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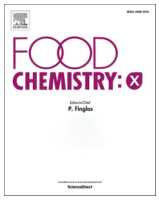

A new perspective on apoptosis: Its impact on meat and organoleptic quality in different animals

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ABSTRACT

Apoptosis serves as the initial phase in the conversion of muscle to meat, driving key biochemical and morphological changes in the postmortem muscle. To effectively improve and control meat quality across different animal species, it is important to gather more information on the mechanisms by which apoptotic potential, mediated through the interaction of apoptosis-related molecules, influences meat quality variations. The apoptotic potential, determined by the balance between apoptotic and anti-apoptotic molecules, such as Ca^{2+}, cytochrome *c*, caspases, and heat shock proteins, varies among different species. A moderate to rapid apoptotic rate can improve textural properties in species with a higher proportion of type I fibers, such as cattle. In contrast, in species with a predominance of type IIB fibers, such as pork and poultry, rapid apoptosis can lead to undesirable quality traits. Therefore, understanding these species-specific apoptotic responses is critical for improving and maintaining meat quality across various species.

1. Introduction

Meat is a critical source of various nutrients that are required in the omnivorous diet of humans and is particularly rich in biologically valuable proteins and functional peptides derived from muscle proteins (Font-i-Furnols & Guerrero, 2014). Recently, consumer-driven macro trends in meat and meat products that are minimally processed and naturally contain beneficial nutrients (Cho et al., 2020; Señorans, Ibáñez, and Cifuentes, 2003; Sloan, 2021). Consumers have begun to consider intangible characteristics, such as cleanliness, environmental friendliness, sustainable farming systems, and carbon footprint, when evaluating and purchasing meat (Warner et al., 2010). However, a substantial number of consumers prioritize eating satisfaction over guaranteed healthy nutrients or animal welfare (Font-i-Furnols & Guerrero, 2014). Accordingly, a primary objective of the meat industry is to produce meat with consistent and assured quality that aligns with consumer expectations.

In a broad sense, meat quality includes attributes that determine its overall desirability for consumption. It is a multidimensional trait that is influenced by the combination of various factors. In addition, as each consumer has different meat quality priorities based on their culinary preferences and values, the criteria for evaluation of preferred and high-quality meat tend to vary depending on the individual, ethnic groups, countries, geographical regions, etc. (Font-i-Furnols & Guerrero, 2014). These factors make it challenging to improve and predict the physico-chemical and sensory quality, such as water-holding capacity (WHC), surface color, appearance preference, tenderness, juiciness, and flavor, to accommodate customer preference (Choi & Kim, 2009). To improve the overall meat quality, a comprehensive definition of environmental and genetic factors that affect quality variation is required, and quality improvement methods should be devised based on these (Damez & Clerjon, 2008).

After exsanguination, a variety of biological, chemical, and structural changes in muscle fiber continuously occur in muscle fibers as skeletal muscles attempt to maintain cellular homeostasis by efficiently producing and using adenosine triphosphate (ATP) (Choi & Kim, 2009). The first phase in the conversion to meat during the postmortem period is the onset of apoptosis, a programmed cell death, which is regulated by various molecules, especially caspases (Brown et al., 2014). Among the apoptosis, intrinsic apoptosis induced under the state of ischemia, hypoxia, and cell cycle arrest is the most important process that contributes to the complex cascade of cellular and biochemical changes during the early postmortem stage (Ertbjerg, 2022; Kemp & Parr, 2012; Ouali et al., 2013). On the other hand, meat from different animals

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varies considerably in its muscle properties due to the relative proportions of fiber types, including slow-twitch oxidative, intermediate, and fast-twitch glycolytic fibers. These can affect the metabolic properties not only in living animals but also during the postmortem period (Choi & Kim, 2009). Apoptotic pathways directly and/or indirectly affect postmortem glycolysis and protein degradation, and apoptotic potentials can influence meat quality trait variations by affecting sensory quality in different ways in various animals (Lee et al., 2022a; Lee & Choi, 2022).

Therefore, this review aims to provide an overview of the apoptotic process and the various related molecules during the postmortem period that influence the metabolic, morphological, and physicochemical properties of meat in different animals. Ultimately, it offers a comprehensive understanding of how postmortem apoptosis differentially impacts meat quality development across various animals to produce high-quality meat that aligns with current consumer trends.

2. Apoptosis pathways

2.1. Cell death

Multi-cellular organisms continually strive to maintain cellular homeostasis by balancing the number of new cells produced by mitosis and the number of cells eliminated as damaged or unnecessary (Brown et al., 2014). Cells exposed to severe physiological and pathophysiological conditions undergo either apoptosis or necrosis, and these two processes are characterized by fundamentally different regulatory mechanisms and morphological and biochemical features (Ertbjerg, 2022). Necrosis is energy-independent, known as uncontrolled cell death, and is triggered accidentally in an unplanned manner, such as exposure to trauma, infection, toxins, or ischemia, thereby causing rapid cell death, without requiring the expression of specific proteins (Sandri & Carraro, 1999). Moreover, necrotic cells generally exhibit edema, organelle damage, and eventual plasma membrane rupture, which releases the cellular contents into the surrounding cells, leading to secondary tissue inflammation (Adams et al., 2001). Unlike necrotic or degenerative cell death, apoptosis is the tightly regulated and controlled death of cells, which usually affects individuals or cell clusters, and it is considered an energy-dependent process that requires ATP (Brown et al., 2014). Another feature of apoptosis compared to necrosis is that the plasma membrane of muscle fibers remains intact until a later stage in the process, thereby preventing secondary tissue damage caused by activation of the inflammatory response (Adams et al., 2001). After initiation of the apoptotic pathway, the expression of anti-apoptotic and apoptotic molecules, especially Ca^{2+}-dependent proteases, B-cell–lymphoma protein 2 (Bcl-2) family members, and heat-shock proteins (HSPs), are selectively increased (Kemp & Parr, 2012). Thereafter, the recruited endogenous enzymes degrade the structural and functional proteins, thus terminating the cellular life cycle (Brown et al., 2014).

2.2. Caspases

Skeletal muscle exhibits complex and unique apoptosis mechanisms due to several factors: i) Muscles are composed of a combination of fiber types with different biochemical properties; ii) muscle fibers are multinucleated; and iii) mitochondria display distinct morphological and biochemical traits depending on the fiber type (Adhihetty & Hood, 2003). Key molecules of signaling mechanisms that induce apoptotic cell death are caspases, a family of cysteine-aspartic acid proteases, and they are involved in a variety of skeletal muscle functions, including amplifying apoptotic signals through caspase interactions (Adhihetty & Hood, 2003). Skeletal muscle contains at least 14 distinct caspases, and caspases are generally classified into three subfamilies based on their functions: initiator, effector, and inflammatory caspases (Ertbjerg, 2022). They can also be classified according to their structure (caspases with a caspase activation and recruitment domain, caspases with a death effector domain, and caspases with a short prodomain) and by their substrate specificity (aspartate- or histidine-specific caspases) (Ertbjerg, 2022).

Depending on their function, the first subfamily is the initiator or apical caspases (Kemp & Parr, 2012). Initiator caspases (caspase 2, caspase 8, caspase 9, and caspase 10) are activated in response to apoptotic stimuli during the early stage of apoptosis (Ertbjerg, 2022). However, they require dimerization of inactive monomeric preforms for apoptosis to occur, as initiator caspases are maintained in inactive states (procaspases) to prevent unintended or premature proteolytic activation (Adams et al., 2001; Dabrowska et al., 2016). The activated initiator caspases cleave inactive pro-effector caspases and active effector caspases (Hyman & Yuan, 2012). This cleavage process triggers the activation of effector caspases and amplifies the apoptotic signal, which induces the execution phase of programmed cell death (Kemp & Parr, 2012). Thus, the initiator caspases are crucial for integrating the various apoptotic signals and transmitting them downstream to the effector caspases (Hyman & Yuan, 2012). Effector caspases (also known as executioner caspases; caspase 3, caspase 6, and caspase 7) belong to the second subset of the caspase family and execute the apoptotic process by cleaving various cellular substrates (Ertbjerg, 2022). These caspases are generally activated through cleavage at a specific aspartic acid residue by initiator caspases and are responsible for performing the actual destruction of the cell by the proteolysis of key cellular substrates, which include structural proteins, DNA repair enzymes, and other essential cellular components (Ertbjerg, 2022). The cleavage of these substrates results in morphological and biochemical feature changes that are associated with apoptosis (Earnshaw et al., 1999). Moreover, inflammatory caspases (caspase 1, caspase 4, caspase 5, and caspase 11) are the third caspase subfamily (Dhani et al., 2021). Unlike apoptotic caspases, including initiator and effector caspases, inflammatory caspases play a significant role in muscle pathology and are activated by chronic inflammatory conditions, infections, etc., leading to cytokine activation and pyroptosis (Dhani et al., 2021).

2.3. Caspase-dependent apoptotic pathways

The caspase-dependent pathway is a commonly employed mechanism for apoptosis and plays an important role in normal muscle growth and maintaining homeostasis (Kroemer & Martin, 2005). However, apoptosis can be induced even without caspases when caspase activation is inhibited or damaged mitochondria do not release sufficient apoptotic molecules (Kroemer & Martin, 2005). This caspase-independent apoptosis serves as an alternative mechanism to eliminate unwanted and potentially harmful cells when caspase-dependent apoptosis fails and can be triggered in response to cytotoxic agents or other death stimuli, such as under conditions of extreme cellular stress (Bröker et al., 2005). In the caspase-independent pathway, various proteins and proteases, including apoptosis-inducing factors, endonuclease G, and cathepsins, are involved, which can induce apoptosis (Bröker et al., 2005).

In contrast, caspase-dependent apoptosis is regulated by various caspases with numerous target cellular substrates in response to various internal and external signals (Dillon & Green, 2016). This form of cell death occurs via three pathways: i) the caspase 12 pathway induces apoptosis by directly stressing the endoplasmic reticulum (ER); ii) extrinsic apoptosis results from the activation of a family of proteins, known as death receptors, by extracellular signals; and iii) the intrinsic pathway is caused by various intracellular stimuli and stress signals (Dillon & Green, 2016; Sierra & Oliván, 2013).

2.3.1. Caspase 12 pathway

The ER is sensitive to changes in homeostasis caused by various stimulus, including glucose deprivation, calcium imbalance, and exposure to free radicals (Lamkanfi et al., 2004). The ER stress, induced by various stimuli, elicits two primary cytoprotective responses: i) attenuation of protein synthesis and ii) upregulation of chaperone-encoding

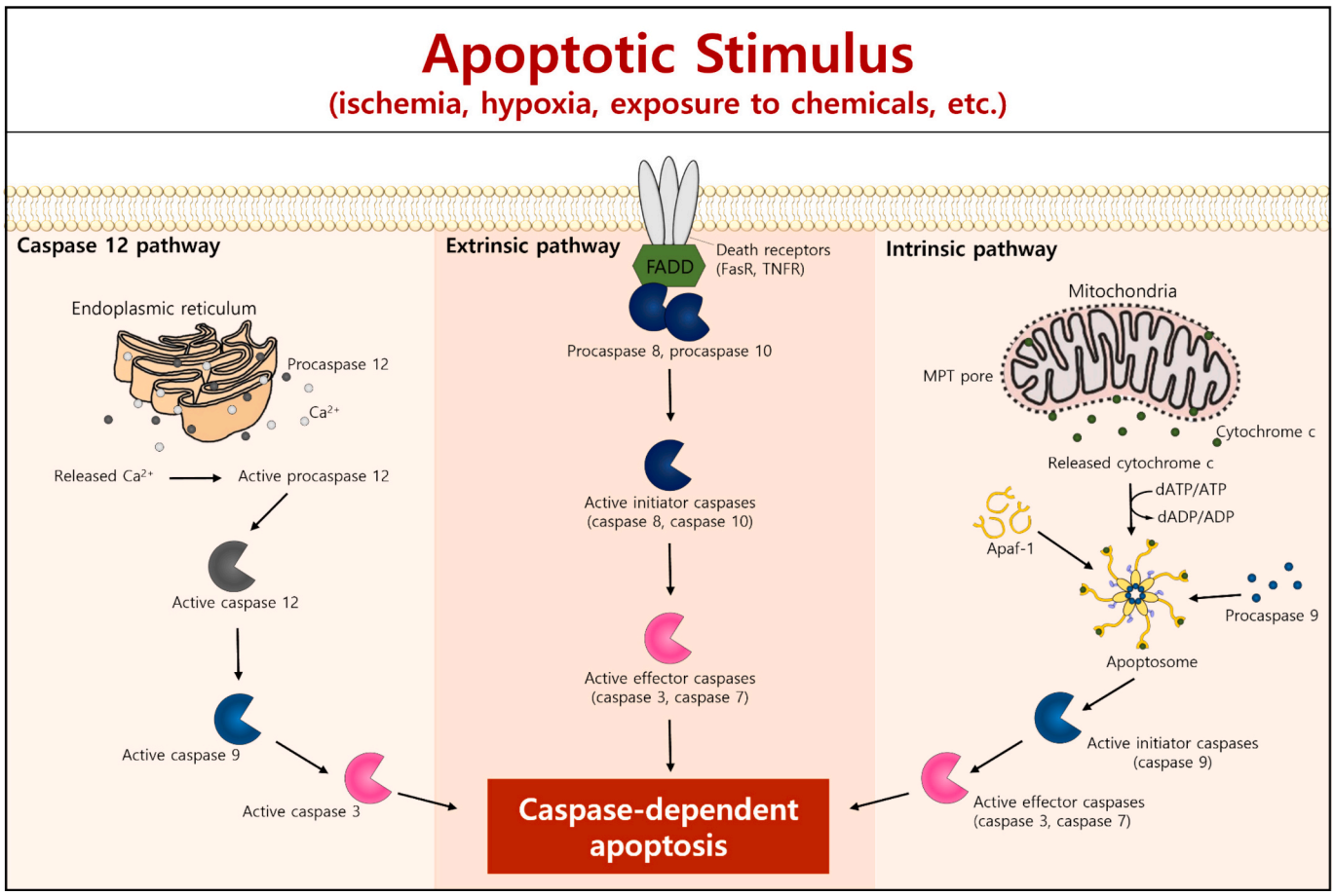

Fig. 1. Schematic representation of the caspase-dependent apoptotic signaling pathways. Caspase-dependent pathways occur via various caspases in response to internal and external signals. There are three pathways: the caspase 12 pathway, which directly stresses the endoplasmic reticulum (ER); the extrinsic pathway, which involves the activation of death receptors from extracellular signals; and the intrinsic (mitochondrial) pathway, which is activated by various intracellular signals, including DNA damage and oncogenic stress. Each pathway activates initiator caspases that are appropriate for the individual pathway and these initiators then activate the effector caspases (caspase 3 and 7) to execute apoptosis. Abbreviations: FADD, Fas-associated protein with death domain; FasR, Fas receptor; TNFR, tumor necrosis factor receptor; MPT, mitochondrial permeability transition; Apaf-1, apoptotic protease activating factor-1; ATP, adenosine triphosphate; dATP, deoxyadenosine triphosphate.

genes that facilitate protein folding in the ER termed the unfolded protein response (UPR) (Lamkanfi et al., 2004). Both responses mitigate the accumulation and aggregation of misfolded proteins within cellular compartments (Lamkanfi et al., 2004). However, excessive levels of these stimuli prevent the UPR from properly regulating the number of unfolded proteins in the cell, leading to apoptosis (Lamkanfi et al., 2004). ER stress-mediated apoptosis recruits adaptor proteins, such as tumor necrosis factor receptor-associated factor 2 and inositol-requiring enzyme 2, which help activate caspase 12 on the ER membrane, a key caspase in this apoptosis (Lamkanfi et al., 2004). Activated caspase 12 cleaves and activates initiator caspase 9, which then catalyzes the proteolytic activation of effector caspases, such as caspase 3, leading to apoptosis (Fig. 1.) (Lamkanfi et al., 2004). In contrast to caspase 1, caspase 12 plays a protective role in regulating inflammation, as it binds to a key inflammatory caspase to prevent its activation, thereby reducing the cleavage and activation of proinflammatory cytokine interleukin-1β (pro-IL-1β) and pro-IL-18 (de la Cadena & Massieu, 2016).

2.3.2. *Extrinsic pathway*

The extrinsic pathway, which occurs due to external trauma, is one of the primary pathways in the blood coagulation cascade and a rapid response system compared to the intrinsic pathway (Adhihetty & Hood, 2003). Key factors that activate the receptor-mediated apoptosis include various forms of cellular stress, such as inflammation, oxidative stress, radiation, chemical exposure, mechanical stress, nutrient deprivation, hyperthermia (Cavalcante et al., 2019). During vascular injury, muscle trauma, or stress, this pathway can interact with the intrinsic pathway to prevent excessive blood loss and promote repair within damaged muscle tissue (Adhihetty & Hood, 2003). The death receptor pathway is triggered by the oligomerization of transmembrane proteins of the death receptor superfamily that are activated by receptor binding of extracellular death ligands, including tumor necrosis factor (TNF)-α and Fas ligands, to the death receptors, such as TNF and Fas receptors (Adhihetty & Hood, 2003). These bindings of death ligands to their receptors recruit procaspase 8 to the plasma membrane, and the accumulation of procaspase 8 results in the formation of a death-inducing signaling complex, which then activates initiator caspase 8 (Adhihetty & Hood, 2003). Caspase 8 activates downstream executioner caspase 3 either directly or indirectly through the mitochondrial pathway, thereby causing the structural and biochemical breakdown of the cell (Salvesen & Dixit, 1999). Additionally, this pathway is associated with changes in mitochondrial permeability and the subsequent events resemble the intrinsic apoptotic pathway described below (Cavalcante et al., 2019).

2.3.3. *Intrinsic pathway*

As outlined in the introduction, the intrinsic apoptosis pathway plays a particularly crucial role in cell death during the conversion of muscle

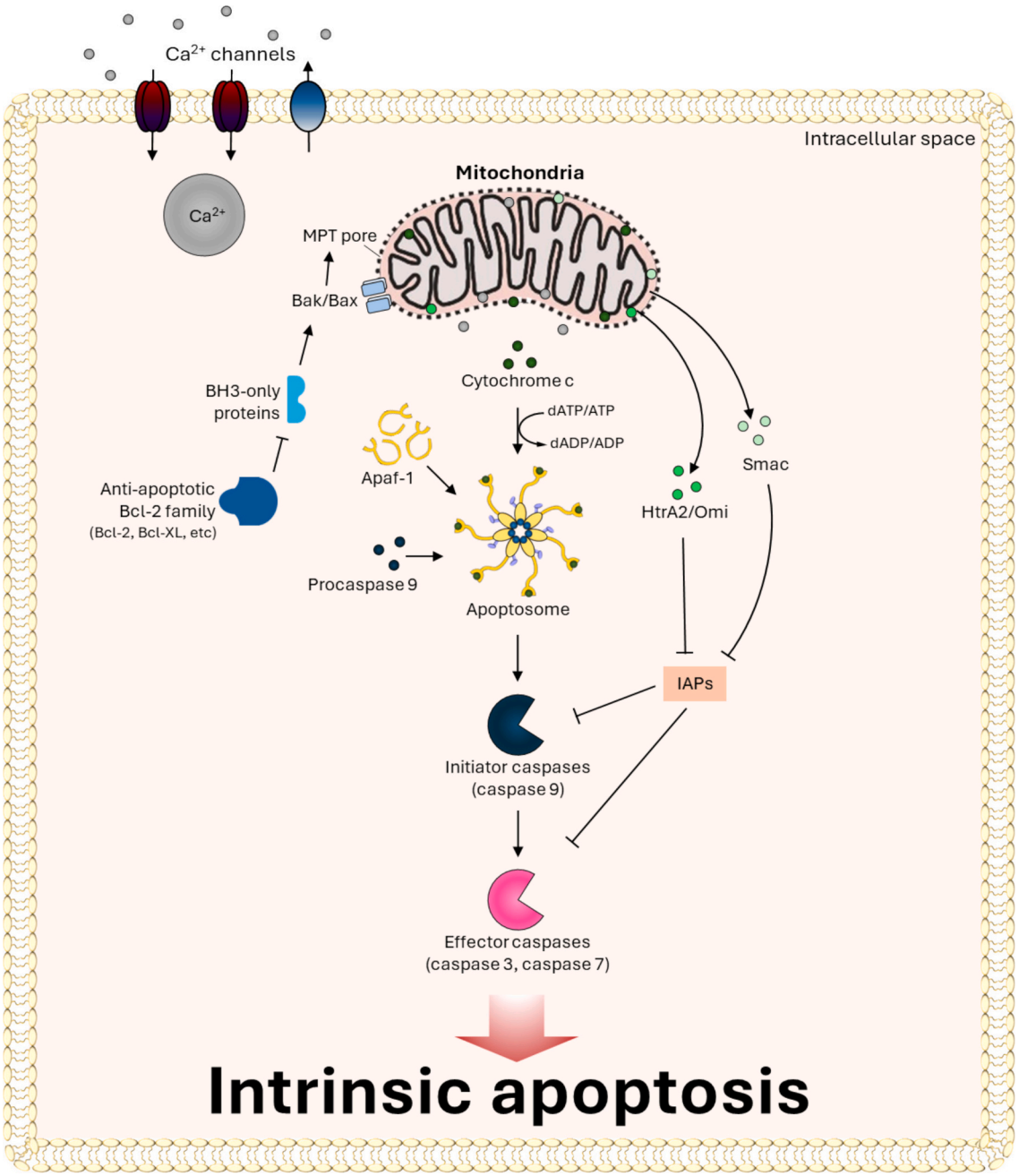

Fig. 2. Summary illustration of the molecular mechanisms of the intrinsic apoptosis pathway. The intrinsic pathway is induced by inserting Bax/Bak into the mitochondrial membrane via BH3-only proteins, followed by the opening of the mitochondrial permeability transition (MPT) pore. Subsequently, cytochrome *c*, Smac/Diablo, and HtrA2/Omi are released through the MPT pore, and the released Smac/Diablo and HtrA2/Omi neutralize the function of the inhibitor of apoptosis proteins (IAPs), which inhibits activation of caspase. Cytoplasmic cytochrome *c* combines with Apaf-1 and procaspase 9 to form an apoptosome, followed by the activation of effector caspases, including caspase 3 and caspase 7, which leads to apoptosis. Abbreviations: Bax, B-cell-lymphoma protein 2 (Bcl-2)-associated X protein; Bak, Bcl-2 antagonist/killer; Smac/Diablo, second mitochondrial activator of caspases/direct IAP binding protein with low pI; HtrA2/Omi, high-temperature requirement protein A2; Apaf-1, apoptotic protease activating factor-1; Bcl-XL, Bcl-2 homolog splice variants; dATP, deoxyadenosine triphosphate; dADP, deoxyadenosine diphosphate.

to meat, relative to other cell death pathways. Intrinsic apoptosis is induced within the mitochondria and is primarily linked to mitochondrial disruption in response to intracellular stress (Dabrowska et al., 2016). This stress includes DNA damage, growth factor deprivation, cytosolic Ca^{2+} overload, oncogenic stress, oxidative stress caused by the excessive production of reactive oxygen species (ROS), and ischemic/hypoxic conditions via oxygen depletion; therefore, it is also known as the mitochondrial apoptotic pathway (Dabrowska et al., 2016). In response to stress signals (Fig. 2.), pro-apoptotic members of the Bcl-2-associated X (Bax) protein subfamily, such as Bax and Bcl-2 antagonist/killer (Bak), are activated, oligomerized, and inserted into the mitochondrial outer membrane, thereby causing it to become permeable (Dabrowska et al., 2016). On the other way, anti-apoptotic family members, especially Bcl-2 and Bcl-XL, inhibit apoptosis by preventing the formation of mitochondrial permeability transition (MPT) pores, whereas the BH3-only proteins inhibit anti-apoptotic proteins through binding, which eliminates their inhibition of Bax and Bak (Warren et al., 2019). Thus, in determining the initiation of apoptosis when cells

undergo apoptotic stimulation, the relative expression levels of these pro- and anti-apoptotic proteins in this pathway are important factors (Adhihetty & Hood, 2003).

During the progression of the intrinsic apoptosis pathway, various specific anti-apoptotic and apoptotic factors also play roles in promoting or inhibiting apoptosis. Through increased MPT pore formation by Bax and Bak, various apoptosis-related molecules, including Ca^{2+}, cytochrome *c*, an inhibitor of apoptosis protein (IAP), a second mitochondria-derived activator of caspases, and high-temperature requirement protein A2, are released into the cytoplasm (D'Arcy, 2019). Among these molecules, released cytochrome *c* binds to apoptotic protease activating factor-1 (Apaf-1), deoxy ATP (dATP), and procaspase 9, which induces a conformational change in Apaf-1, thus causing it to oligomerize into the apoptosome (Concannon et al., 2003; Huang et al., 2016). The formation of a multi-subunit apoptosome complex then recruits and activates procaspase 9, which results in its autocatalytic cleavage and activation, and active caspase 9, in turn, activates downstream executioner procaspases in the form of active effector caspases, particularly caspase 3 and caspase 7 (Concannon et al., 2003). The termination of the intrinsic pathway includes the activation of effector caspases and the subsequent cleavage of cellular substrates, which leads to systematic dismantling and eventual cell death (Kiraz et al., 2016). Conversely, IAPs can bind and directly inhibit both initiator and effector caspases, thereby preventing premature or excessive cell death and ensuring that cell death occurs only under appropriate conditions (Adhihetty & Hood, 2003), whereas the expression level and activity of caspases are positively associated with the rate of apoptosis (Concannon et al., 2003; Huang et al., 2016). This tightly regulated process ensures that apoptosis occurs in a controlled manner, prevents inflammation, and maintains tissue integrity (Kroemer & Martin, 2005).

3. Intrinsic apoptosis and meat quality

3.1. Muscle fiber characteristics and apoptosis in different animals

The rate and extent of apoptosis and postmortem protein degradation can vary depending on the species with different muscle characteristics (Choi & Kim, 2009; Kim et al., 2023). Various functional characteristics of skeletal muscle are mainly influenced by fiber types with different molecular, metabolic, structural, and contractile properties (Matarneh, Silva, & Gerrard, 2021). Type I fibers classified based on their contractile and metabolic characteristics exhibit a redder surface color due to higher levels of myoglobin and blood capillaries, which support greater aerobic metabolism compared to type II fibers (Choi & Kim, 2009). In contrast, type II fibers, especially type IIB fibers, primarily use glucose and glycogen as energy sources to rapidly produce ATP anaerobically and exhibit a greater ATP splitting rate and glycolytic activity than type I fibers (Choi & Kim, 2009). Moreover, type I fibers display a higher density of mitochondria, and their mitochondria are generally larger and contain higher amounts of oxidative enzymes to support efficient aerobic respiration to produce ATP than type IIB fibers (Choi & Kim, 2009).

Meanwhile, in postmortem muscle, exsanguination restricts the blood supply to fibers, causing oxygen deficiency; thus, glycolysis is generally considered the dominant metabolism, and the ATP required for the intrinsic pathway is primarily supplied via glycolytic metabolism (Adams et al., 2001; Lee & Choi, 2022). As ATP levels at the early postmortem period gradually decrease, the mitochondrial membrane potential is disrupted, which releases apoptotic factors through the increased opening of MPT pores (Adams et al., 2001). Accordingly, muscles harboring a higher percentage of type I fibers, such as bovine and ovine muscles, exhibit a slower rate of apoptosis and glycolysis related to lower expression levels and activities of apoptosis-related molecules compared to muscles harboring a higher percentage of type IIB fibers, such as porcine and poultry muscles (Choi & Kim, 2009). Therefore, understanding postmortem muscle changes, especially apoptosis, in different animal types has important implications for explaining quality variations and potential applications in improving the quality characteristics of various meat animals (Kim et al., 2023; Ouali et al., 2013). The following sections provide how the programmed cell death processes differentially affect meat quality development and postmortem glycolysis in animals with different compositions of muscle fiber types.

3.2. Apoptosis and quality characteristics of ruminant muscles

Sensory quality, which consists of tenderness, juiciness, and flavor, can be a key determining criteria that influence consumer experience satisfaction and repurchase, particularly in the context of ruminant meat (Cardona et al., 2023; Font-i-Furnols & Guerrero, 2014; Oh et al., 2019). Among these characteristics, tenderness is generally considered the most important qualitative characteristic from a consumer perspective (Kim et al., 2023). In response to consumer demand, the meat industry and scientists have been exploring the production of beef with improved and consistent tenderness. However, tenderness, a highly variable trait, is widely influenced by the combined interaction of intrinsic and extrinsic factors during the postmortem period (Lee et al., 2022a).

Apoptosis, the first step in converting muscle to meat, may be directly and indirectly associated with tenderness improvement of ruminant meat through structural and biochemical changes (Brown et al., 2014; Lee et al., 2022a). After exsanguination, the increased number of MPT pores because of the ischemia/hypoxia conditions leads to the increased release of Ca^{2+} from the mitochondria, which results in an imbalance in Ca^{2+} homeostasis (Adams et al., 2001). Elevated cytosolic Ca^{2+} activates Ca^{2+}-dependent proteases, such as calpains, cathepsins, and caspases, that are associated with cytoskeletal protein degradation (Ertbjerg, 2022). Meanwhile, various anti-apoptotic molecules, such as Bcl-2, Bcl-XL, and HSPs, are expressed to regulate apoptosis and maintain the structural and functional integrity of mitochondria and muscle fibers (Kemp & Parr, 2012). This complex interplay between these apoptotic and anti-apoptotic factors substantially influences the variation in beef tenderness (Kim et al., 2023).

Table 1 summarizes the various studies on the effects of apoptotic and anti-apoptotic molecules on meat quality variation, especially tenderness, in animals showing a redder surface color due to a higher percentage of type I fibers. Lee et al. (2022a) reported that significant differences in sensory tenderness of Hanwoo *longissimus thoracis* (LT) muscles between the Warner–Bratzler shear force (WBS) groups were associated with the combination of the expression levels of apoptotic and anti-apoptotic molecules at the early postmortem period. Tender beef from the low WBS group (average 50.9 N) showed higher expression levels of apoptotic factors at 45 min postmortem, including cytochrome *c*, initiator caspase 9, and effector caspase 3, compared to tougher beef from the high WBS group (average 67.4 N) ($P < 0.05$; Lee et al., 2022a). In addition, αβ-crystallin, a molecular chaperone that interacts with and inhibits apoptosis-promoting factors in the intrinsic and extrinsic pathways, was lowly expressed (1.00 vs. 2.13, $P < 0.01$) in the low group than in the high group (Lee et al., 2022a). Ma et al. (2022) found that a rapid glycolytic rate induces mitochondrial dysfunction and promotes the release of cytochrome *c*, thereby subsequently enhancing caspase 3 activation and ultimately contributing to improved tenderness of LT muscle in crossbreed bulls. In contrast, it is generally accepted that the calpain system is one of the major proteases that determine beef tenderization through fragmentation of numerous cytoskeletal proteins (Koohmaraie, 1992; Wheeler et al., 1997). During the aging process, the improvement in tenderness cannot be attributed solely to calpains, as their activity is predominantly elevated at the early postmortem period and then decreases (Morgan et al., 1993). In addition to calpains, other endogenous proteases significantly contribute to this process (Lee et al., 2022a). Kim et al. (2023) investigated the underlying factors, especially caspases, contributing to variations in tenderness improvement in the Holstein–Friesian breed, which is renowned for its lower marbling

Table 1
Summary of results of the association between apoptosis-related molecules and meat quality traits in cattle, lamb, and yak during the postmortem.

Animal	Sample preparation	Apoptosis-related molecules	Measurement	Result	Reference
Cattle (steer)	- Breed: Hanwoo - Sample: LT muscle at 45 min & 24 h PM - WBS Groups 1. Low group: mean 50.9 N 2. Medium group: mean 58.9 N 3. High group: mean 67.4 N	Cytochrome *c*, caspase 9, caspase3, caspase 7, αβ-crystallin, HSP20, & HSP27	Histochemical traits, meat quality traits, sensory traits, qPCR, & western blot	- The effect of meat quality on sensory characteristics was fixed in this study. Thus, no significant associations were observed between the sensory quality and meat quality (including marbling) or histochemical traits. - The low group: 1. Greater score for sensory tenderness 2. Higher levels of apoptotic molecules, including cytochrome *c*, initiator caspase, and effector caspase, at 45 min PM 3. Lower level of αβ-crystallin at 45 min PM - The combination of expression levels of apoptotic and anti-apoptotic molecules at the early PM period may be relevant indicators explaining the tenderness variation in Hanwoo cattle	Lee et al., 2022a
Cattle (steer)	- Breed: Luxi yellow cattle × Simmental crossbred - Sample: LT muscle at 0.5, 2, 6, 12, 24, 48, & 72 h PM - Muscle pH Groups 1. Fast decline group: $pH_{6\ h} < 5.8$ 2. Slow decline group: $pH_{6\ h} > 6.2$	Caspase 3	Muscle pH, ROS, mitochondrial membrane permeability, caspase 3 activity, MFI, WBS, etc.	- The fast group: 1. Higher ROS levels at 6–24 h PM 2. Higher mitochondrial dysfunction at 6–72 h except at 48 h PM 3. Increased caspase 3 activity - Faster glycolysis enhanced caspase 3 activity and tenderization by mitochondrial apoptosis during aging.	Ma et al., 2022
Cattle (steer)	- Breed: Holstein-Friesian - Sample: LT muscle at 0, 14, & 28 d of aging - WBS change value (CV) Groups * Categorized by CV * CV = WBS value at 0–14 d 1. Lower CV (LC) group: ranging from 13.3 to 24.0 N 2. Higher CV (HC) group: ranging from 24.6 to 41.7 N	Cytochrome *c*, caspase 9, & caspase 3	Meat quality traits, sensory quality traits, & western blot	- The HC group exhibited a greater tenderness improvement from 0 to 14 d of aging than the LC group. - The HC group: 1. Higher scores of sensory tenderness attributes (softness, initial tenderness, and chewiness) at 14 and 28 d of aging 2. Higher degradation levels of apoptotic factors (cytochrome *c*, caspase 9, and caspase 3) at 14 d of aging 3. Higher degree of desmin and troponin T degradation at 14 d of aging - Greater improvement in tenderness during aging was associated with a higher degree of myofibrillar protein degradation, driven by increased activity of apoptotic molecules.	Kim et al., 2023
Lamb	- Age: 7 mon - Sample: LTL muscle at 0, 3, 6, & 9 d of aging - Live weight: mean 48.1 kg - Genotypes 1. Normal: *C/C*, *C/+*, & *+/+* 2. Callipyge: *+/C*	Calpain, calpastatin, αβ-crystallin, HSP20, and HSP27, caspase 3, & cytochrome *c*	Western blot	- Callipyge genotype: 1. Tougher meat 2. Higher calpastatin activity 3. Lesser μ-calpain autolysis 4. Lower cytochrome *c* and inactive procaspase 3 5. Lower degradation of HSP27 - Delayed onset of apoptosis by anti-apoptotic factor (HSP27) resulted in delayed apoptotic proteolysis, especially caspase 3 activation, and subsequent less tenderization of lamb.	Cramer et al., 2018
Yak	- Weight: 241 to 280 kg - Sample: LL muscle at 6, 12, 24, 72, 120, & 168 h PM - Groups 1. Control: without injection 2. DEVD group: injected with AC-DEVD-CHO (caspase 3 inhibitor)	Caspase 3, caspase 8, & caspase 9	Caspase activities, shear force, MFI, pH, etc.	- During the storage periods: decreased shear force was observed in both groups - The DEVD group (treated with caspase 3 inhibitor): 1. Lower activities of caspase 3, caspase 8, and caspase 9 2. Tougher meat 3. Lower pH value at 120 h PM	Yayuan et al., 2022

(*continued on next page*)

Table 1 (*continued*)

Animal	Sample preparation	Apoptosis-related molecules	Measurement	Result	Reference
Cattle (bull)	- Breed: Luxi × Simmental crossbred - Sample: LT muscle at 0.25, 1, 3, & 7 d PM - Treatment groups 1. Control group: 100 mM NaCl & 2 mM NaN_3 2. Ca group: control + $CaCl_2$ 3. Zn group: control + $ZnCl_2$	Cytochrome *c* & caspase 3	WBS, western blot, etc.	- Inhibited caspase 3 activity may retard tenderization during aging by affecting postmortem glycolysis and reducing protein breakdown. - Ca^{2+} injected sample 1. Increased level of cytochrome *c* 2. Decreased level of caspase 3 precursor 3. Increased level of desmin degradation - Cytosolic Ca^{2+} can accelerated tenderization through increased caspase 3 activation during aging.	Huang et al., 2018
Cattle (bull)	- Breed: Simmental × local Chinese yellow crossbred - Sample: LD muscle at 0, 6, 12, 24, 72, 120, & 168 h PM - Treatment groups 1. Control group: without injection 2. DFO group: 0.1 mM DFO (iron chelator) 3. CA-074 Me group: 10 μM CA-074-Me (cathepsin B inhibitor) 4. Pepstatin A group: 100 μM Pepstatin A (cathepsin D inhibitor)	Bid, Bax, caspase 9, & caspase 3	Lysosomal membrane stability, ROS content, GSH activity, cathepsins activity, mitochondrial membrane permeability, shear force, etc.	- The DFO group 1. Lower ROS content and higher lysosomal membrane stability at 12, 24, and 72 h PM 2. Lower activation of cathepsin B and D at 24 and 72 h PM - The Pepstatin A group: 1. Lowest levels of Bid and Bax during aging, resulting in lower caspase 3 activity aged 0–120 h 2. Highest WBS value aged 120 and 168 h - Accelerated lysosomal-mitochondrial apoptosis may primarily depend on apoptotic factors, especially cathepsin D, to improve tenderness during aging.	Zhang et al., 2019

Abbreviations: LT, *longissimus thoracis*; PM, postmortem; WBS, Warner-Bratzler shear force; HSP, heat shock protein; qPCR, quantitative real-time polymerase chain reaction; ROS, reactive oxygen species; MFI, myofibril fragmentation index; LTL, *longissimus thoracis et lumborum*; LL, *longissimus lumborum*; LD, *longissimus dorsi*; DFO, desferrioxamine; Bid, BH3 interacting domain death agonist; Bax, B-cell-lymphoma protein 2-associated X; GSH, glutathione.

degree and inherent toughness. In this study, beef loin exhibiting greater improvement in tenderness from 0 to 14 d of aging demonstrated a higher degree of myofibrillar protein degradation during the aging period, which was promoted by the increased activity of apoptotic factors such as cytochrome *c*, initiator caspase, and executor caspase, compared to beef loin exhibiting lesser improvement in tenderness (Kim et al., 2023).

To determine the causes of toughness in callipyge lamb, Cramer et al. (2018) compared the levels of apoptotic and anti-apoptotic factors during aging between loin samples from the normal and callipyge groups. They reported that the callipyge lamb samples exhibited higher anti-apoptotic activity compared to the normal lamb samples. This upregulation of the anti-apoptotic activity could be accompanied by decreased activity of caspase 3, thus leading to the delayed onset of apoptosis (Cramer et al., 2018). Therefore, the toughness of callipyge lamb may be associated with a reduced apoptotic rate mediated by an elevated anti-apoptotic response. Similarly to callipyge lamb, delayed cell death in yak muscles may impede tenderization during the aging period, resulting in tougher meat (Yayuan et al., 2022). The *longissimus lumborum* (LL) muscles of yak bulls treated with a caspase 3 inhibitor exhibited reduced caspase activity (caspase 3, caspase 8, and caspase 9) at 12 h postmortem and significantly higher shear force values during aging compared to the untreated LL muscles (Yayuan et al., 2022).

Meanwhile, beef tenderness can be improved by combining the methods of postmortem aging with the acceleration of the apoptotic pathway (Huang et al., 2018; Zhang et al., 2019). Huang et al. (2018) injected $CaCl_2$ or $ZnCl_2$ buffer into beef steaks from Luxi and Simmental crossbred bulls. They found that Ca^{2+} ion injection accelerated tenderization during the aging process by enhancing apoptosis through the increased release of cytochrome *c* and promotion of caspase 3 activity. However, beef samples injected with Zn^{2+} ions exhibited the opposite tendency because of their anti-apoptotic properties (Huang et al., 2018). Thus, in the absence of efficient apoptotic inhibitors, caspases tend to activate in a rapid cascade-like manner. Zhang et al. (2019) suggested that the increased release of cathepsins, which results from impaired lysosomal membrane stability due to the increased levels of ROS, could enhance tenderization during aging. This occurs because cathepsin B and cathepsin D induce the activation of mitochondrial BH3 interacting domain death agonist (Bid) and Bax, and the increased formation of MPT pores by Bid and Bak releases various apoptotic molecules into the cytoplasm, which leads to lysosomal–mitochondrial apoptosis (Zhang et al., 2019).

Overall, ruminant muscles harboring a redder surface color and a higher proportion of type I fibers typically demonstrate lower expression of initiator and effector caspases, indicating a lower apoptotic potential compared to porcine and poultry muscles, which are characterized by a paler surface color and a higher proportion of type IIB fibers. In bovine and ovine muscles, sensory tenderness, the most important of organoleptic traits, can be optimized by controlling a delicate balance between the activities of endogenous proteases and anti-apoptotic factors and facilitating a rapid progression to the resolution phase of rigor mortis. However, to practically apply this knowledge to enhance consumer preference, further research is required to identify optimal treatments, such as aging and calcium injection, that accelerate the intrinsic apoptotic pathway.

3.3. Apoptosis and quality characteristics of porcine and poultry muscles

Rapid growth rates and superior lean meat production observed in modern swine and poultry lines have led to alterations in muscle fiber properties (particularly an increase in large-sized glycolytic fibers), thereby increasing their susceptibility to various stressors (Choi et al., 2013; Lebret and Čandek-Potokar, 2022). This increase in large-sized fibers reduces the space between the muscle fibers and limits the room available for capillaries, which results in a greater glycolytic potential due to lack of oxygen supply (Petracci et al., 2017). Moreover, accelerated ATP depletion due to a rapid rate of glycolysis during the postmortem period is accompanied by an increased rate of intrinsic apoptosis, thus leading to undesirable meat quality characteristics by extensive myofibrillar and sarcoplasmic protein denaturation (Choi & Kim, 2009; Lee & Choi, 2021a). Therefore, unlike animals with a higher percentage of type I fibers, the rapid apoptotic rate induced by apoptotic molecules could negatively impact on the physicochemical characteristics of meat quality in animals with a higher percentage of type IIB fibers, such as pigs, chickens, and turkeys (Lee et al., 2022b; Lee & Choi, 2021a).

Table 2 summarizes the combined effects of apoptotic and anti-apoptotic molecules on the meat quality variation of animals harboring a higher percentage of type IIB fibers. Guo et al. (2016) reported that cytosolic Ca^{2+} levels and the apoptotic potential during the postmortem period were associated with the development of pale, soft, exudative (PSE) in porcine *longissimus* muscle. Cytosolic Ca^{2+} levels are regulated by various molecules in the sarcoplasmic reticulum (SR), such as inositol 1,4,5-triphosphate receptors (IP3Rs), which facilitate Ca^{2+} release from the SR into the cytosol, and sarco/ER Ca^{2+}-ATPase (SERCA), which regulates Ca^{2+} reabsorption into the SR (Lee et al., 2022b). The PSE condition group exhibited higher cytosolic Ca^{2+} levels, which was attributable to a lower expression of SERCA and a higher expression of IP3Rs compared to the normal condition group (Guo et al., 2016). The increased Ca^{2+} levels in PSE pork indicated a higher apoptotic potential, as demonstrated by the elevated expression levels of Bax, cytochrome *c*, and caspase 3 compared to normal pork (Guo et al., 2016). In addition, Yu et al. (2009) reported that PSE meat may be linked to disruptions in the fiber membrane function and permeability, along with reduced expression levels of anti-apoptotic HSPs at the early postmortem period, such as αβ-crystallin and HSP27. These HSPs play crucial roles in maintaining cellular protein homeostasis by preventing irreversible damage to myofibrillar proteins and stabilizing aggregated proteins, thereby reducing their susceptibility to proteolytic denaturation. Conversely, some studies have suggested that HSPs, as representative stress indicators, may be significantly elevated in PSE conditions, and this increase is often associated with animals exhibiting higher susceptibility to stress and faster glycolysis during the early postmortem period (Lee & Choi, 2021a; Liu et al., 2021). Therefore, HSPs may be intricately involved in various processes and conditions, including glycolysis, apoptosis, stress response, and protein modification, leading to divided results in related studies.

Muscles from modern pigs and poultry are generally prone to metabolic-associated disorders and myopathies because of their increased glycolytic potential (Lee & Choi, 2021b). In poultry species, recent significant issues regarding muscular abnormalities associated with the deterioration of sensory and meat quality traits encompass PSE conditions, white striping (WS) feature, and wooden breast (Petracci et al., 2019). Lee and Choi (2021a) reported relationships between the expression levels of anti-apoptotic factors and the development of muscular abnormalities, including PSE and WS features and found that the expression levels of HSPs at 15 min postmortem were significantly increased in PSE condition chickens compared to normal condition chickens. An excessive increase in HSPs during the early postmortem period may be linked to the stress susceptibility of individuals and the impaired quality traits in the PSE broilers (Lee & Choi, 2021a). However, the apoptotic potential has a rather limited effect on the occurrence of WS in broilers, whereas excessive fiber hypertrophy and chronic stress may be associated with the development of WS features (Lee & Choi, 2021a). Similar to the muscles in broilers, a rapid rate of cell death, as measured by the proportion of apoptotic nuclei, could cause deterioration in meat quality traits in duck breast and thigh muscles, including lightness, cooking loss, and tenderness (Zhang et al., 2013). Moreover, excessive oxidative stress may induce a rapid apoptotic rate due to the increased formation of MPT pores and increased activity of caspases (Zhang et al., 2019). Thigh muscles of broilers showing a higher level of ROS formation induced by H_2O_2 injection displayed

Table 2
Summary of results of the association between apoptosis-related molecules and meat quality traits in pig and poultry during the postmortem period.

Animal	Sample preparation	Apoptosis-related molecules	Measurement	Result	Reference
Pig	- Breed: Erhualian × Landrace × Yorkshire crossbred - Live weight: 100 to 120 kg - Sample: *longissimus* muscle - Groups 1. PSE group: $L^* > 50$, pH < 6.0, & drip loss >10 % 2. RFN group: $L^* < 50$, pH > 6.0, & drip loss <10 %	Bax, Bcl-2, cytochrome *c*, & caspase 3	Meat quality traits, western blot, & caspase 3 activity	- The PSE group: 1. Overloaded sarcoplasmic Ca^{2+} status 2. Higher level of Bax & lower level of Bcl-2 3. Higher level of cytochrome *c* 4. Increased activity of caspase 3 - Development of PSE pork was associated with a greater apoptotic potential because of increased cytosolic Ca^{2+} levels resulting from impaired endoplasmic reticulum Ca^{2+} channel.	Guo et al., 2016
Pig	- Breed: F2 offspring of Pietrain × Erhualian - Sample: LD muscle - Treatments 1. Control: no transportation 2. Transport group: 1, 2, or 4 h at 30–40 km/h	αβ-crystallin, HSP27, HSP70, & HSP90	CK activity, LDH activity, meat quality traits, etc.	- Transport treatment: 1. Increased CK & LDH activities 2. Lower initial & ultimate pH values 3. Higher drip loss & lightness values 4. Decreased levels of all HSPs - Stressor-induced meat quality damage in PSE pork may be associated with decreased expression levels of anti-apoptotic HSPs.	Yu et al., 2009
Chicken	- Breed: Ross 308 (male) - Live weight: 1792 ± 301 g - Sample: PM muscle - Groups * Categorized by WS degree & L^* 1. NN group: normal quality without WS 2. NW group: normal quality with WS 3. PN group: PSE quality without WS 4. PW group: PSE quality with WS	αβ-crystallin, HSP70, & HSP90	Carcass traits, histochemical traits, meat quality traits, qPCR, & western blot	- WS traits 1. Greater PM muscle weight and fiber size 2. Limited effect on meat quality traits - PSE traits 1. Higher lightness and WBS values 2. Higher levels of HSPs, except for HSP70, at 15 min postmortem - Anti-apoptotic factors at the early postmortem period were related to chicken breast muscle quality, and higher apoptotic potential can lead to the incidence of PSE conditions.	Lee & Choi, 2021a
Chicken	- Breed: Arbor Acres (male) - Age: 42 d old - Sample: thigh muscle - Treatments 1. Control: without injection 2. Saline injection: 0.75 % physiological saline (1.0 mL/kg of body weight) 3. H_2O_2 injection: 2.5, 5.0, and 10.0 % (1.0 mL/kg of body weight) * Saline or H_2O_2 injection was performed at 16 and 37 d after hatching.	Bcl-2, Bax, caspase 3, caspase 6, caspase 8, & caspase 9	ROS detection, histochemical traits, meat quality traits, oxidative parameters, qPCR, & western blot	- 10 % H_2O_2-injected broilers 1. Highest ROS formation, indicating signs of higher oxidative stress 2. Higher levels of apoptotic molecules, including caspases 3. Significantly lower $pH_{24\ h}$ values and higher shear force values - Apoptosis process was accelerated by excessive ROS stress, and broilers that underwent oxygen stress exhibited undesirable meat quality traits.	Yan et al., 2022
Chicken	- Breed: Ross 308 (male) - Live weight: 1.38 ± 0.10 kg - Sample: PM muscle & blood serum - Groups * Clustered by serum AST activity 1. Low group: average of 195 U/L (ranging from 179 to 210 U/L) 2. Medium group: average of 235 U/L (ranging from 211 to 259 U/L) 3. High group: average of 287 U/L (ranging from 260 to 335 U/L)	AST, Ca^{2+}, cytochrome *c*, caspase 9, & caspase 3	AST activity, Ca^{2+} content, serotonin content, qPCR, meat quality traits, & sensory quality traits.	- The low group: 1.Higher serum Ca^{2+} level and a lower serotonin level 2. Higher levels of cytochrome *c* and caspases 3. Lower pH values and a higher L^* value at 24 h, indicating PSE quality 4. Lower sensory juiciness and overall acceptability scores - Poor meat quality traits and the occurrence of PSE condition can be influenced by increased levels of apoptotic molecules regulated by serum Ca^{2+} levels in broiler PM muscles.	Lee et al., 2022b
Duck	- Live weight: approximately 2.0 kg - Sample: breast and thigh muscles at 0.5, 4, 8, & 12 h postmortems	Apoptotic nuclei	Meat quality traits, histochemistry, etc.	- Duck breast and thigh muscles 1. Apoptosis occurs in duck muscles at the quite early PM 2. As apoptotic nuclei increase, the intercellular space decreases, and cell shrinkage increases 3. Apoptosis levels were associated with the meat quality traits, including color, WHC, and WBS values.	Zhang et al., 2013

Abbreviations: PSE, pale, soft, and exudative; L^*, lightness; RFN, reddish, firm, and non-exudative; Bcl-2, B-cell-lymphoma protein 2; Bax, Bcl-2-associated X; LD, *longissimus dorsi*; HSP, heat shock protein; CK, creatine kinase; LDH, lactate dehydrogenase; PM, *pectoralis major*; qPCR, quantitative real-time polymerase chain reaction; H_2O_2, Hydrogen peroxide; ROS, reactive oxygen species; AST, aspartate aminotransferase; WHC, water-holding capacity; WBS, Warner–Bratzler shear force.

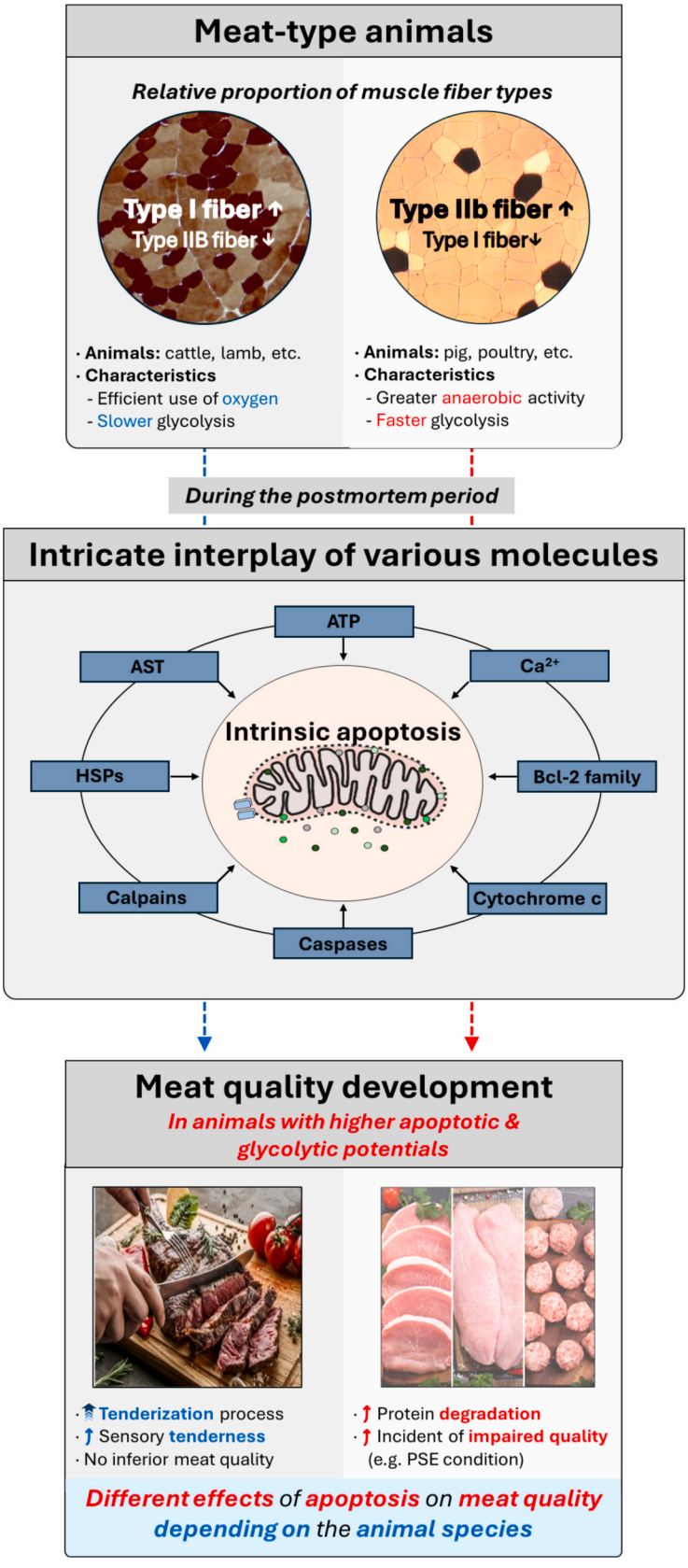

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Fig. 3. Comparison of the effects of postmortem apoptosis on meat quality traits in different meat-type animals. After exsanguination, which implies a state of ischemia/hypoxia, skeletal muscle is converted into meat by initiating the intrinsic apoptosis pathway. This includes a complex interplay of apoptosis-related molecules, which influences the conversion process during the postmortem period. The expression levels of these molecules influence the apoptotic and glycolytic potentials, and their effect on meat quality development varies depending on the meat-type animals. Muscles exhibiting a redder surface color, such as bovine and ovine muscles, have a slower rate of apoptosis as well as glycolysis due to a higher proportion of type I fibers compared to muscles showing a paler surface color due to a higher proportion of type IIB fibers, such as porcine and poultry muscles. The rate of cell death process can have varying effects on meat quality development in animals with a higher percentage of type I or type IIB fibers. For example, a moderate to rapid apoptotic rate in beef and lamb is generally associated with improved tenderness. Conversely, in pork and chicken, a rapid apoptotic rate is often linked to a higher glycolytic potential and accelerated ATP depletion, which can lead to undesirable quality traits, such as pale, soft, exudative conditions. The histochemical images in the top box: left, the *longissimus thoracis* muscle from a Hanwoo steer using acid ATPase staining; right, the *longissimus dorsi* muscle from a crossbred pig using acid ATPase staining. Abbreviations: Bcl-2, B-cell-lymphoma protein 2; HSPs, heat shock proteins; AST, aspartate aminotransferase; PSE, pale, soft, and exudative.

higher expression levels of initiator and effector caspases, which resulted in a rapid apoptotic rate and resulting in undesirable meat quality traits compared to thigh muscles without H_2O_2 injection (Yan et al., 2022). Lee et al. (2022b) suggested that elevated Ca^{2+} levels were also linked to the development of PSE in broilers by accelerating the postmortem intrinsic pathway. To investigate this, serum Ca^{2+} levels, expression levels of Ca^{2+}-channel genes and apoptotic-associated molecules, and the activity of serum aspartate aminotransferase (AST, which is crucial for maintaining mitochondrial integrity by regulating intracellular Ca^{2+} levels) were analyzed. *Pectoralis major* (PM) muscles from the low AST group (average of 195 U/L) exhibited a higher level of serum Ca^{2+}, which suggests that more Ca^{2+} was released into the sarcoplasm ($P < 0.01$) compared to the high AST group (average of 287 U/L) (Lee et al., 2022b). Disruptions in Ca^{2+} homeostasis are associated with alterations in mitochondrial morphology, which subsequently lead to the release of cytochrome *c*. This release acts as a key trigger of the apoptotic proteolysis during the quite early stages of apoptosis (Marchi et al., 2018; Wang et al., 2019). In addition to a higher level of Ca^{2+}, the low AST group presented higher levels of RyR and caspases at 15 min postmortem than the high AST group ($P < 0.05$). The low AST group showing a higher apoptotic potential had lower pH (5.70 vs. 5.86, $P < 0.001$), higher lightness (55.3 vs. 52.3, $P < 0.01$), and lower sensory acceptability values as determined by trained panelists (5.35 vs. 5.87, $P < 0.05$) at 24 h postmortem compared to the high AST group (Lee et al., 2022b), which is indicative of the presence of PSE conditions with undesirable organoleptic traits (Carvalho et al., 2014; Qiao et al., 2002). Moreover, Lee and Choi (2022) confirmed that PM muscles with a rapid glycolytic rate exhibited an increased apoptotic potential compared to those with a normal glycolytic rate. This is because the increase in apoptotic potential was due to the accelerated glycolysis and subsequent depletion of ATP during the early postmortem period (Lee & Choi, 2022).

Taken together, in poultry and porcine muscles, elevated cytosolic Ca^{2+} levels, caused by calcium channel dysfunction and extensively released from mitochondria, are closely associated with increased levels of apoptotic molecules and decreased anti-apoptotic molecules. This heightened apoptotic potential is accompanied by an acceleration of the glycolytic rates due to ATP depletion, which negatively affects myofibrillar and sarcoplasmic protein integrity. As a result, undesirable meat quality traits can develop, such as reduced WHC, lighter muscle surface, and lower sensory acceptability. Therefore, glycolysis and apoptosis in postmortem muscle are interconnected processes that jointly determine the biochemical and physical changes in poultry and porcine meat. In these species compared to ruminants, reducing the apoptotic rate during the early postmortem period requires treatments that directly stabilize cellular and mitochondrial integrity. Practical treatments to minimize apoptotic activity include rapid carcass chilling to slow enzymatic processes, regulating the pH decline rate by reducing and controlling preslaughter stressors, managing calcium levels to prevent excessive protease activation, using antioxidants to alleviate oxidative stress, etc.

4. Conclusion

Meat quality is a highly complex attribute influenced by various environmental and genetic factors, requiring species-specific improvement treatments that account for differences in skeletal muscle characteristics to improve quality traits. This review provides deep insight into the mechanisms of postmortem apoptosis that influence meat quality, offering a comprehensive explanation of how apoptotic molecules contribute to the development of key quality attributes in different meat animals. Among the apoptosis pathways, the intrinsic pathway plays an essential role in regulating the complex morphological and biochemical changes during the conversion of muscle to meat. These changes are determined by the intricate interactions between apoptosis-related molecules, especially Ca^{2+}, ATP, cytochrome *c*, caspases, the Bcl-2 family, and HSPs (Fig. 3.). The apoptotic potential, as determined by the relative expression levels of anti-apoptotic and apoptotic molecules, can exert different effects on meat quality characteristics depending on the animal type. In animals characterized by a higher proportion of type I fibers, such as cattle and lamb, where improvement in sensory quality is particularly important to increase consumer satisfaction, moderate to rapid apoptotic rates typically accelerate the degradation of structural proteins, thereby contributing to desirable tenderness attributes. However, the rapid apoptotic rate in postmortem muscles of animals with a higher proportion of type IIB fibers, such as pork and poultry meat, is associated with high glycolytic potential and can result in undesirable quality traits, such as PSE conditions. Therefore, understanding the species-specific responses to apoptosis is crucial for developing strategies in meat production to improve and maintain the quality attributes of animals with different characteristics.

CRediT authorship contribution statement

Boin Lee: Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Young Min Choi:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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