

The role of the *CAPN1* gene in the genetic improvement of livestock meat production

Uloga *CAPN1* gena u genetskom unapređenju proizvodnje mesa domaćih životinja

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ABSTRACT

The development of molecular genetics has enabled direct analysis of the livestock genome, as well as the study of specific gene functions. Some studies have observed correlations between candidate genes and fattening and meat traits in livestock under specific production systems. However, in the Republic of Croatia, research on the association between specific genes (genotypes) and growth intensity or carcass quality in livestock is limited. This review summarizes previous findings on the association between the *CAPN1* gene and growth performance, carcass characteristics, and meat quality across various livestock species, aiming to consolidate current knowledge about the effects of specific genetic variants of the *CAPN1* gene and highlight their practical applications in breeding programs. Previous studies have confirmed associations between the *CAPN1* gene and growth intensity, carcass traits, and meat quality in cattle, pigs, and poultry; however, such studies are significantly less common in small ruminants. Genotyping of key *CAPN1* SNPs enables the early selection of animals that are better suited for meat tenderness, marbling, and growth, thereby improving production efficiency. Future research should focus on validating these associations in local breeds and production systems.

Keywords: *CAPN1*, growth intensity, carcass and meat characteristics, livestock

SAŽETAK

Razvojem molekularne genetike omogućena je izravna analiza genoma domaćih životinja, kao i proučavanje funkcije određenih gena. U pojedinim istraživanjima zapažena je povezanost kandidat gena s tovnim i mesnim odlikama domaćih životinja u specifičnim tehnologijama tova. Međutim, u Republici Hrvatskoj skroman je broj istraživanja o povezanosti određenih gena (genotipova) s intenzitetom rasta i kvalitetom trupova domaćih životinja. Ovaj pregledni rad ima za cilj prikazati rezultate dosadašnjih istraživanja o povezanosti *CAPN1* gena s rezultatima tova i odlikama trupa i mesa različitih vrsta domaćih životinja, prikazati trenutna saznanja o djelovanju pojedinih genetskih varijanti *CAPN1* gena te njihovu praktičnu primjenu u programima oplemenjivanja. Dosadašnja istraživanja potvrdila su povezanost *CAPN1* gena s intenzitetom rasta, odlikama trupa i mesa junadi, svinja i pilića, a znatno je manji broj ovakvih istraživanja u malih preživača. Buduća istraživanja trebala bi se usmjeriti na validaciju ovih povezanosti u domaćim pasminama i proizvodnim sustavima.

Ključne riječi: *CAPN1*, intenzitet rasta, odlike trupa i mesa, domaće životinje

INTRODUCTION

Meat production and consumption are key components of the agricultural and food industries in both the European Union (EU) and the Republic of Croatia. In recent decades, meat production in many European countries, including Croatia, has faced challenges such as a decline in the number of farms, reduced self-sufficiency, and a high dependence on imports. According to statistics (CAAF, 2024a; CAAF, 2024b), Croatia has experienced a decline in meat production, while consumption remains high, leading to decreased self-sufficiency, particularly in the cattle and pig breeding sectors. A similar trend is observed at the EU level, where production practices are shifting toward greater efficiency, while simultaneously raising concerns about environmental challenges associated with intensive farming. In this context, exploring new approaches in agricultural production is necessary to address issues related to self-sufficiency and sustainability within the meat production sector. Modern strategies aimed at enhancing meat production efficiency include genotyping animals to identify genetic determinants of high productivity and enabling targeted selection (Terry et al., 2020). However, successful application of these strategies requires consideration of genotype by environment (G×E) interactions, since the phenotypic effects of favorable single-nucleotide polymorphisms (SNPs) can vary across different environmental conditions. One promising avenue involves genetic improvement with a particular focus on the calpain gene (*CAPN1*), which plays a crucial role in determining meat quality, especially during the meat aging process (Koochmaraie, 1996; Li et al., 2013; Węglarz et al., 2020). The *CAPN1* gene encodes a family of enzymes responsible for the breakdown of proteins in meat, which directly affects the texture and tenderness of the meat (Page et al., 2002; Shi et al., 2011; Li et al., 2013). Research indicates that selection based on variations in the *CAPN1* gene can improve both quantity (Sun et al., 2013; Ardicli et al., 2017a; Ardicli et al., 2017b; Ardicli et al., 2019; Ropka-Molik et al., 2016) and quality (Ardicli et al., 2017a; Al-Shebany et al., 2025), making meat production more competitive and cost-effective. This paper provides an overview of the

current status of meat production and self-sufficiency in Croatia and the EU, with an emphasis on the challenges and opportunities that genomics and biotechnology offer for improving this sector. Furthermore, it discusses the potential of the *CAPN1* gene as a biotechnological tool to address key challenges in the livestock sector, including the enhancement of growth performance and meat quality, reduction of production costs, and improvement of self-sufficiency.

MEAT PRODUCTION IN THE REPUBLIC OF CROATIA

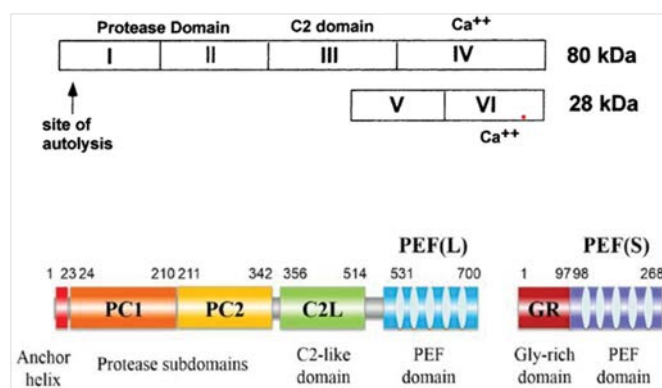
Meat production in the Republic of Croatia is undergoing significant structural changes. In the cattle sector, there has been a decline in the number of cows, which affects the overall production because most of the fattening calves come from dairy cows, while beef breeds constitute only 12.5% of the total cattle population (CAAF, 2024a). Croatia accounts for 0.6% of total EU beef production (43,000 tonnes), mostly focused on the domestic market, with self-sufficiency at 74%, meaning more than a quarter of the demand is met through imports. Due to the decline in domestic cow numbers and the shortage of calves, calves are imported from Hungary, Romania, the Czech Republic, and Slovakia to meet production needs (CAAF, 2024a). Producers are adapting genotypes and production technologies to meet increasing consumer demands (Berry, 2021) and to ensure economic viability (Konjačić et al., 2013). In the pig sector, production has also declined due to market instability and global issues such as African swine fever and the war in Ukraine, with Croatia accounting for 0.37% of EU pork production (125,000 tonnes) and a self-sufficiency rate of 52%, significantly below the EU average and countries like Poland (CAAF, 2024b; CBS, 2024). Poultry production has shown a slight but steady growth of 0.65% in 2023 (from 716,000 to 721,000 tonnes), dominated by broilers (84.4%), with turkey and duck accounting for 12.7% and 2.6%, respectively (CAAF, 2024c). Croatia is still not fully self-sufficient in poultry production, with 83% coverage of domestic demand compared to the EU average of

110%, while Poland reaches 335% (CAAF, 2024c). Poultry imports increased by 3.2%, while exports dropped by 41.4% in 2023 (CBS, 2024). Sheep and goat farming constitute about 10% of the total livestock population, with indigenous breeds dominating sheep farming (75%) and foreign breeds prevailing in goat farming (67.4%) (CAAF, 2024c). The EU recorded a 2.3% rise in sheep meat production, and Croatia increased its production by 12.2% to 6,112 tonnes. Croatia's self-sufficiency in sheep meat is about 81%, close to the EU average of 84%, while countries like Ireland have much higher rates, up to 756% (MAFFRC, 2024). Despite tradition and their importance for rural development, these sectors face challenges such as unfavorable climate, high feed costs, and market difficulties, requiring investments in modernization, market expansion, and the support of sustainable practices, including organic production and preservation of traditional breeds.

THE CALPAIN (CAPN1) GENE

Calpains are calcium-dependent cysteine proteases that regulate various essential cellular processes. They are classified into conventional calpains (μ -calpain – CAPN1 and m-calpain), which are active at physiological calcium concentrations, and non-typical calpains (e.g., CAPN3, CAPN9), which have specific functions in certain tissues. Their activity is tightly regulated by calcium levels and the endogenous inhibitor calpastatin (Suzuki et al., 2004). Calpain (CAPN1) consists of two subunits: a large catalytic subunit (~80 kDa) containing four distinct domains (I-V) and a smaller regulatory subunit (~30 kDa) referred to as V and VI (Sorimachi and Suzuki, 2001), which are outlined in Figure 1. The first domain (I) corresponds to the N-terminal region, which contains an anchor helix that is cleaved upon activation of the enzyme. The second domain (II) harbors the proteolytic active site, including the catalytic triad composed of cysteine, histidine, and asparagine, and is subdivided into two parts, IIa and IIb, resembling the structural organization of other cysteine proteases such as cathepsin B and L. Domain III adopts a β -sandwich fold and contributes to membrane association and regulation of the proteolytic function of calpain. Domain IV, known

as PEF(L), belongs to the penta-EF-hand protein family and is responsible for calcium binding and interaction with the small subunit through dimerization. In the smaller regulatory subunit, domain V is rich in glycine residues, which provides structural flexibility and makes it prone to self-cleavage during activation. Domain VI, a penta-EF-hand domain homologous to domain IV of the catalytic subunit (PEF(S)), mediates dimerization through EF-hand motif interactions, ensuring proper assembly and regulation of the calpain complex (InterPro, 2025).



(modified according to Perrin and Huttenlocher, 2002; InterPro, 2025)

Figure 1. Diagram of CAPN1 structure

CAPN1 exists in an inactive form, and an increase in intracellular Ca^{2+} triggers conformational changes enabling peptide bond hydrolysis in proteins. There are two main isoforms of calpain: μ -calpain (CAPN1), which requires low concentrations of calcium (3-50 μM), and m-calpain (CAPN2), which requires significantly higher concentrations (400-800 μM) for half-maximal activation (Goll et al., 2003). The regulation of CAPN1 activity is tightly controlled, involving the endogenous inhibitor calpastatin (CAST), a specific protein that binds to CAPN1 and prevents excessive activation and unwanted protein degradation. CAST is ubiquitously expressed across various cellular compartments and contains multiple domains that confer potent and specific inhibition of CAPN1 and CAPN2. Interestingly, CAPN2 can degrade CAST, adding a layer of regulatory control over the calpain-calpastatin proteolytic system (Sazontova et al., 1999). Besides calcium regulation, CAPN1 activity is also modulated by phosphorylation and interactions with membrane structures, with active CAPN1 predominantly

localized at the plasma membrane where precise spatial and temporal control of its proteolytic function is achieved (Perrin and Huttenlocher, 2002; Sorimachi and Ono, 2012). *CAPN1* mediates limited proteolysis rather than complete protein degradation; it selectively cleaves its substrates to modulate their function, stability, localization, and intracellular signaling. Targets of *CAPN1* include cytoskeletal proteins such as talin and vinculin, transcription factors including p53 and c-Fos, and various enzymes such as protein kinase C and caspases. Through these actions, *CAPN1* regulates numerous cellular processes, including migration, proliferation, differentiation, and apoptosis (Ujan et al., 2018). In the *post-mortem* context, *CAPN1* is the principal protease responsible for the degradation of myofibrillar proteins, contributing to meat tenderization during aging. The activity of *CAPN1* during this postmortem interval is tightly regulated by calpastatin inhibition and autolytic degradation of calpain itself (Sorimachi and Ono, 2012). This regulatory mechanism permits controlled proteolysis critical for meat quality post-slaughter. Collectively, the calpain-calpastatin system is a key regulator of proteolytic processes in muscle tissue, playing essential roles both in physiological cellular functions and in the *post-mortem* proteolytic events that influence the nutritional and physical properties of meat.

Table 1 shows the chromosomal location of the *CAPN1* gene in animal species, based on their reference

genomes. In most mammals, including cattle (*Bos taurus*), pigs (*Sus scrofa*), sheep (*Ovis aries*), and goats (*Capra hircus*), the *CAPN1* gene comprises 23 exons and 22 introns. In contrast, in chickens, this gene has one fewer exon and intron, and its overall length is considerably shorter compared to that in mammals (NCBI, 2025a). Although the core regions of the *CAPN1* gene are conserved, birds possess unique calpain variants whose sensitivity to calcium lies between μ - and m-types, known as μ /m-CAPN, designated as *CAPN1.5*. These molecular differences likely reflect adapted functions of calpain proteins in muscle physiology and *post-mortem* tissue degradation, which are key to understanding muscle plasticity and meat quality (Shu et al., 2015).

The expression and functionality of the *CAPN1* gene are strongly influenced by genetic variations, some of which, single-nucleotide polymorphisms (SNPs), are associated with economically important production traits. This gene has been linked to growth performance in several livestock species, including cattle (Miquel et al., 2009; Tait et al., 2014; Ardicli et al., 2017a; Ardicli et al., 2017b), poultry (Felício et al., 2013), and pigs (Ropka-Molik et al., 2016). However, such associations have not yet been confirmed in sheep and goats. Different SNPs within this gene can affect calpain activity, consequently altering the rate of myofibrillar degradation and influencing meat quality (Zhang et al., 2008) in commercial production systems.

Table 1. Location of the *CAPN1* gene in different animal species

Animal species	Location/Locus	Number of exons	Number of introns	Gene length	Source
Cattle (<i>Bos taurus</i>)	BTA29 NC_037356	23	22	27 518 bp	NCBI, 2025b
Pig (<i>Sus scrofa</i>)	SSC2 NC_010444	23	22	26 898 bp	NCBI, 2025c
Poultry (<i>Gallus gallus</i>)	GGA39 NW_024095974	22	21	15 178 bp	NCBI, 2025a
Sheep (<i>Ovis aries</i>)	OAR21 NC_056074	23	22	26 541 bp	NCBI, 2025d
Goat (<i>Capra hircus</i>)	CHI29 NC_030836	23	22	27 745 bp	NCBI, 2025e

Table 2 presents the locations of the *CAPN1* gene and its most frequently identified and studied SNPs across livestock species. Comparison of studies on SNPs in the *CAPN1* gene among different domestic animal species reveals the highest consistency in cattle. The SNP *CAPN1* 316 has been the most frequently investigated and is consistently associated with meat tenderness in meat breeds such as Angus, Hereford, Simmental, and others, confirming its value for marker-assisted selection. Other SNPs (*CAPN1* 530, 4751) have also been studied, covering various European and tropical breeds. In pigs and poultry, diverse SNPs have been examined, but results are heterogeneous and often breed-specific. Although associations with meat quality and growth exist, the lack of standardization limits wider application. Research on sheep and goats is limited but demonstrates genetic diversity and potential selective value of specific variants (e.g., *CAPN1* 471G>A in goats, *CAPN4* in sheep). Cattle currently represent the most stable model for applying *CAPN1* SNPs, while further standardized research is needed for other species to ensure reliability and practical applicability.

Association of CAPN1 gene polymorphisms with growth performance, carcass characteristics, and meat quality in cattle

Numerous studies have confirmed the association between the *CAPN1* gene and fattening performance as well as meat quality in beef production (Table 3). *CAPN1* 316 polymorphisms play an important role in cattle growth and fattening. Studies show that the GG genotype often results in better growth performance, with higher body weights, faster daily gains, and shorter fattening periods, especially in the Simmental breed (Ardicli et al., 2017a) as well as other breeds (Miquel et al., 2009; Tait et al., 2014). Selection goals in beef production include increasing growth intensity and optimizing carcass traits that directly influence economic viability (Santana et al., 2014; Raza et al., 2019, 2020). Konovalova et al. (2023) highlight that effects vary depending on sex. In Aberdeen Angus heifers, the CC genotype is associated with lower birth weight but higher weight at 6 months (compensatory growth), while the CG genotype shows the best post-weaning gains. In

bulls, genotype effects on growth were not statistically significant. Kusumawati et al. (2022) showed that the CC genotype in Kazakh White-headed cattle results in 6.9% higher body weight at 12 months and 7.4% greater daily gain compared to GG, along with improved carcass traits and a more favorable fatty acid composition. Bulls of the Kazakh Whiteheaded breed with the rare CC genotype of *CAPN1* 316 had higher body weight, daily gain, and greater protein and fat content in the muscle, along with lower water content, compared to the more common GG genotype (Plakhtukova et al., 2020). Couto et al. (2025) reported that the *CAPN* gene did not affect the growth of Nellore cattle. These differences in *CAPN1* genotype effects likely depend on genetic background, breed, sex, and management, which are crucial for the proper application of this genetic marker in selection programs. Regarding carcass traits and meat quality, the *CAPN1* 316 CC genotype in Aberdeen Angus is associated with significantly greater meat tenderness and better tenderness scores compared to CG and GG (Gill et al., 2009). This genotype is also linked to higher hindquarter weights (+5.33% compared to GG). In addition, Li et al. (2013) reported that the CC genotype is associated with a higher intramuscular fat content and greater marbling. These meat qualities have a positive effect on flavour and juiciness (Thompson, 2004). IMF content is also modulated by a livestock diet and management practices. Christensen et al. (2011) confirmed a clear correlation between fat content and physical properties of meat, most notably tenderness. Mengistie et al. (2021) state that meat tenderness and marbling score are the most economically important parameters in beef production. Corva et al. (2007) analyzed SNP 316 and SNP 530 and found that the CC genotype at SNP 316 produces 11-17% more tender meat, while the GG genotype at SNP 530 is associated with tougher meat (11.5% higher shear force). Curi et al. (2009) observed that the CT genotype at *CAPN1* 4751 is linked with significantly greater meat tenderness and a higher myofibrillar fragmentation index, whereas Avilés et al. (2015) did not find significant effects of *CAPN1* genotypes on tenderness in Charolais and Limousin breeds.

Table 2. The most commonly identified SNPs of the CAPN1 gene in different species

Animal Species	Chromosome	SNP	Breed / Line	Source
Cattle (<i>Bos taurus</i>)	BTA29	CAPN1 316; CAPN1 530	Piedmontese × Angus, Jersey × Limousin	Page et al., 2002
		CAPN1 316; CAPN1 530	Angus x Hereford x Limuzin	Corva et al., 2007
		CAPN1 316	Brangus and Angus	Miquel et al., 2009
		CAPN1 316	Aberdeen Angus	Gill et al., 2009
		CAPN1 4751	Nellore; Angus × Nellore; Rubia Gallega × Nellore; Canchim; Brangus; Braunvieh	Curi et al., 2009
		CAPN1 316	Angus; Hereford; Simmental; Limousin; Charolais	Li et al., 2013
		CAPN1 316; CAPN1 4751	¼ Angus, ¼ Hereford, ¼ Red Poll, ¼ Pinzgauer	Tait et al., 2014
		CAPN1 316	Simmental	Ardicli et al., 2017a
		CAPN1 316	Holstein	Ardicli et al., 2017b
		CAPN1 316	Kazakh Whiteheaded Cattle	Kusumawati et al., 2022
		CAPN1 316; CAPN1 530	Aberdeen Angus	Konovalova et al., 2023
Pig (<i>Sus scrofa</i>)	SSC2	g.157T>C	Duroc × (Landrace × Large White)	Gandolfi et al., 2011
		g.4479A>G; g.4526A>T; g.4529_4530delAG	Pietrain; Polish Landrace; Polish Large White; Puławska	Ropka-Molik et al., 2014
		g.1429G>A	Pietrain; Polish Landrace; Polish Large White; Puławska	Ropka-Molik et al., 2016
		rs81358667G > A	Iberian pig	Fernández-Barroso et al., 2020
Poultry (<i>Gallus gallus</i>)	GGA3	C2546T, G3535A, C7198A	Broilers	Zhang et al., 2008
		g.2456T>A; g.2460C>T; g.2554T>C; g.2629C>T	Broilers	Felicio et al., 2013
		A31563625G; C31563918T; C31566680T; A31570225C	Broilers	Sun et al., 2013
		G3535A; G9950A; A31563625G; C31563918T; C31566680T	Da-Heng broiler	Zhou et al., 2017
		C2546T; G3535A; C7198A	Qingyuan partridge (QY); Recessive White (RW)	Shu et al., 2015
		NM_001044672.1	Autochthonous breed Leung Hang Khao	Molee et al., 2018

Continued. Table 2

Animal Species	Chromosome	SNP	Breed / Line	Source
		NM_001044672.1	Slow-growing chicken	Kubota et al., 2019
		c.82.C>T	Ross-308	Abdul-Kareem and Raysan, 2022
Sheep (<i>Ovis aries</i>)	OAR14	NM_001044672.1	Zel	Dehnavi et al., 2012
		NM_001044672.1	Barki; Rahmani; Ossimi	Mahrous et al., 2016
	OAR29	c.82.C>T	Bandur rams	Kumar et al., 2016
		CAPN1 rs408790217 rs403953588 rs430307080 rs418818682	Santa Inês	Machado et al., 2020
OAR7	g.24962426T>C	New Zealand Romney	Fang et al., 2013; Talebi et al., 2022	
Goat (<i>Capra hircus</i>)	CHI29	5543 T/C, 5707 C/T, 4638 T/C, 4689 C/T, 6415 T/G, 6493 T/C, 6520 T/C, 6524 C/G, 6531 A/G 6533 T/G	Barbari, Beetal, Ganjam, Sirohi, Black Bengal, Osmanabadi and Malabari)	Singh et al., 2020
		CHI1 CHI16	CAPN7 CAPN2, CAPN8	Boer, Kalahari Red, Savanna
	CHI29	CAPN1 471 G>A	Iraqi goat	Al-Shebany et al., 2025

In summary, the CAPN1 316 SNP is a key genetic marker linking growth and production traits with meat quality. While the GG genotype favors faster growth and greater body weight, the CC genotype is associated with better meat quality, especially tenderness and intramuscular fat content. The CG genotype exhibits variable effects depending on breed, sex, and management conditions, which should be considered during selection.

Association of CAPN1 gene polymorphisms with growth performance, carcass characteristics, and meat quality in pigs

The CAPN1 gene, encoding the calpain-1 protease, is crucial for regulating various physiological processes in pigs. Located on SSC2, near the RELA gene (transcription factor p65) (Nonneman et al., 2011), certain CAPN1 variants influence growth intensity and meat quality

traits, especially tenderness (Goll et al., 2003; Sentandreu et al., 2002). Due to market demand for higher meat quality and economic importance, CAPN1 serves as a valuable molecular marker in pig breeding (Table 4). Gandolfi et al. (2011) found the g.157T>C polymorphism did not significantly affect calpain activity in Italian Duroc × (Landrace × Large White) crossbreds. However, pigs with the TC genotype had a larger average myofibrillar particle diameter (4.82 μm vs. 3.96 μm for TT) and higher redness (a*) values at early post mortem times (e.g., 6 hours: TC = 7.30, TT = 5.92; $P < 0.05$), indicating its potential use for selecting meat color. This SNP showed no significant effect on some physical and technological meat properties like pH, drip loss, shear force, and cooking loss. Ropka-Molik et al. (2014) identified seven CAPN1 polymorphisms in Pietrain, Polish Landrace, Polish Large White, and Puławska breeds.

Table 3. Association of the CAPN1 gene with growth performance, carcass characteristics and meat quality in cattle

SNP	Genotype frequency	Breed	Trait (Genotype + Effect)	Source
CAPN1 316	CC – 0.13 CG – 0.53 GG – 0.34	Angus x Hereford x Limousin	<ul style="list-style-type: none"> • CC genotype of SNP 316 has 11% and 17% lower WBSF values (7.86 kg) compared to CG (8.73 kg) and GG (9.21 kg) ($P < 0.05$) • GG genotype of SNP 530 has tougher meat (WBSF = 8.90 kg and 7.98 kg) ($P < 0.05$) • No polymorphism affected growth rate 	Corva et al., 2007
CAPN1 530	AA – 0.01 AG – 0.21 GG – 0.78			
CAPN1 316	CC – 0.05 CG – 0.35 GG – 0.61	Aberdeen Angus	<ul style="list-style-type: none"> • CC genotype had a lower tenderometer score (22.25 kPa, $P < 0.01$), more tender meat, and +5.33% larger hindquarter (75.67 kg, $P < 0.05$) vs GG (25.18 kPa, 71.84 kg) 	Gill et al., 2009
CAPN1 316	CC – 0.03 CG – 0.36 GG – 0.61	Brangus and Angus	<ul style="list-style-type: none"> • GG genotype has 46% tougher meat vs CC (WBSF – 6.29 kg; 4.41kg, $P < 0.05$) • GG genotype has +10 % higher ADG (GG – 0.76 kg/d; CG – 0.7 kg/d; CC – 0.69 kg/d, $P < 0.05$) • GG genotype has +10.8% and +4.7% higher final BW (GG – 399.23 kg; CG – 381.34 kg; CC – 360.23 kg, $P < 0.05$) 	Miquel et al., 2009
CAPN1 4751	TT – 0.802 CT – 0.188 CC – 0	Nellore, Angus × Nellore, Rubia Gallega × Nellore, Canchim, Brangus, Braunvieh	<ul style="list-style-type: none"> • CT genotype significantly improves tenderness (77.53 kgf/cm² vs. 69.47 kgf/cm²) and myofibrillar degradation ($P < 0.05$) • No significant effects on fat thickness, IMF, or muscle area • CC genotype not observed 	Curi et al., 2009
CAPN1 316	CC – 0 – 0.11 CG – 0.06 – 0.49 GG – 0.4 – 0.94	Angus, Hereford, Simmental, Limousin, Charolais	<ul style="list-style-type: none"> • CC genotype has +30% and +26% higher IMF (3.32 %) vs GC (2.31 %) and CC (2.38 %), $P < 0.05$ • CC genotype has +26% and +22% higher marbling score (2.9) vs GC (2.31) and CC (2.38), $P < 0.05$ 	Li et al., 2013
CAPN1 316	not published	Limousin, Charolais, Retina	<ul style="list-style-type: none"> • no association found between this gene and beef tenderness 	Aviles et al., 2015
CAPN1 316	CC – 0.06 CG – 0.43 GG – 0.51	Holstein	<ul style="list-style-type: none"> • GG genotype shows better growth performance (higher BW, ADG, shorter fattening period) ($P < 0.05$) • BW: GG – 448.65 kg; CG – 445.12 kg; GG – 405.34 kg 	Ardicli et al., 2017b
CAPN1 316	CC – 0 CG – 0.15 GG – 0.85	Simmental	<ul style="list-style-type: none"> • GG genotype shows better growth performance, $P < 0.05$ • GG shows higher BW (623,5 kg), ADG (1.52 kg/d) and shorter fattening period (259.8 d) vs. CG (575 kg; 1.35 kg/d; 311.7 days, $P < 0.05$) 	Ardicli et al., 2017a

Continued. Table 3

SNP	Genotype frequency	Breed	Trait (Genotype + Effect)	Source
CAPN1 316	CC – 0.03 – 0.06 CG – 0.13 – 0.22 GG – 0.72 – 0.81	Kazakh Whiteheaded Cattle	<ul style="list-style-type: none"> • bulls with the CC genotype have higher BW (379.2 kg, $P < 0.05$), ADG (948.4 g/day, $P < 0.01$), more protein (22.45%, $P < 0.01$) and fat (2.89%, $P < 0.05$) in MLD muscle, and lower water content (73.47%, $P < 0.05$) vs GG • GG: BW – 359.9 kg; ADG – 883.2 g/day; protein – 21.12%; fat – 2.38%; water content – 75.02% 	Plakhtukova et al., 2020
CAPN1 316	CC – 0.06 CG – 0.81 GG – 0.13	Kazakh Whiteheaded Cattle	<ul style="list-style-type: none"> • CC genotype had +6.9% BW (374 kg) at 12 months compared to GG (349 kg), $P < 0.05$ • CC had +7.4% ADG (948.2 g/day), and +9.1% dressing percentage vs GG (883 g/day), $P < 0.01$ • animals with the CC genotype exhibited the highest preslaughter live weight (380.2 kg), whereas CG individuals averaged 371.3 kg and GG animals 362.3 kg, $P < 0.05$ • the same pattern was observed for slaughter weight - CC: 219.6 kg, CG: 209.9 kg, GG: 198.6 kg, $P < 0.05$ 	Kusumawati et al., 2022
CAPN1 316	CC – 0.078 CG – 0.406 GG – 0.516	Aberdeen Angus (heifers)	<ul style="list-style-type: none"> • CC genotype heifers had lower birth weight (2.89-3.38 kg) compared to GC/GG ($P < 0.05$) • CC genotype had +8.11 to 11.5 kg higher BW at 6 months of age (CC – 176.14 kg; CG – 164.64 kg; GG -168.03 kg) • CC had lower post-weaning gain (740 g/day) compared to GC (800 g/day) and GG (790 g/day) 	Konovalova et al., 2023

SNP – single nucleotide polymorphism; WBSF – Warner-Bratzler shear force; ADG – average daily gain; BW – body weigh; IMF – intramuscular fat; MLD – *Musculus longissimus dorsi*

Five were located in introns, one in the 3' untranslated region, and one in the promoter region. In a population of 451 gilts from four pig breeds, deviations from the Hardy-Weinberg equilibrium were observed for the g.25676C>T mutation (all breeds), g.1429G>A (Puławska), and g.4479A>G; g.4526A>T; g. 4529_4530delAG) (Polish Large White), indicating possible selection pressure. In a larger study of 860 pigs across five breeds (Polish Landrace, Polish Large White, Pietrain, Duroc, and Puławska), the g.1429G>A polymorphism in the third intron significantly influenced production and carcass traits (Ropka-Molik et al., 2016).

The GG genotype was linked to shorter fattening periods (79.1 days) and younger slaughter age (166.6 days), but also higher fat deposition with thicker backfat (1.51 cm vs. 1.40-1.46 cm in GA/AA). The GA and AA genotypes had greater ham weight (around 9.2 kg vs. 9.05 kg for GG), larger loin eye areas (up to 54.0 cm² in AA vs. 52.6 cm² in GG), and higher muscle percentages (61.2% vs. 60.6%), demonstrating the A allele's positive effect on musculature and fat reduction. These findings highlight the g.1429G>A SNP's potential as a breeding marker for improved muscle mass, reduced fat, and optimized fattening duration. Fernández-Barroso et al. (2020)

Table 4. Association of the CAPN1 gene with growth performance, carcass characteristics and meat quality in pigs

SNP	Genotype frequency	Breed	Trait (Genotype + Effect)	Source
g.157T>C	CC - 0 CT - 0.34 TT - 0.66	Duroc × (Landrace × Large White)	<ul style="list-style-type: none"> • effect on meat color • CT genotype – higher meat redness (a*) at 1 (9.71), 4,5 (7,81) and 6 h (7,30) post mortem vs TT (8.06; 6.28; 5.92), (P < 0.05) • no effect on meat pH, drip loss, shear force, and cooking loss 	Gandolfi et al., 2011
g.1429G>A	GG - 0.07 GA - 0.30 AA - 0.63	Pietrain, Pulawska, Duroc, PLW	<ul style="list-style-type: none"> • GG – fastest growth (889.3 g/day), shortest fattening (79.1 days), lowest slaughter age (166.6 days), thickest backfat (1.51 cm), smallest loin area (52.6 cm²), lowest lean % (60.6%), lowest ham weight (9.05 kg) (P < 0.05) • GA – best balance: highest ham weight (9.23 kg), thinnest backfat (1.40 cm), highest lean % (61.2%), highest primal cuts weight (23.9 kg), high ADG (886.8 g/day), moderate fattening (82.2 days) • AA – largest loin area (54.0 cm², P < 0.01), high muscularity, good ham weight (9.20 kg), lean (61.2%), but slowest growth (874.3 g/day), longest fattening (84.4 days), oldest slaughter age (174.8 days) 	Ropka-Molik et al., 2016
rs81358667G > A		Iberian pig	<ul style="list-style-type: none"> • associated with meat tenderness • the influence of CAPN1 allelic variants has not been investigated 	Fernández-Barroso et al., 2020

ADG – average daily gain

reported that in Iberian pigs, the SNP rs81358667G>A significantly influenced cooked meat Shear force, reinforcing CAPN1's role in meat tenderness and its utility in selection programs.

In summary, the TC genotype of SNP g.157T>C is associated with improved meat color in Duroc × Landrace × Large White crosses. The GG and GA genotypes of SNP g.1429G>A are linked to faster growth, shorter fattening periods, thicker backfat, and better muscle development in Pietrain, Puławska, and Duroc breeds. These genotypes are valuable markers for enhancing meat quality and growth performance. Research is also exploring CAPN1 interactions with other genes like IGF2 and MSTN for further improvement possibilities.

Association of CAPN1 gene polymorphisms with growth performance, carcass characteristics, and meat quality in poultry

The CAPN1 gene plays a significant role in poultry growth performance and meat quality, with multiple SNP variants demonstrating associations with important production traits across diverse breeds. Due to rising global demand for poultry meat, breeding programs focus not only on growth rates and carcass yield but increasingly on qualitative traits such as tenderness, juiciness, and marbling, where CAPN1 polymorphisms offer promising markers. Felício et al. (2013) reported the g.2554T>C SNP in broilers, where the C allele increased meat lightness and leg muscle weight. Sun et al. (2013) found that the TT genotype at C31566680T significantly improved live and carcass weights (+8.5% and +6.1%) and muscle yields compared to CC and CT genotypes. Shu et al. (2015) identified SNP G3535A as crucial: in Qingyuan Partridge chickens, AA genotypes showed 14% lower shear force and 9% higher intramuscular fat versus GG, indicating enhanced tenderness and juiciness. However, Zhou et al. (2017) found breed-dependent differences in Da-Heng broilers, where the GG genotype had higher body weight but also increased fat and lower meat quality compared to AA, illustrating the inherent trade-offs breeders face between production and quality traits. Zhou et al. (2017) further identified SNPs C7198A, G7324A, and G9950A

with distinct effects on growth and carcass composition, including fat deposition and muscle mass, emphasizing the complex genetic regulation at this locus. While some genotypes favored better growth performance, they often showed compromised meat quality, highlighting the importance of balanced selection strategies. Molle et al. (2018) linked genotypes in indigenous Leung Hang Khao chickens to differences in meat firmness and drip loss, with the A2A2 genotype associated with firmer but less tender meat. Kubota et al. (2019) studied slow-growing broilers, finding genotype-related variation in early body weight and muscle distribution. Genotype BB had the highest live weight and thigh muscle mass, while AB excelled in breast muscle mass. In Ross-308 broilers, Abdul-Kareem and Raysan (2022) demonstrated that at the c.82.C>T locus, CC genotype birds had superior water-holding capacity, flavor, juiciness, and tenderness compared to TT genotypes. Recent research by Bungsrissawat et al. (2024) on Betong chickens aligned with these findings, showing the BB genotype correlated with increased meat lightness, possibly influencing consumer preference.

Nevertheless, not all studies report uniform effects. Differences among breed and genotype interactions, sample sizes, and phenotyping methodologies complicate direct comparisons. Some favorable alleles occur at low frequencies within populations, limiting their immediate applicability. Moreover, the genetic influence of CAPN1 often involves trade-offs between enhancing growth traits and maintaining or improving meat quality, necessitating integrative breeding strategies that consider both market demands and genetic diversity.

Future research should focus on validating CAPN1 markers across diverse genetic backgrounds, exploring interactions with other growth-related genes such as MSTN and IGF1, and standardizing phenotypic assessments. Combining molecular insights from CAPN1 polymorphisms with traditional selection could optimize genetic gains, helping poultry producers meet increasing global demand for high-quality meat efficiently and sustainably.

Table 5. Association of CAPN1 Gene SNPs with growth performance, carcass characteristics, and meat quality in poultry

SNP	Genotype frequency	Breed / Hybrids	Trait (Genotype + Effect)	Source
g.2554T>C	TT - 0.302 TC - 0.463 CC - 0.234	Broilers	<ul style="list-style-type: none"> Meat lightness (L*), redness (a*), leg weight C allele: +0.39 L*, increased leg and drumstick weight 	Felício et al., 2013
C31566680T	CC - 0.72 CT - 0.25 TT - 0.02	Broilers	<ul style="list-style-type: none"> TT genotype: +8.5% and +4.2% higher LW ($P < 0.05$) vs. CC and CT LW: TT - 1.28 kg; CT - 1.23 kg; CC - 1.185 kg TT genotype: +6.1% and higher CW (1.05 kg) vs. CC (0.99 kg), $P < 0.01$ CT: +4.8% breast meat and +5.4% leg and drumstick weight vs. CC Breast meat weight: CT - 131.68 g; CC - 125.22 g Thigh weight: CT - 72.68g; CC - 68.95g 	Sun et al., 2013
G3535A	AA - 0.74 GA - 0.24 GG - 0.02 AA - 0.08 GA - 0.40 GG - 0.52	Qingyuan Partridge (QY) Recessive White (RW)	<ul style="list-style-type: none"> AA: 14% lower WBSF (2.37 kg), 2% less water loss (0.30 %), 9% higher IMF (1.51 %) vs. GG ($P < 0.05$) GG: shear force - 2.46 kg; water loss - 0.31 %; IMF -1.42 % GA: shear force - 2,32 kg; water loss - 0.29 %; IMF -1.44 % AA: 5-7% better results than GA for all traits 	Shu et al., 2015
G3535A	AA - 0.28 GA - 0.532 GG - 0.26	Da-Heng broilers	<ul style="list-style-type: none"> GG: best overall trait performance GG had greater subcutaneous fat thickness (4.22 mm) and meat firmness (2.81 kgN), which were 27.5% and 14.2% higher than AA (3.31 mm for subcutaneous fat thickness; 2.46 kgN for meat firmness) ($P < 0.05$) higher water loss in GG (74.72%) compared to AA (70.83%) ($P < 0.01$) 	Zhou et al., 2017
C7198A	AA - 0.109 CA - 0.278 CC - 0.617	Da-Heng broilers	<ul style="list-style-type: none"> AA: highest values for FW (2589.96 g), CW (2389.15 g), and breast muscle weight ($P > 0.05$) CC genotype had a significantly higher meat yield (84.22%) than AA (82.15%), with a 2.5% difference ($P < 0.05$) the abdominal fat weight in CC (44.21 g) was 106% higher than in AA (21.44 g) AA genotype had the lowest abdominal fat percentage (0.77%) ($P < 0.01$) and significantly lower water loss (72.76%) ($P < 0.05$), indicating that AC and CC genotypes result in lower meat quality 	Zhou et al., 2017
G7324A	AA - 0.113 GA - 0.415 GG - 0.463	Da-Heng broilers	<ul style="list-style-type: none"> AA and AG genotypes had significantly higher FW (~2640 g) than GG (2205.52 g), a 16.6% difference ($P < 0.05$), and significantly higher CW (~18%, $P < 0.01$) 	Zhou et al., 2017

Continued. Table 5

SNP	Genotype frequency	Breed / Hybrids	Trait (Genotype + Effect)	Source
G9950A	AA - 0.099 GA - 0.612 GG - 0.291	Da-Heng broilers	<ul style="list-style-type: none"> • GG genotype had significantly higher FW (2768.23 g), CW (2558.58 g), and breast muscle weight (167.02 g) compared to AG and AA ($P < 0.01$) • no significant differences were found in abdominal fat, tenderness, or water loss 	Zhou et al., 2017
NC_006090.1	A1A1 - 0.59 A1A2 - 0.15 A2A2 - 0.26	Indigenous Leung Hang Khao	<ul style="list-style-type: none"> • A1A2: +2.4% body weight (1479 g) vs. A1A1 (1449 g, $P > 0.05$) • A2A2: +6.7% shear force vs. A1A1 ($P < 0.05$), A2 allele contributes to increased firmness (reduced tenderness). • A2A2: +4.7% drip loss (2.69%) vs. A1A1 and A1A2 (2.57%) ($P > 0.05$) 	Molee et al., 2018
NC_006090.1	AA - 0.448 AB - 0.177 BB - 0.376	Slow-growing broilers	<ul style="list-style-type: none"> • BB genotype led to the highest LW (755.11 g), up to 3% more than AA (733.02 g) and over 5% more than AB (721.46 g) in early weeks ($P < 0.05$) • AB: highest average breast muscle mass (51.33 g), which is ~1.8% more than AA (50.43 g) and ~7.4% more than BB (47.54 g), $P < 0.05$ • BB had the highest thigh muscle mass (47.04 g), compared to AB (46.07 g) and AA (45.57 g), a 3.2% difference favoring BB for thigh weight ($P > 0.05$) 	Kubota et al., 2019
c.82.C>T	CC - 0.52 CT - 0.34 TT - 0.14	Ross-308 broilers	<ul style="list-style-type: none"> • CC was superior in WHC (0,25) vs CT (0,43) and TT genotype (0,71) ($P < 0.01$) • CC: best sensory traits (flavor $P < 0.05$; juiciness, tenderness ($P < 0.01$)) • TT: lowest scores for all sensory traits • no differences in meat color (CC showed higher color values around 10.33-15.61%) 	Abdul-Kareem and Raysan, 2022
not reported	AA - 0.48 AB - 0.343 BB - 0.608	Betong chickens	<ul style="list-style-type: none"> • BB: greater meat lightness (L^*) 	Bungsrissawat et al., 2024

LW - live weight; FW - final weight; CW - carcass weight; WHC - water holding capacity; IMF - intramuscular fat; WBSF - Warner-Bratzler shear force.

Association of CAPN1 gene polymorphisms with growth performance, carcass characteristics, and meat quality in sheep and goats

Research on candidate genes such as CAST (Nassiry et al., 2006), MSTN (Thepa et al., 2024), and DGAT1 (Vrbanić et al., 2020; Khan et al., 2021) related to production traits is abundant, but studies on the CAPN1 gene remain limited, especially in sheep (Zhang et al., 2013). However, some evidence suggests CAPN1 acts as a key regulator of physiological processes in sheep

and goats, with certain variants significantly affecting production traits and meat quality. Calpains are critical for *post-mortem* tenderization by degrading muscle proteins (Huff-Lonergan et al., 1996). Most research focuses on CAPN1 variants linked to growth traits (body weight, average daily gain) and meat tenderness (Kumar et al., 2016; Mahrous et al., 2016). Meat quality traits such as color, intramuscular fat (marbling), and water-holding capacity are important to consumers, and genetic improvements in these should be prioritized across meat

types. However, genetic variation in candidate genes in sheep remains insufficiently explored (Grochowska et al., 2017). Many studies suffer from small sample sizes, limited breed diversity, and a lack of standardized protocols for phenotyping and genotyping, which affects their reliability and comparability. Therefore, larger, varied sheep breeds and standardized methods are needed. The *CAPN1* small subunit (*CAPNS1* or *CAPN4*) has been extensively studied in sheep for its impact on growth and meat quality. Dehnavi et al. (2012) identified two SSCP variants (AA and AB) in the *CAPN4* gene fragment in Iranian Zel sheep, with the AB genotype associated with significantly higher body weight (30.37 kg vs. 27.91 kg for AA; $P < 0.01$), suggesting an additive effect of the B allele that may promote muscle growth through enhanced proteolytic activity. Similarly, Mahrous et al. (2016) reported a C>T substitution (SNP 44) in Egyptian sheep breeds linked to increased body weight, final weight, and daily gain, with the TT genotype demonstrating superior performance, possibly due to improved protein turnover regulation. This SNP is considered a valuable molecular marker for breeding programs targeting better growth. In Polish Merino sheep, Grochowska et al. (2017) associated the same *CAPN4* gene region with intramuscular fat, water loss, and meat lightness, traits crucial for meat quality and consumer appeal, as marbling enhances juiciness and flavor while lower water loss improves texture and shelf life. Machado et al. (2020) identified 45 variants in the *CAPN1* gene in Santa Inês sheep, mostly intronic but potentially causal for growth and carcass traits. Variants like rs408790217 were linked to increased height and reduced fat thickness, desirable for lean carcasses, while others (rs403953588, rs430307080) were related to increased muscle mass, benefiting yield and quality. Conversely, Kumar et al. (2016), Fang et al. (2013), and Valencia et al. (2022) found no significant associations between some *CAPN1* variants and growth traits in various sheep breeds (Bandur, New Zealand Romney, Colombian Hair Sheep). Still, TT genotypes tended to show better growth metrics, suggesting subtle or breed-specific genetic effects that require larger and more diverse populations for reliable detection.

Research on the *CAPN1* gene in goats is limited, but it indicates its potential role in meat quality. Several new SNPs, particularly in intron 17 and exons 9 and 14 of *CAPN1*, including the non-synonymous 5707 C→T mutation in exon 9, may affect protein function and influence meat tenderness, offering valuable markers for selection in Indian goat breeds (Singh et al., 2020). These genetic variations have significant potential for use in selection programs aimed at improving meat quality in various Indian goat breeds (Singh et al., 2020). In the study by Ncube et al. (2022) conducted on three South African goat breeds, Boer, Kalahari Red, and Savanna, SNPs were identified on chromosome *CHI1* (*CAPN7*) and chromosome *CHI16* (*CAPN2* and *CAPN8*) that were significantly associated with carcass traits such as hot and cold carcass weight and subcutaneous fat thickness. Although *CAPN1* was not among the identified genes, the presence of significant associations with other calpain genes confirms the importance of the calpain system in the genetic regulation of meat quality in goats. Al-Shebany et al. (2025) reported that in Iraqi goats, *CAPN1* variants at position 471 showed genotype-related differences in meat physical traits. Animals with the AA genotype showed higher drip loss in both thigh and back cuts, while the GA genotype was associated with increased cooking loss, especially in the thigh and shoulder. No significant differences were observed in thawing loss or water holding capacity in the thigh. These findings suggest that AA and GA genotypes may negatively affect water retention in meat and could serve as genetic markers for meat quality selection. Sensory evaluation revealed limited effects of *CAPN1* polymorphisms on meat quality. The GG genotype scored better on juiciness and flavour in specific cuts, but no significant differences in tenderness or overall acceptability were observed across genotypes. This suggests *CAPN1* variation influences certain sensory traits but is not a key determinant of overall meat sensory quality.

Previous studies have investigated the role of *CAPN1* and *CAPN4* gene polymorphisms in sheep and goats, aiming to identify genetic markers associated with growth traits and meat quality. These studies suggest

Table 6. Effect of Significant CAPN1 Gene SNPs on growth performance, carcass characteristics, and meat quality

SNP / Variant	Genotype frequency	Breed	Trait (Genotype + Effect)	Source
CAPN4 nt 44 C>T	CC - 0,50 CT - 0,50 TT - 0	Barki	<ul style="list-style-type: none"> • TT genotype: +11.85% and +8.40% birth weight (3.87 kg) vs. CC (3.46 kg) and CT (3.57 kg) • TT: +21.18% and +11.23% BW (59.44 kg) vs. CC (49.05 kg) and CT (53.44 kg) 	Mahrous et al., 2016
	CC - 0,37 CT - 0,44 TT - 0,19	Rahmani	<ul style="list-style-type: none"> • TT: +19.54% and +7.52% daily gain (128.67 g/day) vs. CC (107.64 g/day) and CT (119.67 g/day) 	
	CC - 1 CT - 0 TT - 0	Ossimi	<ul style="list-style-type: none"> • CT genotype showed moderate advantages over CC, with differences of: + 3.18 % for birth weight, + 8.95 % for FW, and + 11.18 % for daily gain 	
rs408790217		Santa Inês sheep	<ul style="list-style-type: none"> • multiple effects on withers and rump height, and reduced fat thickness 	Machado et al., 2020
rs403953588 rs430307080		Santa Inês sheep	<ul style="list-style-type: none"> • associated with increased muscle mass (loin eye area) 	Machado et al., 2020
rs418818682		Santa Inês sheep	<ul style="list-style-type: none"> • associated with traits such as post-weaning body weight, fat thickness, and final weight 	Machado et al., 2020
A 192 bp (exons 5 and 6)	AA - 0,672 AB - 0,295 BB - 0,033	Bandur rams	<ul style="list-style-type: none"> • no significant associations between CAPN1 loci polymorphisms and growth traits (BW, FW, ADG) were observed 	Kumar et al., 2016
CAPN1 (471 G>A)	not reported	Iraqi goat breed	<ul style="list-style-type: none"> • AA genotype (7.45 %) outperformed GA (5.52 %) and GG (5.49 %) in drip loss ($P \geq 0.05$) in thigh • the GA genotype (41.46 %) outperformed GG (44.72%) and AA (41.64 %) in the cooking loss ratio ($P \geq 0.05$) in the thigh • GA and AA genotypes showed higher values compared to GG (GG: 39.91%, GA: 43.93%, AA: 44.85 %) in shoulder cut in cooking loss ($P \geq 0.05$) • no significant differences in the thawing loss ratio and WHC in the thigh cut • AA genotype (6.83 %) outperformed GA (5.53 %) and GG (5.54 %) in the drip loss ratio in back cut ($P \geq 0.05$) 	Al-Shebany et al., 2025

ADG – average daily gain; BW – body weight; FW – final weight; WHC - water holding capacity

CONCLUSION

that specific genotypes may influence body weight, daily gain, fat deposition, and water-holding capacity in a breed-dependent manner. Although the number of studies remains limited, the findings indicate that certain CAPN1 and CAPN4 polymorphisms may hold potential as selection markers in small ruminants. However, further research with larger sample sizes and standardized phenotypic evaluation is needed to confirm their practical applicability in breeding programs.

The CAPN1 gene has proven to be an important molecular marker associated with numerous production and quality traits of meat in various domestic animal species. Research on cattle, pigs, poultry, sheep, and goats indicates that polymorphisms in this gene can significantly affect growth rate and meat quality. The most extensive research has been conducted in cattle, where CAPN1 gene variants have been linked to improved tenderness and marbling of the meat, as well as increased growth

rate and shorter fattening duration. Although studies in small ruminants are still in the preliminary phase, current evidence in cattle suggests that the *CAPN1* gene could also be included in selection programs to improve production traits. Allelic variants of the *CAPN1* gene show significant effects on production and quality traits in sheep and goats. As confirmed by numerous studies, understanding these genetic influences can contribute to improving breeding programs for these species. The application of molecular markers in selection programs is becoming an increasingly important strategy for enhancing the efficiency and quality of production. Given the strong economic importance of meat quality traits, molecular markers like *CAPN1* have gained wide recognition, yet their practical adoption in routine breeding programmes is still restricted in numerous species and regions. Future research should prioritize the validation of these associations across diverse breeds, genetic backgrounds, feeding systems, climatic conditions, and other production environments, with the aim of developing livestock populations that are both genetically superior and economically efficient.

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