# Ruminant meat tenderness. I. Overview of factors affecting meat tenderness. Review

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**Abstract**

The aim of the present article was to make an overview of tenderness of meat from large and small ruminants and to outline some factors that affect it. At present, the tenderness of meat is one of its most important quality traits. It is assumed that tenderness along with juiciness are perhaps the essential and most relevant criteria that determine the consumers' acceptance of the product. If the meat is tough and does not meet consumers' demands, it will not be bought by them and vice versa, tender meat will satisfy consumers and will result in repeated purchase of the same product. What is more, surveys indicate that people tend to pay more for more tender meat. The article is focused on some factors, e.g. the calpain system, *rigor mortis*, animal breed and sex, muscle fibre type, fat and connective tissue content and their impact on meat tenderness. The literature overview demonstrates that meat tenderness varies within a broad range dependent on numerous factors. Future efforts have to be targeted to factors affecting meat tenderness variations. The restriction of impact of factors leading to altered met tenderness becomes a main concern in many meat processing enterprises.

***Key words:*** meat tenderness of ruminants; factors influencing tenderness

## Introduction

The meat tenderness is a measure of the resistance exerted during cutting, mincing, chewing (Hwang et al., 2002). Tenderisation is a term describing the events associated with meat tenderness improvement, which could be determined only after the *rigor mortis* resolution. Meat tenderisation occurs after proteolysis of muscle proteins. The evaluation of meat tenderness could be done either instrumentally or by sensory panel groups. Among commonly used instrumental methods are units based on shear force tests. The sensory approach uses a trained group of people that continuously improve their accuracy in assessment of certain meat properties (Kaić and Žgur, 2017). The tenderness is a primary meat quality trait that guarantees consumers' satisfaction and would contribute to a repeated purchase (Warner et al., 2021; Gagaoua and Picard, 2020; Bekhit et al., 2014; Ouali et al., 2013; Maltin et al., 2003). Meat tenderness is perhaps the most important factor determining consumption contentment and therefore, an essential challenge to acceptability of meat purchased by consumers (Matney et al., 2021; Zhu et al., 2021; Miller, 2020; Holloway and Wu, 2019; O'Quinn et al., 2018; Miller et al., 2001). O'Quinn et al. (2018) found out that tenderness rated as unsatisfactory by consumers would likely result in unacceptable taste for 69% of them. According to some authors, meat tenderness depends on the amount and quality of connective tissue (Leal-Gutierrez et al., 2018; Kaić and Žgur, 2017; Chang, 2012; Houbak et al., 2008; Huidobro et al., 2005; Koohmaraie et al., 2002). In the view of others, it depended on meat marbling (Leal-Gutierrez et al., 2018; Kaić and Žgur, 2017; Houbak et al., 2008) while thirds affirm that sarcomere length influences meat tenderness (Kaić and Žgur, 2017; Chang, 2012; Maltin et al., 2003; Koohmaraie et al., 2002; Morton et al., 1999). There are researchers that consider the myofibrillar protein degradation contributes to meat tenderisation (Leal-Gutierrez et al., 2018; Kaić and Žgur, 2017; Houbak et al., 2008; Maltin et al., 2003) as well as teams that have observed a breed influence to meat tenderness (Huidobro et al., 2005; Maltin et al., 2003).

The presented data make clear that tenderness as a meat quality trait varies within a broad range and depends on numerous factors (Polkinghorne et al., 2008). With this regard, the solution to the problem with meat tenderness variation is a main meat industry priority due to consumers' demands (Gagaoua et al., 2018; Marais, 2007). It is reported that the improvement of carcass meat tenderness will lead to greater interest in consumers, higher price and more frequent consumption (Santos et al., 2021; Warner et al., 2021; Felderhof et al., 2020; Kaić and Žgur, 2017; Špehar et al., 2008; Platter et al., 2005; Lusk et al., 2001). The aim of the present article was to make an overview of the literature on ruminant meat tenderness and to analyse the more important factors that affect it.

## Muscles and their structure

The meat sold on retail markets is produced from skeletal muscles of animals (Gunenc, 2007). Animal muscles (Figure 1) are wrapped in a dense connective tissue sheath – epimysium, whose ends blend with the tendon inserted into skeleton bones (Jorgenson et al., 2020; Marinova and Popova, 2011; Gunenc, 2007). Groups of muscle bundles radiate into the muscles surrounded by an envelope called perimysium. Muscle bundles are the main structural and functional units of muscles. The number of muscle fibres within a bundle varies from 30 to 80 (Marinova and Popova, 2011). The individual muscle fibres are enveloped in a connective tissue sheath called endomysium (Marinova and Popova, 2011; Gunenc, 2007). Muscle fibres are composed by myofibrils (Figure 2) – the main structural and functional unit of muscle fibres. Each muscle fibre contains approximately 1000 myofibrils which realise the contraction and re-

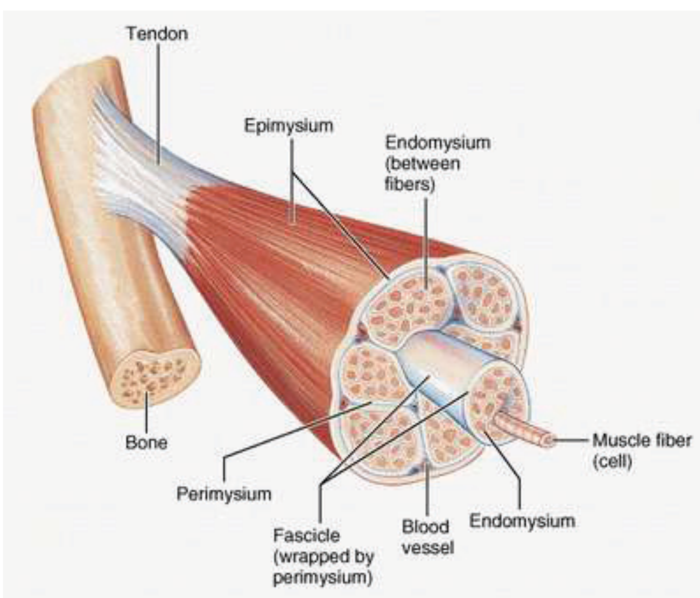


**Fig. 1.** Structure of muscles in domestic animals (Medicalook, 2012)

laxation of muscles. Myofibrils are suspended in a fluid termed sarcoplasm, containing water-soluble (sarcoplasmic) proteins (Marinova and Popova, 2011). The thickness and chemical composition of myofibrils differ. Thicker myofibrils are composed of myosin and thinner ones: of actin. In muscle, myofibrils are divided into regularly alternating dark and light bands (discs). Some discs appear dark under visible light and are called anisotropic (A-discs) and are doubly refractive. Other discs, termed isotropic (I-discs) appear light and are not doubly refractive. The dark and light myofibril areas of each muscle fibre (A- and I-discs) are aligned and give its striated appearance. The length of A-discs is constant while that of I-discs depends on the stage of muscle fibre contraction. The A-discs are divided by a H-line, whereas I-discs: by a Z-line. The Z-line is a dense membrane, to which myofibrils are attached. They occupy not only the I-disc area, but pass in between actin and myosin filaments in the A-disc area. In these zones, actin and myosin filaments are interrelated by cross-bridges, originating from myosin. These filaments contain ATP (Petkov et al., 2000).

The sarcomere (Figure 2) is the main structural, functional and contractile unit of myofibrils. It is a repeating unit between two Z-lines (Marinova and Popova, 2011; Gunenc, 2007). The sarcomere consists of one A-disc, bordered from both sides by a half I-disc.

## Meat proteins

The red meat (especially lamb) is a valuable source of proteins. It contains 15–25% proteins (Van Heerden et al., 2007; Biesalski, 2005).

Muscle proteins may be divided into three groups (Yu et al., 2017; Koohmaraie et al., 2002):

- Sarcoplasmic (water-soluble) proteins. They comprise approximately 30–35% of all muscle tissue proteins. Glycolytic enzymes and

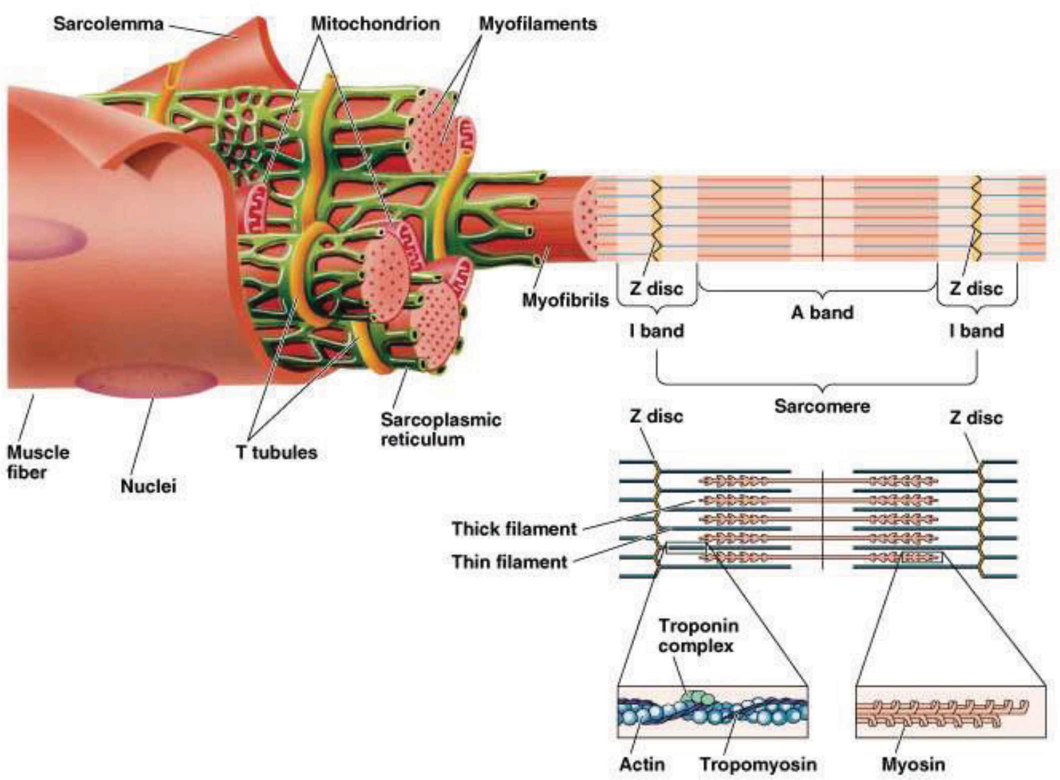


**Fig. 2.** Structure of muscle fibres' myofibrils
(https://www.pinterest.com/pin/167899892338251634/, available by 20. 2. 2023)

myoglobin are their main representatives (Yu et al., 2017);

- Myofibrillar proteins (soluble in saline solutions). They make up about 55–60% of meat proteins (Yu et al., 2017). Actin and myosin are the myofibrillar proteins with the highest proportions. Other important myofibrillar proteins are tropomyosin, troponin, nebulin and titin (Yu et al., 2017; Linke and Krüger, 2010; Ottenheijm and Granzier, 2010);
- Connective tissue proteins. The main proteins from this group are collagen and elastin. These proteins are insoluble in water and saline solutions. They make up the thin envelope of muscle fibres e.g. the sarcolemma. Collagen and elastin are the main constituents of intracellular substance of the connective tissue and are outlined with substantial mechanical strength (Vasilev, 2003).

## The calpain system and meat tenderness

The calpain system includes two $Ca^{2+}$-dependent proteases and a third polypeptide – the calpastatin. Calpains are among the most extensively studies proteases by meat science. It is demonstrated that the proteolytic activity of the calpain system contributes to the tenderisation of beef and lamb through degradation of the structure of muscles (Azari et al., 2012; Kemp et al., 2010; Koohmaraie and Geesink, 2006; Sentandreu et al., 2002; Huff-Lonergan et al., 1996). Koohmaraie (1994) affirms that the calpain system is the most relevant factor that influences beef tenderness. Calpains are a large group of intracellular cysteine proteases. In skeletal muscles, the calpain system comprises three proteases – μ-calpain (that requires low calcium content), m-calpain (requiring high calcium content) and calpain 3. The first two calpains (μ- and m-calpains) are calcium-activated, e.g. they require $Ca^{2+}$ in order to be activated (Kar et al., 2010; Kemp et al., 2010). It is proved that μ- and m-calpains are present in every cell of vertebrate animals (Goll et al., 2003). Previous studies show that μ- and m-calpains are located intracellularly under the form of intracellular depots (Coria et al., 2018; Varricchio et al., 2013). Raynaud et al. (2005) found out that μ-calpain is concentrated in titin, assuming that this protein is the reservoir of the cell. Many calpain substrates attaching to the sarcolemma: desmin, nebulin, titin, filamin and troponin-T, are localised and proteolysed during meat tenderisation (Coria et al., 2018; Varricchio et al., 2013).

Authors collective (Coria et al., 2018) reports a hypothesis, that during extended aging m-calpain is responsible for additional tenderisation of meat, whereas μ-calpains contribute to early posslaughter tenderisation improvement.

Calpastatin is the only acknowledged endogenous and specific protein inhibitor of calpain proteases that regulated the rate and extent of post mortem tenderisation (Azari et al., 2012; Wendt et al., 2004; Kocwin and Kuryl, 2003).

There is a significant evidences that calpains is linked to the tenderisation of pork, lamb and beef. Correlations between the different tenderisation rates between species (beef < lamb < pork) have shown vice versa relation to the ratio of calpastatin calpain (beef > lamb > pork) (Kemp et al., 2010; Koohmaraie et al., 1991).

Doumit and Koohmaraie (1999) reported a strong negative correlation between calpastatin and meat tenderisation degree. The high calpastatin activity results in reduced calpain activity and hence, tenderness improvement (Marais, 2007; Sazili et al., 2004).

The decreased expression of calpains or increased expression of calpastatin is associated with tougher meat (Coria et al., 2020). It is reported that feeding may alter the protein expression of the calpain system. Thus, Therkildsen (2005) observed that μ-calpain decreased after long-term restriction of feeding. It was also evidenced that the differences in ration constituents altered the calpastatin content in skeletal muscles of cattle (Du et al., 2004). Feeding strategies may modulate the turnover of muscle protein, muscle energy levels at slaughter and the water holding capacity (WHC), which may lead to meat tenderness changes (Coria et al., 2020; Andersen et al., 2005).

As already mentioned, the μ- and m-calpains are the primary proteins involved in meat tenderisation. They however do not degrade the main connective tissue constituent – the collagen. The reason is that the triple helical structure of natural collagen makes it resistant to most proteases (Kaur et al., 2021; Purslow, 2005).

### Association of meat tenderness with *Rigor mortis*, sarcomere length and pH values

Postmortem rigidity – *Rigor mortis*, is a process characterised with stiffening of slaughter carcass muscles when all energy stores are depleted (Greaser and Guo, 2012). *Rigor mortis* is one of the main causes for sarcomere shortening. The latter is induced at the time of stiffening and formation of permanent cross-bridges between actin and myosin. The energy for contraction is produced by glycogen and creatine phosphate degradation. The degradation provides ATP for myosin binding to actin forming the actomyosin complex (Chang, 2012). The muscles become tough and rigid, they are hardly salted and inappropriate for culinary processing.

The course of muscles stiffening is not the same for all muscles. The cause of *rigor mortis* is the cease of oxygen flow to muscles, switching the biochemical processes to anaerobic respiration and as a result, a rapid glycogen degradation occurs. The pH begins to decrease and meat becomes acidic. When meat pH reaches 5.20–5.40 (the isoelectric point of muscle proteins), actin and myosin bind to form actomyosin, responsible for meat stiffening (Vasilev, 2003).

The complete rigidity takes different time depending on the specificity of animals and environmental conditions (Vasilev, 2003). At 4 °C, the rigidity of slaughter carcasses of small ruminants occurs after 12–16 hours. It develops faster in the muscles of young animals and more slowly – in muscles of fattened animals. The postmortem rigidity is most pronounced in skeletal muscles, at a lower extent – in the heart and is almost imperceptible in smooth muscles.

The decrease of meat pH results from glycogen degradation to lactic acid. The values decrease from 7.2 in live animals to about 5.4–5.5 in carcass muscles. In general, meat with higher pH has higher shear force values (e.g. it is tougher). Similarly, meat with lower pH has lower shear force values and is more tender (Chang, 2012). Silva et al. (1999) established that the tenderness of beef at the 1$^{st}$, 6$^{th}$ and 13$^{th}$ day of storage increases linearly parallelly to increase of ultimate pH value from 5.5 to 6.7. In the view of Li et al. (2014) and Hamoen et al. (2013) beef tenderness has long been associated with meat pH values. They found out that the tenderness meat with high (over 6.2) and low (under 5.8) pH is acceptable. Moreover, Silva et al. (1999) and Dutson (1983) reported that the extent of tenderisation was pH-dependent. With this regard, the tenderisation of meat with high pH occurred faster as compared to meat with low pH.

### Association of meat tenderness with animal breed and sex

It is demonstrated that ruminant meat tenderness is influenced by genetics. Beef tenderness is an extremely important meat quality trait. One of the essential factors influencing the total number of muscle fibres, fibre cross section area and muscle fibre type within the species, is breed (Lefaucheur, 2010). According to Monsón et al. (2005), breed has a considerable impact on beef tenderness and juiciness. That is why, the interest to genetic selection for improvement of meat tenderness is great (Hanzelková et al., 2011). According to researchers, there are cattle breeds as Pinzgauer, South Devon, Jersey and Piedmontese, whose meat is more tender compared to meat of other breeds (Koohmaraie et al., 1995).

Monsón et al. (2005) investigated the tenderness of beef in four different cattle breeds - Blonde d'Aquitaine, Holstein, Limousin and Brown Swiss. They found out that after 14-day ageing, the meat of Blonde d'Aquitaine attained up to 83.0% of the total tenderidation, that of Brown Swiss – 89.5%, whereas in Holstein meat total tenderisation was obtained. Total tenderisation in Limousin beef meat took 7 days.

Another study (Neath et al., 2007) determined the difference in meat tenderness between water buffalo meat and beef during postmortem aging. Female Philippine Carabao x Bulgarian Murrah buffaloes were compared to female Brahman x

Philippine Native cattle. The authors concluded that the tenderness of water buffalo meat was superior to that of beef.

Aleksić et al. (2011) conducted sensory analysis of beef from three different genotypes – Domestic spotted x Charolais, Domestic spotted x Limousin and Domestic spotted breed of Simmental type. The study affirmed that beef tenderness was the best in the Domestic spotted breed of Simmental type – 5.43 kg/cm$^2$, followed by genotypes Domestic spotted x Limousine and Domestic spotted x Charolais, with 5.99 kg/cm$^2$ and 7.10 kg/cm$^2$ respectively.

Petričević et al. (2017) analysed the technological properties of meat of female cattle from two different genotypes – domestic Simmental breed and its crosses with Charolais. The authors found out that meat tenderness was statistically significantly better in Simmental x Charolais crosses.

Marino et al. (2013) and Chambaz et al. (2003) also acknowledged the impact of breed on beef tenderness. Chambaz et al. (2003) reported that the meat from Angus and Limousin was more tender than that from Simmental cattle.

As already noted, meat tenderness is perhaps the most relevant meat quality parameter. The deviations in meat tenderness are the main reason for discontent among consumers and therefore, should be controlled to improve consumers satisfaction and the repeat purchase decision (Špehar et al., 2008).

At a global scale, some sheep breeds have been selected for years to obtain animals with excellent meat flavour, low fat content and very tender meat. Examples are the specialised French meat sheep breeds, whose representatives are Mouton Charolais and Ile de France. The analysis of meat from these sheep breeds has shown a very good tenderness and low fat content (Ivanov, 2019; Ivanov et al., 2017).

A study on meat quality from male and female Simmental cattle was performed. The animals were fed the same diet and slaughtered at the same age. The authors concluded that meat tenderness of female cattle was superior to that of males (Petričević et al., 2015). The same tendency was confirmed by Andrade et al. (2021), reporting that the meat of female buffaloes was more tender than that of males. Similar is the conclusion of Rodrigues et al. (2011) and Johnson et al. (1995) according to which the meat of female goats is more tender than that of males. Gularte et al. (2000) as well as Velasco et al. (2000), also found that the meat of female lambs was more tender than that of males.

## Association of meat tenderness with muscle fibre type

Skeletal muscles are classified into several groups depending on their colour, constriction rate and energy metabolism (Marinova and Popova, 2011). According to their colour the muscles are red or white, according to contraction speed they are either slow-twitch or fast-twitch, and in relation to the energy metabolism: oxidative and glycolytic types.

Muscle fibres differ by their morphology, contractile and metabolic properties (Lee et al., 2010). Contractile and metabolic properties are differentiated with regard to muscle fibre type and therefore, the quality of fresh meat depends on this type.

In general, four types of muscle fibres are distinguished (Joo et al., 2013; Schiaffino et al., 1989):

Slow oxidative fibres – type I;

Fast oxidative-glycolytic fibres – type IIA;

Fast glycolytic fibres – types IIX and IIB.

All these types are observed in muscles of most of animals, and their composition may determined the prevailing metabolic events and muscle colour (Ryu and Kim, 2005). Red muscles contain a higher proportion of red fibres and are mainly associated with movement. They are outlined with higher content of myoglobin, capillaries and mitochondria, and have an oxidative metabolism. These are the so-called type I muscle fibres (slow oxidative) and type IIA (fast oxidative) fibres. Unlike them, white muscles are mainly composed of white muscle fibres, playing a predominantly supportive function. White fibres contain few myoglobin and their metabolism is of the glycolytic type – type IIB fibres (fast glycolytic fibres). The differences of fibres; colour and type are important for consequent processing of meat (Marinova and Popova, 2011).

Lefaucheur (2010) reported that the diameter of muscle fibres increased in the following order: I = IIA < IIX < IIB. According to Wang and Li (1994), the tenderness of meat is good if fibres are thin, the density is high and fat content – higher. This means that fibres from types I and IIA are more tender than fibres from types IIX and IIB (Lian et al., 2013).

Hammond (2017) stated that the different types of muscles, made of different muscle fibre types, have various tenderness. Thus, the *muscles Longissimus thoracis*, *Triceps brachii*, *Gluteus medius*, *Rectus abdominus and Semitendinosus*, may be influenced by proteolytic degradation, whereas collagen traits may influence the tenderness of *m. Pectoralis profundus*.

Variations in the shear force values of different sheep muscles were documented also by Xu et al. (2018).

Picard et al. (2014) found out that in cattle breeds with faster glycolytic metabolism (such as French breeds), the *Longissimus thoracis muscle* was the most tender. The higher proportion of glycolytic fibres may improve the tenderness of some muscles through enhancement of ageing due to the higher calpain/calpastatin ratio in the meat of species with slaw meat ageing, e.g. cattle and sheep (Zamora et al., 1996).

Janz et al. (2006), demonstrated that the shear force that is indicative for beef tenderness has decreased (corresponding to more tender meat) from the anterior to the posterior part of *Musculus Longissimus Lumborum*. Conversely, Derington et al. (2011) detected increased shear force by 29% for steaks in the same direction (from the anterior to the posterior part).

## Association of meat tenderness with connective tissue content

Muscles are made of muscle fibres, which are attached to each other and organised by connective tissue (Marais, 2007).

The amount, distribution and composition of meat connective tissue are substantially variable according to muscle location in the carcass and age. It is demonstrated that connective tissue had an effect on meat tenderness (Marais, 2007; Purslow, 2005). The toughness of connective tissue is often termed background toughness because it does not change during meat storage (Marais, 2007).

Intramuscular connective tissue is composed of collagen and elastin protein fibres, surrounded by a proteoglycan (PG) matrix. The overall content of collagen in beef may vary from 1% to 15%, and that of elastin – within a narrower range: from 0.6% to 3.6% (Bendall, 1967). Schönfeldt and Strydom (2011) found out that the age of animals had not impact on collagen content, but its solubility was definitely age-dependent. In general, the tenderness and solubility of collagen decrease significantly with age regardless of the muscle. The shear force resistance was found to increase considerably with age in seven of 14 studied meat cuts.

In the view of Jeremiah et al. (2003), the collagen content of beef is negatively associated with sensory tenderness of meat. The authors concluded that additional studies of more muscles were necessary to identify the relationship of collagen characteristics with meat tenderness.

Meat sensory tenderness could not be distinguished from shear force (Chriki et al., 2013). The authors affirmed that sensory tenderness was associated with total collagen content, intramuscular fat content, average cross-sectional area of fibres, whereas shear force was closely associated with insoluble collagen content. Tenderness variations according to Maltin et al. (2003) might be explained with collagen content (up to 33% of variations in tenderness are attributed to fat and collagen content). Astruc (2014) also found out that the connective tissue influenced meat tenderness through it composition and structure, especially in cattle, in which collagen was deemed the principal factor determining shear force. There are, however, substantial differences between crude and cooked meat as tenderness was concerned. The shear force of crude meat correlated strongly with its collagen content (Nishimura, 2015). For cooked meat, the correlation between collagen content, solubility and meat shear force was unclear and varied with regard to muscle type and cooking conditions (Sifre et al., 2005, Ngapo et al., 2002).

## Association of meat tenderness with intramuscular fat content

The minimum amount of intramuscular fat for meat acceptance by consumers is reported to be 3–4% for beef (Savell and Cross, 1986) and about 5% for mutton (Hopkins et al., 2006).

According to Terlouw et al. (2021), Gagaoua et al. (2019) and Bonny et al. (2018), the highly marbled veal may be at the background of the higher meat tenderness. There are also literature reports which did not confirm any relationship between intramuscular fat content and meat tenderness (Geay et al., 2001). Conversely, later studies demonstrated a positive correlation between fat content and tenderness of meat (Xu et al., 2020; Oury et al., 2009; Picard et al., 2007; Wood et al., 2008). Their results were supported by Ueda et al. (2007), by observing a negative correlation between fat content and shear force values, indicative for meat tenderness. They found out that the increase in intramuscular fat from 5% to 35% resulted in reduced shear force of cooked *longissimus* from Japanese Black cattle with a 1.5 $kg/cm^2$. Maltin et al. (2003) also affirmed that a certain percentage of tenderness variation may be explained by meat fat content.

Chartrin et al. (2006) also showed that the increase in fat content of duck breast muscle from 1.7% to 8.5% resulted in improved meat tenderness and flavour.

## Conclusion

The performed literature overview demonstrated that meat tenderness varied among species, breeds and between sexes within a breed. Meat tenderness was influences by different factors, some having a positive and others – a negative impact.

Among the studied factors, the calpain system and fat content exerted a positive influence on tenderness. The prevailing opinion in the scientific literature is that high meat fat content results in lower shear force values and therefore, improve its tenderness.

It is evidenced that some factors e.g. *rigor mortis* and connective tissue content, have a negative effect on tenderness of meat from large and small ruminants. During *rigor mortis*, stiffening of carcass musculature occurs after depletion of all energy stores. *Rigor mortis* is one of the main causes for sarcomere shortening, which takes place during the stiffening and formation of permanent cross-bridges between actin and myosin. The energy for shortening comes from glycogen and creatine phosphate degradation. This degradation provides ATP for binding myosin to actin into actomyosin complex, responsible for meat toughness. Collagen and elastin as connective tissue constituents, also worsen tenderness. This is due to the structural strength of these two proteins.

Muscle fibre type is another important factor with impact on tenderness. The different muscle types made of different muscle fibers, have a variable tenderness. It is demonstrated that in ascending order, muscle fibre diameter may be ranged as follows: I = IIA < IIX < IIB. This means that fibres from types I and IIA are more tender than types IIX and IIB.

The knowledge on the mechanism of action of different factors on meat tenderness may contribute to reduce the variation of this meat quality element. The control on factors influencing meat tenderness, as much as possible, will inevitably lead to tenderness improvement and consequently, increased selling price and sales of more tender meat. Improvement of meat tenderness through regulation of influencing factors should become main concern in meat processing enterprises in the future.

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