SF and tenderness (sensory and/or shear force). Although many genes, such as, *MSTN, LEP, FABP4, LIPE, FASN, GH1, PPARG* and *SCD* are responsible in a positive or negative way for the FA expression in meat, the *LEP, FASN* and *SCD* are the most involved in FA composition. The mentioned genes are the most highlighted in the current literature and therefore this review will focus on them.

3.1. ADIPOQ (Adiponectin)

ADIPOQ is located in chromosome 1 and, of the 7 traits associated with this gene, 6 are related to meat quality (Table 1). This gene encodes adiponectin, which is a peptide hormone that is involved with lipid synthesis and fat accumulation in adipose tissue (Nelson and Cox, 2012). Although it also appears to be implicated in regulating bone development (Berner et al., 2004). Despite few findings in the literature, *ADIPOQ* is related to the degree of marbling, carcass weight (CW), *Longissimus* muscle area (LMA), BFT and IMF in cattle derived from *Bos taurus* (Morsci et al., 2006; Barendse, 2011; Choi et al., 2015). However, no significant association has been observed in zebu animals (Fonseca et al., 2015; Royer et al., 2016).

On the other hand, Morsci et al. (2006) investigating the association of *ADIPOQ* and somatostatin (*SST*) gene polymorphisms in Angus breed, did not observe a direct effect of the *ADIPOQ* on the marbling degree. Both genes are located within the bovine chromosome 1. Nevertheless, significant associations were detected for *SST*, suggesting that *ADIPOQ* has no direct effect on marbling, but may be located in the vicinity of a QTL that affects marbling, such as *SST*. Furthermore, several SNPs with significant effects on the degree of marbling are found in chromosome 1 (Wang et al., 2020).

3.2. MSTN (Miostatin)

Located in chromosome 2, the genetic variation in the *MSTN* gene (also known as *GDF8* gene) is associated with an increase in the number of muscle fibers in cattle, which generates double-muscled animals or muscle hypertrophy (Haruna et al., 2020). Grobet et al. (1998) identified a series of variants in the myostatin gene as being responsible for the trait of double-muscled phenotype. They observed that several breeds, such as Belgian Blue White, Blonde d'Aquitaine, Charolais, Gasconne, Limousin, Maine-Anjou, Parthenaise, Piedmontese, and some Spanish breeds such as Asturiana de los Valles and Rubia Gallega, are recognized as carriers of specific variants that predispose to this genetic condition.

Table 1

The main genes related to meat quality traits with statistically significant effect (adapted from NCBI and Animal QTL database). Some carcass quality traits are also included.

Gene[†]	Name	Chr	Traits	References
ADIPOQ 7 traits with 17 QTL found	Adiponectin	1	Marbling; CW IMF LMA; BFT	Choi et al., 2015 Barendse, 2011 Choi et al., 2015; Morsci et al., 2006
POU1F1 8 traits with 9 QTL found	POU class 1 homeobox 1	1	Gristle length[‡] Muscle pH (8th day *post-mortem*)	Gill et al., 2010 Ribeca et al., 2014
SST 8 traits with 15 QTL found	Somatostatin	1	CW Marbling	Kim et al., 2003 Morsci et al., 2006
MSTN 57 traits with 102 QTL found	Myostatin	2	CW MUFA; CL; BFT; RFT Dressing percentage SF%; DL; fat cover; fat percentage; intermuscular fat percentage; WHC Fat color Insoluble collagen content Tenderness (sensory panel); MC (L*) IMF LMA Yield grade Meat percentage	Allais et al., 2010; Esmailizadeh et al., 2008; Martínez et al., 2010; Sellick et al., 2007 Esmailizadeh et al., 2008 Allais et al., 2010; Martínez et al., 2010 Martínez et al., 2010 Han et al., 2012 Allais et al., 2010 Allais et al., 2010; Esmailizadeh et al., 2008 Allais et al., 2010; Esmailizadeh et al., 2008; Martínez et al., 2010; Saatchi et al., 2014; Sellick et al., 2007 Esmailizadeh et al., 2008 Saatchi et al., 2014 Martínez et al., 2010; Sellick et al., 2007
PRKAG3 9 traits with 16 QTL found	Protein kinase, AMP-activated, gamma 3 non-catalytic subunit	2	MC (L*, a*, b*); muscle pH (8th day post-mortem) CW, Gristle length[‡] CL	Ribeca et al., 2014 Gill et al., 2010 Reardon et al., 2010
RORC 3 traits with 15 QTL found	RAR-related orphan receptor C	3	IMF Marbling RFT	Avilés et al., 2013; Barendse et al., 2010 Barendse et al., 2007a, 2010 Barendse et al., 2007a
LEPR 4 traits with 6 QTL found	Leptin receptor	3	BFT LMA	Ferraz et al., 2009 Da Silva et al., 2012; Ferraz et al., 2009
CACNA2D1 7 traits with 14 QTL found	Calcium channel, voltage-dependent, alpha 2/delta subunit 1	4	CW; Meat percentage Dressing percentage; BFT Fat color	Hou et al., 2010 Hou et al., 2010; Yuan and Xu, 2011 Yuan and Xu, 2011
LEP 90 traits with 316 QTL found	Leptin	4	C20:0; C14 index; C18 index; C10:0; C15:1*cis*-10; C20:2 *cis*-11; C12:0; C18:3 *n*-3; C17:0; C14:0; C15:0 CW C22:5 Dressing percentage; muscle pH (24h *post-mortem*) DL C20:5 *n*-3 (EPA) Fat color BFT LMA Marbling MC (a*) MC (b*) MC (chroma) C18:1 *cis*-9; MUFA; SFA C14:1 *cis*-9; C18:0 C16:0; C16:1 *cis*-9 RFT	Orrù et al., 2011 Kawaguchi et al., 2017; Tian et al., 2013 Papaleo Mazzucco et al., 2016 Tian et al., 2013 Pintos and Corva, 2011 Papaleo Mazzucco et al., 2016; Orrù et al., 2011 Melucci et al., 2012; Tian et al., 2013 Collis et al., 2012; Silva et al., 2014; Souza et al., 2010; Woronuk et al., 2012 Collis et al., 2012; Da Silva et al., 2012; Tian et al., 2013 Melucci et al., 2012 Melucci et al., 2012; Silva et al., 2014 Silva et al., 2014 Li et al., 2013 Kawaguchi et al., 2017; Papaleo Mazzucco et al., 2016; Orrù et al., 2011 Kawaguchi et al., 2017; Orrù et al., 2011 Kawaguchi et al., 2017 Da Silva et al., 2012

Table 1 (*continued*)

Gene[†]	Name	Chr	Traits	References
IGF1 26 traits with 41 QTL found	Insulin-like growth factor 1 (somatomedin C)	5	Meat percentage; BFT CW	Islam et al., 2009 Mullen et al., 2011
PPARA 7 traits with 7 QTL found	Peroxisome proliferator-activated receptor alpha	5	Juiciness; muscle pH (24h *post-mortem*)	Gill et al., 2010
CAST 26 traits with 92 QTL found	Calpastatin	7	DL; MC (a*, b*) Juiciness MC (L*, a*, b*) Muscle iron content Muscle pH (24 and 48h *post-mortem*) WBSF BFT RFT Tenderness (sensory panel)	Ribeca et al., 2013 Lee et al., 2014 Reardon et al., 2010 Casas et al., 2014 Reardon et al., 2010; Ribeca et al., 2013 Allais et al., 2011; Barendse et al., 2007b, 2008; Barendse, 2011; Calvo et al., 2014; Curi et al., 2009; Enriquez-Valencia et al., 2017; Leal-Gutiérrez et al., 2018; Lee et al., 2014, 2019; Pinto et al., 2010; Ribeca et al., 2013 Abo-Ismail et al., 2018 Collis et al., 2012 Allais et al., 2011; Avilés et al., 2015
POMC 10 traits with 26 QTL found	Proopiomelanocortin	11	DL; muscle pH (24h *post-mortem*) BFT Marbling LMA Tenderness (sensory panel) CW	Ribeca et al., 2014 Liu et al., 2013 Seong and Kong, 2015 Gill et al., 2010; Liu et al., 2013; Seong and Kong, 2015 Gill et al., 2010 Ribeca et al., 2014
TG 11 traits with 21 QTL found	Thyroglobulin	14	Marbling IMF Muscle pH (8th day *post-mortem*); MC (a*, b*); DL; CW	Gan et al., 2008; Hou et al., 2011; Royer et al., 2016 Bonilla et al., 2010; Thaller et al., 2003 Ribeca et al., 2014
FABP4 22 traits with 40 QTL found	Fatty acid binding protein 4, adipocyte	14	C14:0; C16:0; C20:4 *cis*-5, 8, 11, 14 BFT; C14:1 *cis*-9; MUFA; *n*- 6/*n*-3 IMF Marbling Meat texture Quality grade CW	Maharani et al., 2012 Goszczynski et al., 2017 Avilés et al., 2013; Barendse et al., 2009 Blecha et al., 2015; Lee et al., 2010; Shin et al., 2012 Blecha et al., 2015 Shin et al., 2012 Lee et al., 2010
CRH 8 traits with 13 QTL found	Corticotropin releasing hormone	14	LMA Marbling Muscle pH (8th day and 24h *post-mortem*) BFT	Seong and Kong, 2015 Wibowo et al., 2007 Gill et al., 2010; Ribeca et al., 2014 Wibowo et al., 2007
DGAT1 71 traits with 304 QTL found	Diacylglycerol O-acyltransferase 1	14	CL IMF LMA; RFT Marbling BFT CW	Ribeca et al., 2014 Li et al., 2013; Thaller et al., 2003; Wu et al., 2012 Collis et al., 2012 Li et al., 2013 Avilés et al., 2013 Ribeca et al., 2014

Table 1 (*continued*)

Gene[†]	Name	Chr	Traits	References
CPE 5 traits with 9 QTL found	Carboxypeptidase E	17	CL	Reardon et al., 2010; Ribeca et al., 2014
			MC (a*, b*); muscle pH (8th day and 24h *post-mortem*)	Ribeca et al., 2014
			Meat flavor score (sensory panel)	Reardon et al., 2010
LIPE (HSL) 4 traits with 5 QTL found	Lipase, hormone-sensitive	18	C18:1 *cis*-9; C21:0; MUFA	Goszczynski et al., 2014
FASN *41 traits with 259* QTL found	Fatty acid synthase	19	C14 index; C16 index; C18 index; C18:2 *cis*-9 *cis*-12; C18:3 *n*-3; marbling; BFT	Oh et al., 2012a
			UFA; REA; WBSF	Kim et al., 2017
			MUFA	Bartoň et al., 2016; Kim et al., 2017; Matsuhashi et al., 2011; Oh et al., 2012a
			MUFA/SFA	Abe et al., 2009; Bartoň et al., 2016; Kim et al., 2017; Matsuhashi et al., 2011; Oh et al., 2012a
			C14:0	Abe et al., 2009; Bartoň et al., 2016; Bhuiyan et al., 2018; Hayakawa et al., 2015; Kim et al., 2017; Maharani et al., 2012; Matsuhashi et al., 2011; Papaleo Mazzucco et al., 2016; Oh et al., 2012a; Sasago et al., 2017
			C14:1 *cis*-9	Abe et al., 2009; Bartoň et al., 2016; Hayakawa et al., 2015; Matsuhashi et al., 2011; Oh et al., 2012a; Sasago et al., 2017
			C18:1 *cis*-9	Abe et al., 2009; Bartoň et al., 2016; Hayakawa et al., 2015; Maharani et al., 2012; Papaleo Mazzucco et al., 2016; Oh et al., 2012a; Sasago et al., 2017
			C16:0	Abe et al., 2009; Bartoň et al., 2016; Kim et al., 2017; Matsuhashi et al., 2011; Papaleo Mazzucco et al., 2016; Oh et al., 2012a
			C16:1 *cis*-9	Abe et al., 2009; Hayakawa et al., 2015; Matsuhashi et al., 2011; Papaleo Mazzucco et al., 2016; Sasago et al., 2017
			SFA	Bartoň et al., 2016; Kim et al., 2017; Oh et al., 2012a
			C18:0	Abe et al., 2009; Oh et al., 2012a
			CW	Rempel et al., 2012
GH1 34 traits with 81 QTL found	Growth hormone 1	19	DL; muscle pH (8th day and 24h *post-mortem*)	Ribeca et al., 2014
			LMA	Gill et al., 2010
			C14:0; C14:1 *n*-5 *cis*-9; C18:1 *n*-9 *cis*-9; C16:0; C16:1 n-7 *cis*-9	Matsuhashi et al., 2011
			CW	Matsuhashi et al., 2011; Ribeca et al., 2014
GHR 41 traits with 168 QTL found	Growth hormone receptor	20	CL; muscle pH (8th day *post-mortem*)	Ribeca et al., 2014
			BFT	Baeza et al., 2011; Garrett et al., 2008
			IMF	Baeza et al., 2011; Reardon et al., 2010
			LMA	Baeza et al., 2011; Cardoso et al., 2014
			MC (L*); muscle protein percentage; tenderness (sensory panel)	Reardon et al., 2010
PPARG 12 traits with 13 QTL found	Peroxisome proliferator-activated receptor gamma	22	BFT; tenderness (sensory panel)	Fan et al., 2011
			MUFA; SFA	Oh et al., 2012b
			C18:0; C18:1 *cis*-9	Goszczynski et al., 2016
			WHC	Fan et al., 2011, 2012
MC4R 11 traits with 18 QTL found	Melanocortin-4 receptor	24	Muscle pH (8th day *post-mortem*); WBSF; CL	Ribeca et al., 2014
			BFT	Huang et al., 2010; Liu et al., 2010; Seong et al., 2012
			Marbling	Liu et al., 2010; Seong et al., 2012
			CW	Liu et al., 2010; Ribeca et al., 2014

Table 1 (*continued*)

Gene[†]	Name	Chr	Traits	References
SCD 34 traits with 117 QTL found	Stearoyl-CoA desaturase (delta-9-desaturase)	26	IMF	Reardon et al., 2010; Wu et al., 2012
			C18:3 *n*-3	Orrù et al., 2011
			MC (L*, a*, b*); pH muscular (48h *post-mortem*)	Reardon et al., 2010
			MC (chroma, a*, b*)	Li et al., 2013
			Meat firmness; C14:0	Matsuhashi et al., 2011
			MUFA	Bartoň et al., 2010; Matsuhashi et al., 2011; Orrù et al., 2011
			MUFA/SFA	Bartoň et al., 2010
			C14:1 *cis*-9	Bartoň et al., 2010; Maharani et al., 2012; Matsuhashi et al., 2011; Wang et al., 2019
			C18:1	Bartoň et al., 2010; Kim et al., 2017; Matsuhashi et al., 2011; Orrù et al., 2011
			SFA	Bartoň et al., 2010; Kim et al., 2017
			WBSF	Wu et al., 2012
			C18:0	Bartoň et al., 2010; Kim et al., 2017; Matsuhashi et al., 2011; Orrù et al., 2011
			Tenderness (sensory panel)	Avilés et al., 2015
			UFA	Kim et al., 2017
CAPN1 19 traits with 79 QTL found	Calpain 1	29	DL	Ribeca et al., 2013
			Fat color; MC (L*)	Melucci et al., 2012
			IMF	Barendse, 2011; Li et al., 2013
			Juiciness	Lee et al., 2014
			LMA	Pintos and Corva, 2011
			Marbling	Li et al., 2013; Melucci et al., 2012
			MC (a*)	Melucci et al., 2012; Pintos and Corva, 2011
			MC (b*)	Melucci et al., 2012; Pintos and Corva, 2011; Ribeca et al., 2013
			MCS	Liu et al., 2015
			Muscle iron content	Casas et al., 2014
			WBSF	Allais et al., 2011; Barendse, 2011; Barendse et al., 2007b; Bonilla et al., 2010; Curi et al., 2009, 2010; Gill et al., 2009; Lee et al., 2014, 2019; Page et al., 2002; Pinto et al., 2010
			Tenderness (sensory panel)	Allais et al., 2011; Gill et al., 2009; Lee et al., 2014
IGF2 15 traits with 32 QTL/ found	Insulin-like growth factor 2	29	BFT; LMA	Sherman et al., 2008
			CW	Berkowicz et al., 2011

Abbreviations: BFT, Back Fat Thickness (12th rib); CL, Cooking Loss; Chr, chromosome; CW, Carcass Weight; DL, Drip loss; IMF, Intramuscular Fat; LMA, *Longissimus* muscle area; MC, Meat Color; MCS, Meat Color Score; MUFA, Monounsaturated Fatty Acids; PUFA, Polyunsaturated Fatty Acids; QTLs, Quantitative Trait Locus; RFT, Rump Fat thickness; SF%, Subcutaneous Fat Percentage; SFA, Saturated Fatty Acids; UFA, Unsaturated Fatty Acids; WBSF, Warner-Bratzler Shear Force; WHC, Water Holding Capacity.

[†] The number of traits and QTLs mentioned are relative by the end of September 2024.

[‡] Connective tissue amount.

Martínez et al. (2010) observed that Asturiana de los Valles breed presented the double-muscled genotype and had reduced water-holding capacity (WHC), lower proportion of fat cover and reduced fat content in LMA. However, double-muscled animals had the greatest carcass yield and *Longissimus* muscle weight and area, as well. Although the reduced fat content and low WHC could negatively affect the sensory attributes of the meat compared to other genotypes with greater fatness, the authors concluded that these animals provide higher economic returns in intensive production systems due to their higher CW and conformation, higher efficiency and lower feeding costs (due to better feed conversion). Besides, tenderization which is highly appreciated by consumers is high at low ageing periods in this breed (Campo et al., 1999).

On the other hand, the low amount of IMF and the different proportion of FA, can be considered positive in terms of human health. Belgian Blue White animals with double-muscled genotype have lower total FA content compared with animals with normal genotype, and higher proportion of polyunsaturated FA (PUFA), resulting in improved polyunsaturated/saturated fat ratio and lower *n*-6 /*n*-3 (Raes et al., 2001). Unfortunately, this trait is associated with reduced fertility, dystocia and stress susceptibility (Arthur, 1995; Allais et al., 2010; Fiems, 2012), which must be taken into account when selecting animals for this trait.

3.3. RORC (retinoic acid receptor-related orphan receptor C)

The retinoic acid receptor-related orphan receptor C (*RORC*) is a steroid and thyroid hormone receptor, which binds retinoic acid as well as thyroid hormone (Barendse et al., 2007a; Mullen et al., 2009). Although there are relatively limited reports in the literature associated with meat quality, *RORC* gene, located in the chromosome 3, is strongly related to marbling score and IMF traits. Barendse et al. (2007a) observed that the T allele (g.3290T>G SNP) has been associated with increased marbling in a large sample (1.750) of Angus and Shorthorn animals. The positive effect of *RORC* on marbling score (measured by AUS-MEAT) and IMF percentage (measured by near-infrared spectrometry), also has been observed in Angus and Hereford breeds and in *Bos indicus* (Brahman) (Barendse et al., 2010).

Similarly, Avilés et al. (2013) reported a significant association of the T allele and genotype TT of the same SNP with IMF in Charolais, Limousin and Retinta breeds. However, Avilés et al. (2015) observed no associations between SNP in *RORC* gene and sensory attributes assessed by consumers (tenderness and overall acceptability) in the same breeds. The lack of association could be attributable to the limited number of animals used in the study (161 in total).

3.4. LEP (Leptin)

Located in chromosome 4, the *LEP* gene encodes leptin hormone, which acts on receptors controlled by the *LEPR* (Leptin receptor) gene in the hypothalamus to suppress appetite. Due to this, it affects the regulation of feed intake and therefore it is related with body composition, energy balance and body weight (Nelson and Cox, 2012; Tian et al., 2013). Serum leptin concentrations were positively correlated with marbling score, SF and USDA quality grade, but a negative correlation was observed for LMA (Geary et al., 2003). These findings mean that leptin could be used as an indicator for assessment of carcass composition in the live animal and can be very useful in breeding programs.

Furthermore, research suggests that leptin polymorphisms fit into the group of important genetic factors influencing carcass performance and meat quality in beef cattle, such as marbling grade in Hereford (Melucci et al., 2012), carcass yield and IMF in Simmental crossbreds (Tian et al., 2013), BFT in Nelore (Souza et al., 2010; Silva et al., 2014) and effects on weights in Chianina and Marchigiana breeds (Sarti et al., 2019).

Although the *LEP* gene was found to be associated with IMF (Tian et al., 2013; Papaleo Mazzucco et al., 2016), the lack of association has

also been reported in the literature for Aberdeen Angus, Belgian Blue, Blonde d'Aquitaine, Charolais, Friesian, Hereford, Limousin, Salers and Simmental breeds (Pannier et al., 2009; Li et al., 2013; Papaleo Mazzucco et al., 2016). Nevertheless, the *LEP* gene (g.73C>T SNP) has a significant association with overall acceptability of Limousin breed meat aged for 7 days, suggesting that the gene has an effect on some measurements of sensory meat quality (Avilés et al., 2015).

3.5. CAST (Calpastatin) and CAPN (Calpain)

Located respectively in the chromosomes 7 and 29, *CAST* and *CAPN* are one of the most important genes for meat production and composition, for presenting allelic variants that are associated with productive traits of meat quality. Meat tenderness assumes a prominent position among the quality characteristics most required by the consumer. Several studies have correlated the lower tenderness in *Bos indicus* muscle with a higher concentration of *CAST*. This occurs since CAST inhibits the action of *CAPN* during the *post-mortem* muscle proteolysis process (Goll et al., 2003; Alves et al., 2006; Botero et al., 2011; Robinson et al., 2012), since the *CAST* gene can result in more calpastatin protein and consequently higher calpain inhibition rate. This suggests that *CAPN* is mainly responsible for the meat tenderness increase during the *post-mortem* process (Alves et al., 2006; Barendse et al., 2007b).

The heritability for *CAST* activity was found to be 0.65 (considered high h^2) and a genotypic correlation of 0.5 with Warner-Bratzler Shear Force (WBSF) (Shackelford et al., 1994), which means that it is possible to improve meat tenderness through animals selected against *CAST*. This was evidenced by Leal-Gutiérrez et al. (2018), who found significantly higher tenderness in crossbreed animals with more than 80 % Angus blood in comparison with Brahman cattle. As expected, animals with higher genetic proportion of Brahman had higher frequency of alleles belonging to *CAST* genes, and the higher the proportion of Angus blood, the higher the allele frequency of the *CAPN* gene, with significant values of 3.91 kg vs. 4.45 kg of WBSF for animals with less than 20 % Angus blood. The researchers found four *CAST* gene markers (ARSUS-MARC116, Cast5, rs730723459 and rs210861835) significantly associated with meat tenderness. Furthermore, a variant of the *CAST* gene (g.98535683A>G SNP) that increases the meat toughness was found in the Pirenaica and Parda de la Montaña breeds (Calvo et al., 2014). Enriquez-Valencia et al. (2017) confirmed this effect later in Nelore breed (*Bos indicus*) and its crosses with *Bos taurus*. In particular, animals carrying this genetic variant have up to 22 % tougher meat than the other genotypes (Calvo et al., 2014; Iguácel et al., 2019).

Leal-Gutiérrez et al. (2015) found high relationship between the Cast5 marker and WHC in raw meat, but no relation with cooking losses (CL). In addition, there are many studies that evidence the relationship of *CAST* and *CAPN* genes with meat quality, mainly for tenderness (in Table 1, see WBSF for *CAST* and *CAPN1*). Thus, as proposed by Shackelford et al. (1994), a rapid genetic response could be achieved through the selection of animals against *CAST*, given its high heritability. However, more recent studies report that low *CAST* expression can influence higher residual feed intake, which can affect growth efficiency and muscle deposition, and may compromise meat quality (Novo et al., 2021; Zorzi et al., 2013).

These polymorphisms can be useful to the meat industry as genetic markers to identify tough meats and plan appropriate handling procedures for these carcasses. In animals carrying the variant, a long maturation period may be advisable in order to obtain more tender meat and reduce the variability of this parameter as demanded by consumers. Furthermore, it is possible to apply this knowledge to select animals, as it is being done by the Farmers Association of Parda de Montaña beef (ARAPARDA) in Spain, which works with the pre-selection of breeders based on the genetic marker (Iguácel et al., 2019).

The current understanding of the calpain-calpastatin system in bovine muscle goes beyond the simplistic view of *CAST* as merely a *CAPN* inhibitor. New insights suggest that calpastatin's isoforms, genetic

variability, and physiological conditions significantly modulate this interaction, affecting muscle physiology, growth, and meat quality. Further research is required to fully map how different *CAST* profiles influence muscle tissue under various conditions, both pre- and postmortem.

3.6. POMC (Proopiomelanocortin)

POMC is located in chromosome 11, and as well as *LEP* and *MC4R* (Table 1), act as appetite regulators. A SNP (288C>T) in the *POMC* gene was previously associated with average daily weight gain and final CW in Charolais cross steers (Buchanan et al., 2005; Deobald and Buchanan, 2011). With progress of research, this gene was also significantly associated with tenderness in Aberdeen Angus (Gill et al., 2010), muscle pH in the Piedmontese breed (Ribeca et al., 2014), marbling in Korean Hanwoo cattle (Seong and Kong, 2015) and with ultrasound in BFT and LMA in Chinese cattle (Liu et al., 2013).

These findings make the *POMC* a candidate QTL gene for production and quality traits and, if validated in other cattle breeds, this marker could be incorporated into breeding programs to improve the rate of progress in carcass traits and meat quality.

3.7. TG (Thyroglobulin)

Located in chromosome 14, *TG* gene encodes thyroglobulin, a precursor of the thyroid hormones, triiodothyronine (T3) and tetraiodothyronine (T4), implicated in the development of adipose cells (Ailhaud et al., 1992). It is often argued in the literature that *TG* is considered a candidate gene for QTLs because it is positively related to the marbling grade, mainly in meat from *Bos taurus* (Barendse et al., 2004; Casas et al., 2007; Gan et al., 2008; Hou et al., 2011).

Shin and Chung (2007), Gan et al. (2008) and Hou et al. (2011) found a positive association between CC genotype (C422T, G133C and T354C SNPs respectively) and meat marbling in several *Bos Taurus* breeds (Simmental, Angus, Hereford, Charolais, Limousin, Qinchuan, Luxi, Jinnan and Korean cattle). In the same way, research carried out with a population of purebred Angus and Shorthorn cattle, as well as yours crossbreeds including Charolais, Shaver, Limousin, Simmental, Santa Gertrudis and Red Composite, revealed a stronger association between TG5 SNP and marbling score (Barendse et al., 2004).

On the other hand, lack of association of *TG* gene with marbling was detected in several breeds, such as in purebred Piedmontese cattle (Ribeca et al., 2014), early weaned Simmental steers (Rincker et al., 2006), Limousin, Charolais, Friesian, Simmental, Angus, Hereford, Belgian Blue, Blonde d'Aquitaine and in Salers (Renand et al., 2007; Pannier et al., 2010). Ribeca et al. (2014) also observed that the C allele of 1696C>T SNP had an unfavorable effect in purebred Piedmontese breed, as it was associated with increased drip losses (DL) and a* in meat.

In Brahman cattle, the *TG* gene (X05380.1:g-422C>T SNP) was associated to BFT and LMA, but not to marbling (Casas et al., 2005; Carvalho et al., 2012). On the other hand, Royer et al. (2016) found strong association of 4 SNPs (rs110501231 C/T, rs133980693 G/A, 135, 059,985 C/T and rs378567477 T/C SNP) with marbling score for a Brahman population. While research programs have been developed in several countries for various breeds to detect QTLs for meat quality traits, the association between the detected QTL and the target traits appeared to be different according to the breed. Although these candidate genes may be useful in selected populations, they do not appear to have wide applicability in predicting marbling or IMF levels in a large cattle population.

3.8. DGAT1 (Diacylglycerol O-acyltransferase 1)

Located in chromosome 14, *DGAT1* gene encodes d*iacylglycerol O-acyltransferase 1*, an enzyme responsible for catalyzing the final step of triglyceride synthesis. It was first related to milk fat content (Grisart et al., 2002; Spelman et al., 2002). However, Thaller et al. (2003) suggested that *DGAT1* gene would also be associated with muscle fat deposition, once they observed very consistent results of IMF content for the KK genotype in the K232A SNP in German Holsten cattle. Similarly, Avilés et al. (2013) observed a positive association for BFT with K232A SNP, which was more expressive in the KK genotype than in KA, given that the KK homozygote was in higher frequency in the Charolais and Limousin animal groups, and KA in the Retinta breed. Li et al. (2013) observed association of K232A SNP with the degree of marbling in Angus, Simmental and Charolais, where animals with the heterozygous genotype KA displayed a higher IMF content than homozygous AA genotype. In contrast, Karolyi et al. (2012) did not find an effect of K232A SNP on IMF in Simmental breed.

3.9. Genes involved with fatty acid composition in meat

Consumers have become increasingly concerned about the relationship between diet and health. This consensus generates a demand for functional foods, as it is known that FA consumed through food have an important influence as risk factors in the development of certain diseases, as well as in their prevention. The consumer's interest lies not only in the amount of fat in the meat, but also in its composition, which is important for its quality, palatability, and nutritional value (Bhuiyan et al., 2018). Furthermore, fat content can positively influence the sensory attributes of beef, such as tenderness, flavor and juiciness. However, from a health perspective, consumers may consider the high fat content as undesirable, although meat is rich source of protein, vitamins and minerals (O'Quinn et al., 2012; Joo et al., 2013).

Pasture-fed animals produce leaner meat with a healthier FA profile, including conjugated linoleic acid (CLA), and the main sources for humans are beef and dairy products. However, this meat can be less tender and juicy and have a very distinctive flavor when compared to meat from grain-feed animals. It is therefore important to note that flavor preferences differ between cultures. Nevertheless, in addition to the importance of maintaining a balanced diet in terms of quantity and quality, it is essential to consume meat with a low proportion of n-6/n-3 FA and low levels of SFA to promote a healthy diet (Simopoulos, 2016; Santos et al., 2021; Pogorzelski et al., 2022).

In this sense, research has been undertaken with the intention to enhance FA profile in ruminant meat, aiming to increase concentrations of beneficial FA to improve human health and reduce FA that could have some detrimental effect (Scollan et al., 2006, 2014; Poli et al., 2019). Some *trans* FA have well-known adverse effects and the advice is to eliminate it from the human diet, together with the reduction of saturated FA (SFA), replacing them with a combination of PUFA and monounsaturated FA (MUFA). As a result, the risk of cardiovascular diseases can be reduced (Michas et al., 2014).

Investigations confirm the impact of several genes on meat FA content, especially those considered important from a healthcare point of view. Kim et al. (2017) verified a positive association of the *FASN* gene (g.16024A>G SNP) with C18:1, unsaturated FA (UFA) and MUFA content and a negative correlation with SFA in muscle from Hanwoo steers (Korean cattle). Oh et al. (2012a) observed that the AA genotype of the *FASN* gene (g.17924G>A) had high levels of SFA and low levels of MUFA, as well as a low marbling score. The higher MUFA and lower SFA values in meat of purebred Angus and Fleckvieh animals was significantly associated with the GG genotype of the g.17924A>G SNP in the *FASN* gene (Zhang et al., 2008; Bartoň et al., 2016).

Goszczynski et al. (2014) demonstrated the association of *LIPE* gene with MUFA and C18:1 content, as the AC genotype was 2.2 and 2.6 % higher than AA, respectively in meat of Angus-Hereford crossbreed. The *PPARG* gene encodes a key transcription factor involved in adipogenesis. Besides being related to tenderness and BFT (Fan et al., 2011), *PPARG* has been associated with higher values of MUFA and lower SFA in the GG and GT genotypes (NM_181,024.2:c.1523G>T SNP) in Hanwoo

cattle (Oh et al., 2012b). Other SNPs on the *PPARG* gene were also associated with FA composition in meat of Angus, Hereford and their crossbreeds (Goszczynski et al., 2016).

Orrù et al. (2011) detected four SNPs of the *LEP* gene associated with FA content of meat (g.3157A>G, g.3100C>T, g.978C>T and g.3257C>T). The G allele of g.3157A>G had the most influence, contributed to increasing MUFA (+1.1 %), C18:1 n-9 (+1.2 %) and to reducing C18:0 (-1.1 %) and all the short-medium chain SFA. In addition to marbling, Papaleo Mazzucco et al. (2016) observed that the TT genotype from the *LEP-E* SNP had a significantly higher content of C18:1 n-*9* and MUFA and lower SFA than CT, and the animals with the highest TT frequency were Angus, ½ Angus – ½ Hereford and Limousin sires × Angus-Hereford (F1). Similarly, *LEP-P* was also associated with C18:1 *n*-9 and MUFA, with higher levels for the CC (higher genotype frequency for ¾ Angus - ¼ Hereford, ¼ Angus - ¾ Hereford and Limousin sires × Angus-Hereford), while for C20:5 *n*-3 the highest levels were observed in TT genotype.

The *SCD* gene is involved in inserting a double bond between carbons 9 and 10 in the SFA chain, which affects the FA composition of membrane phospholipids, triglycerides and cholesterol esters. *SCD* is also an essential enzyme in the endogenous production of the isomer *cis-9, trans-11* of Conjugated Linoleic Acid (CLA), which is normally found in the fat of the milk and meat of ruminant animals and is considered beneficial to human health in several respects, as well (Bauman et al., 2000; Nelson and Cox, 2012). Research conducted on Simmental young bulls revealed that besides a significant increase in 0.93 % for C18:1 *n*-9, the g.10329C>T SNP of *SCD* gene affected the desaturation of FA into MUFA (Orrù et al., 2011).

Eight SNPs (G702A, C762T, T878C, T1905C, C3143T, A3351G, A3537G and A4736G) were identified in Japanese Black cattle from *SCD* gene (Taniguchi et al., 2004). The T878C SNP causes a substitution of valine to alanine in the coded protein, and this change has been associated with a higher MUFA percentage in IMF. This significant association has also been found in Japanese Black cattle (Ohsaki et al., 2009; Matsuhashi et al., 2011) Fleckvieh bulls (Bartoň et al., 2010), Brangus steers (Baeza et al., 2013) and Hanwoo steers (Kim et al., 2017).

4. Conclusions

The genes presented in this review are the most important so far associated with economically important traits, which have a significant impact on the meat industry. Although several genes have been found to be closely related to carcass and meat quality, there are still a large number of QTLs of economic interest to be identified and analyzed. The main challenges remain in fully understanding the complex interactions between these genes and their effects on economically important traits, especially in different cattle breeds and production system. Ongoing research into gene polymorphisms and their relationships with sensory and health-related attributes is essential to optimize selection strategies. Even though genetic analyses are costly and laborious, the use of molecular markers provides the increase of favorable genes in the population, and their advancement is becoming more concrete and acceptable as a measure of economic importance. Genetic markers and genomic tools offer great potential for improving beef quality. By integrating these findings into breeding strategies, it is possible to improve the beef production that best match and target both industry standards and consumer demands.

CRediT authorship contribution statement

Jakeline Vieira Romero: Writing – review & editing, Writing – original draft, Conceptualization. **José Luis Olleta:** Writing – review & editing. **Virginia Celia Resconi:** Writing – review & editing. **Pilar Santolaria:** Writing – review & editing, Project administration, Funding acquisition. **María del Mar Campo:** Writing – review & editing, Supervision, Project administration.

Declaration of competing interest

None.

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