Relationships between loin physical, meat quality and intramuscular collagen characteristics of carcasses from crossbred swine populations

by

Prince Opoku

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Animal Science

Department of Agricultural, Food and Nutritional Science
University of Alberta

ABSTRACT

Carcass and meat characteristics are of great importance to the pork industry as they determine the ultimate returns from animals produced. Making genetic progress in these traits requires them to be measurable, heritable and have adequate additive genetic variability. Estimates of genetic parameters must therefore be assessed to determine heritability and level of additive genetic variation for use in selection programs. In the first study, phenotypic data from 500 pedigreed crossbred pigs from Duroc sires and hybrid Large White × Landrace sows from two different swine genetics companies were used. Fixed effects (slaughter batch, sex and company), and a random additive effect were fitted in bivariate animal models to estimate phenotypic and genetic parameters in ASReml. Moderate heritabilities were obtained for loin compositional traits ranging from 0.21±0.10 for bone weight to 0.44±0.11 for loin eye weight with low estimates of 0.09±0.08, 0.19±0.08, 0.13±0.09 obtained for bone percent, loin weight and fat trim weight, respectively. Meat quality traits were low to moderately heritable with the highest estimate being found for intramuscular fat (0.42±0.13). The heritability estimates for percentages of heat soluble and insoluble collagen were 0.12±0.09 and 0.15±0.09, respectively, while 0.33±0.12 was found for total collagen content. Moderate heritability implies the possibility of improving these traits through selective breeding. Strong negative genetic correlations between moisture and fat traits and a further negative correlation between fat and muscling traits confirmed that selection for improved muscling over time negatively affects fat traits and may then decrease meat eating quality. The strong genetic correlations of lightness (L^*) with soluble collagen (0.68±0.30) and insoluble collagen (-0.71±0.35) suggest possible pleiotropic gene effects on these traits. Warner-Bratzler shear force (WBSF) had moderate genetic correlations with insoluble collagen (0.42±0.16) and soluble collagen (-0.38±0.10), suggesting a potential relationship between some of the genes impacting these traits. Genetic correlations between WBSF and collagen characteristics indicated that despite the relative youthfulness of pigs at slaughter, genetic selection for collagen solubility may decrease WBSF.

In the second study, the contributions of company, sex and loin physical and collagen characteristics to measures of pork carcass and meat quality in a Canadian context were examined. Results from this study indicated that intramuscular collagen characteristics influenced loin cooking loss and further revealed that Warner-Bratzler shear force (WBSF) values were driven more by denaturation of myofibrillar proteins than by intramuscular fat content. Means separation analysis also showed WBSF to increase with increased muscularity and reduced backfat which suggests that selection for rapid growth rate with its associated reduction in calpain activity may decrease pork tenderness. This study further implicates pH and intramuscular fat content as part of the traits influencing insoluble collagen percent indicating that deposition of fat in the perimysium may be a potential disruptor of crosslink formation. Step- wise regression indicated that pH is not a reliable sole predictor of meat quality in loin that has been frozen and then thawed and thus other variables in addition to pH are needed to reliably predict frozen/thawed pork quality. Drip loss predicted most of the variation in tenderness which indicated that pork samples in the present study may have undergone myofibrillar protein oxidation during frozen storage or dehydration during cooking. The results indicated that sex has no significant influence ($p>0.05$) on loin compositional and meat quality traits while source of animal has a significant ($p<0.01$) influence on loin composition, pH, drip loss (%), cooking loss (%) and collagen characteristics.

In summary, the genetic parameters estimated in this study will make it feasible to predict response to genetic selection on loin and collagen characteristics and further add to the already established research database on meat quality traits. The results of this study also provide insights on variables with potential for predicting pork quality and suggest that although the populations studied were obtained from the same breed combinations differentiation in terms of loin compositional, meat quality and collagen characteristics would not be expected based on sex but would be expected in terms of animal origin.

Acknowledgements

Throughout the writing of this thesis I have received a great deal of assistance and support. I would first like to thank the Natural Sciences and Engineering Research Council (NSERC), Hypor Incorporated and Genesus Genetics for generously supporting this research.

Further, I would like to express my utmost gratitude to my supervisor Dr. Heather Bruce for giving me the opportunity to study at the University of Alberta, and for the time, effort and academic advice she provided throughout this study. The door to Dr. Bruce's office was always open whenever I had a question about my research or ran into a trouble spot. She consistently allowed this thesis to be my own work but steered me in the right the direction whenever she thought I needed it.

I would also like to express gratitude to Dr. Leluo Guan for the suggestions and guidance she provided me for the completion of this work. I further thank Professor Graham Plastow for his constructive comments and criticisms. I further thank Dr. Changxi Li and Dr. Arthur Gilmour whose expertise was invaluable during my statistical analysis.

Also, I would like to extend my thanks to Dr. Bimol Roy for his guidance during my laboratory work, Dr. Huaigang Lei for help during my statistical analysis and Dr. Robert Mukiibi who have provided me with invaluable assistance and support throughout the course of my studies.

Finally, I would really like to thank Rabaa Hamed, Jiyuan Li, Patience Coleman and all my lab mates and friends for their support and for providing happy distractions to rest my mind outside of my research. This experience would not have been the same without them.

In addition, I would also like to thank my family for their wise counsel, sympathetic ear, encouragement and their many sacrifices that have allowed me to reach this stage in my life. My father, Kwame Panin, My mother, Akua Konadu, my sisters, Diviana Amadie-Panin and Munich Konadu-Panin and Niece, Elsie Nana Achia Panin. I thank God for making everything come together in the end.

Table of Contents

List of Tables

List of Figures

List of Abbreviations

BP	Bone percent
BWT	Bone weight
CL	Cooking loss percent
ECM	Extracellular matrix
FOF	Foss crude fat
FOM	Foss crude moisture
FOP	Foss crude protein
FTW	Fat trim weight
IMCC	Intramuscular connective tissue characteristics
IMF	Intramuscular fat
ISOLC	Insoluble collagen percent
LEP	Loin eye percent
LEW	Loin eye weight
LOINA	Minolta a^*
LOINB	Minolta b^*
LOINC	Minolta chroma
LOINH	Minolta hue
LOINL	Minolta L^*
LWT	Loin weight
MC	Moisture content (%)
MTW	Meat trim weight
MRA	Metmyoglobin reducing activity

PSE	Pale, soft, and exudative
RTP	Rib trim percent
RTW	Rib trim weight
SOLC	Soluble collagen percent
TCOL	Total collagen (mg/g raw meat)
TFP	Thick fat percent
TFW	Thick fat weight
WBSF	Warner-Bratzler shear force (N)

Chapter 1

1.0 Introduction

Swine domestication from wild boar subspecies in Asia and Europe approximately 9000 years ago is known to have been of critical importance in establishing a secure supply of protein to various human civilizations (Bosse 2018; Guiffra et al., 2000). Indeed, pork is currently the most consumed meat worldwide accounting for about 40% of the world's meat consumption (USDA, 2017; Rothschild and Ruvinsky, 2011). Pork consumption per capita worldwide as of 1961 was 8.0 kg but saw a steady rise to 16.0 kg by 2013 (FAO, 2017; Ritchie and Roser, 2019). This increase was most likely driven by the exponential rise in the worldwide population leading to an increase in pork production from 24.8 million tons in 1961 to 112.3 million metric tons in 2013, representing an over 4-fold increase (FAO, 2017; Ritchie and Roser, 2019). In Canada, production went from 535,940 in 1961 to 2.53 million tons in 2013. Expectedly, OECD/FAO (2018) projected a 15% increase in global meat production over the next decade using the average of 2015-2017 as the base and this increase was anticipated to be driven mainly by developing countries. Concomitant with this increase, over the next ten years a rise in the global demand for mutton/lamb and beef while a decrease in the demand for pork and poultry is projected (OECD/FAO, 2018). This will most probably be due to the fact that consumers of meat in most developing countries, over the years, preferred pork and poultry due to the relatively lower market prices of their end products. However, projected growth in consumer incomes over the next decade is expected to fuel a shift in their preference to more costly meat like that from sheep and cattle (USDA, 2018; OECD/FAO, 2018). It is therefore crucial and critical that commercial pig producers and processors endeavor to boost production efficiency and most importantly produce pork that meets the high standards of consumers so that they remain competitive with producers of other species in the global livestock and animal protein markets (Salas and Mingala, 2017).

Genetic improvement of animal performance traits like litter size, lean percent, carcass weight, average daily gain, and growth rate that are economically vital to producers has conventionally been the focus of swine breeding programs (Kanis et al., 2015). However, this trend is gradually shifting as consumers are progressively allocating less importance to price in their purchasing decisions and attaching more value to traits and issues like pig welfare and health, healthiness of pork, organoleptic properties and overall eating quality (Tsakiridou et al., 2010; Ciobanu et al., 2011). Meat quality is therefore progressively exerting much influence on processor and consumer decisions and thus on the direction of the swine industry (Lonergan et al., 2001). Indeed, research studies are showing that selection for traits of economic importance to producers like feed efficiency, lean percent, and carcass weight could negatively affect pork quality (Miar et al., 2014; Lonergan et al., 2001). The increase in demand for pork products of good quality has led to an increase in research by animal breeders and meat scientists to discover ways of improving meat quality (Ciobanu et al., 2001). Breeders are also increasingly becoming interested in the relationships existing between and among animal performance indicators, carcass, meat, and eating quality, and specific muscle histochemical and biochemical traits for incorporation as traits for selection in their breeding programs (Suzuki et al., 2005; Larzul et al., 1997).

Swine skeletal muscle tissue mass usually falls between 40 to 60% of their live weight (Kauffman and Warner, 1993) and are composed of a number of tissues. These include muscle fibers, vascular, nervous, adipose and connective tissues (Listrat et al., 2016). The ratio and characteristics of muscle fibers, intramuscular fat and intramuscular connective tissues play key roles in determining various quality dimensions (Listrat et al., 2016). Quality can be divided into 3 subclasses: carcass quality, meat quality and eating quality. Carcass quality usually includes factors that critically affect the market price of carcasses, and some of these factors are carcass fat cover, bone to meat ratio and carcass weight (Smulders, 1986) while meat quality encompasses all the serviceability/processeability, organoleptic, healthiness/nutritional and microbiological aspects of meat at fabrication, purchase or examination (Hoffman, 1973). Eating quality, a subset of meat quality, on the other hand, is defined by three cardinal traits: juiciness, tenderness, and flavor (Mateescu, 2005).

Intramuscular fat content has been implicated in species to species flavor differences and juiciness (Hornstein and Crowe, 1960) while muscle fiber density and intramuscular connective tissue variability have been shown to influence meat texture (Zheng et al., 2018; Thompson, 2004). For many years, numerous researchers in the field of meat science have endeavored to find the link between muscle texture and its composition (Dransfield, 1977). The role of intramuscular connective tissues or its major protein collagen has been a topic of much debate. Indeed, a critical reason for the increase in research studies focusing on the inherent characteristics of intramuscular connective tissues has been because of meat texture variability (Voutila et al., 2007). There is a consensus on the role of collagen in raw meat toughness but some skepticism as to its role in cooked meat toughness. Proponents of the hypothesis that collagen plays an only minor role on cooked meat toughness like Purslow (2018) suggest that myofibrillar proteins drive meat toughness at high cooking temperatures with the collagens essentially gelatinizing at these temperatures. However, other research studies like that of Light et al. (1985) suggest that although collagen molecules shrink at high temperatures, meats with high percentages of heat resistant trivalent cross-links tend to have stable matrices compared to those with more heat labile crosslinks (which form gelatin) (Bailey and Light, 1989). Based on this argument, it is suggested that the proportion of heat insoluble to heat soluble collagen influences meat toughness and texture to a greater degree than previously thought (Purslow, 2018). Adequate additive genetic variability in collagen traits if obtained, may pave way to the manipulation of its characteristics through selective breeding, as this is yet to be undertaken. Indeed, studies (Brock et al., 2000) on the effects of selection for increased leanness on muscle fiber type characteristics has shown that selection for reduced backfat thickness results in an increase in glycolytic muscle fibers and a decrease in oxidative fibers, and the magnitude of these changes is dependent on generation (selection period duration) and muscle type. This trend is problematic as these changes tend to affect the metabolic properties of muscles (Brock et al., 2000) and thus, muscles with higher glycolytic fibers are known to yield poor quality meat. It therefore is crucial to undertake a study to characterize the genetic relationships among V, meat quality and intramuscular collagen characteristics to test the hypothesis that because genetic relationships exist amongst them, a genetic approach may be a better tool for managing meat quality. Characterization of pork collagen has been limited most likely because pigs are relatively immature (slaughtered based on physiological age rather than chronological age) at slaughter and thus the proportion of heat-resistant collagen cross-links which would contribute to cooked pork toughness is expected to be low. However, some studies still suggest that intramuscular collagen contributes to immutable background toughness in meat irrespective of maturity level (Purslow, 2005).

The objective of this chapter was to explore the contribution of genetics, breeding and management practices to pork quality, and how collagen contributes to meat quality and is affected by genetics and management practices. To understand this contribution, the structure and composition of pork muscle and how it relates to pork quality must first be considered and appreciated.

1.1 Chemical composition and structural features of muscles

Generally, post-rigor muscle that is yet to undergo its postmortem degradative transformations will usually be comprised of 75% water, approximately 19% protein, about 2.5% fat and 3.5% non-protein soluble substances (Voyle, 1979; Mateescu, 2015). The structural integrity of muscle is maintained by 3 layers of connective tissues: there is the epimysium which sheathes the whole muscle, the perimysium which surrounds bundles of muscle fibers and the endomysium which surrounds each individual muscle fiber (Bailey and Light, 1989).

1.1.1 Muscle water

About 5-12% of the overall water content of muscle is in the space of the extracellular matrix while the rest (88-95%) is held in the myofibers (between the myofibrils, within the myofibrils, and between the myofibrils and cell membrane) (Voyle, 1979). Approximately 5% of the total water volume in muscle is bound to hydrophilic sites on myofibrillar proteins (Lee, 2012). The rest is categorized either as free water (immobilized due to myofibrillar protein configuration) or loose water, which is the water expressed during water holding capacity measurements (Hamm, 1961).

1.1.2 Muscle protein

There are three basic classifications of muscle proteins. These are myofibrillar, sarcoplasmic and stroma proteins (Xiong, 1997). This classification is based on their solubility characteristics (Xiong, 1997). Myofibrillar proteins are salt-soluble and sarcoplasmic proteins water soluble while stroma proteins are insoluble (Greaser and Guo, 2015). Figure 1.1 depicts the muscle protein fractionation into these three solubility categories.

Myofibrillar and sarcoplasmic proteins tend to be intracellular while stroma proteins are usually extracellular (Greaser and Guo, 2015). The major myofibrillar proteins by percent composition are myosin (43%), actin (22%) and titin (8%) (Greaser and Guo, 2015) while myoglobin and hemoglobin are the most important sarcoplasmic proteins (Papadopoulos, 2000). Stroma proteins fundamentally constitute the muscle connective tissue component and include elastin, collagen, and reticulin as well as the proteins in myocyte organelle membrane systems (Smulders, 1986).

1.1.3 Muscle fat

Fat reserves in mammals can be found in a number of internal and external anatomical locations where they serve as energy depots (Lebret, 2008). Two main types of adipose cells are known so far, these are white and brown adipose cells. The main differences between these two cells are that brown adipose cells besides their brown color, tend to have comparatively higher mitochondria, cytoplasm, and a greater level of vascularization (Swatland, 1994). Nascent fat tissues tend to have a higher proportion of connective tissue, water and a lower proportion of lipid; however as animals age dietary energy is diverted increasingly into fat growth, and the lipid portion increases while the proportions of connective tissue and water decrease (Aberle et al, 1977). The main systemic locations of adipose tissue with respect to muscles are between (intermuscular) and within muscle (intramuscular). Intramuscular fat content varies with breed, genotype, growth rate and nutrition (Lebret, 2008). For instance, Duroc and Meishan pigs have higher fat contents than Landrace or Large White pigs (Shingfield et al., 2013). Castrated males in the studies of Franco et al. (2014) and Alonso et al. (2009) had higher intramuscular fat contents compared to entire females. Ramirez and Cava (2007), Kim et al. (2018) and Sundrum et al. (2011) however found no effect of sex on intramuscular fat content. These differences in the results from these studies underscore the need to take into consideration how sex influences this trait in swine populations.

1.2 The extracellular matrix (ECM)

The extracellular matrix is known to be a sophisticated 3-dimensional network of macromolecules found in the extracellular space (Kaushal et al., 2014). It is the non-cellular component found within all organs and tissues, where it offers not only vital physical scaffolding for the cellular constituents but also launches crucial biomechanical and biochemical cues (Kular et al., 2014). It provides structural support for all mammalian tissues and organs, playing crucial roles in cell proliferation, migration, differentiation, signaling, and survival (Hynes, 2002; 2009). The importance of the ECM can be seen from the number of syndromes that occur from genetic abnormalities in certain ECM proteins (Jarvelainen et al., 2009). These include macromolecular network is mostly composed of laminins, proteoglycans, elastin, glycoproteins, collagens and hyaluronan (Sainio and Järvelainen, 2014; Ruoslathi, 1988) secreted by a wide array of cell types such as chondrocytes, osteoblasts, fibroblasts, endothelial cells, epithelial cells, adipocytes and tenocytes (Kaushal et al., 2014; Sainio and Järvelainen, 2014; Milz et al., 2009). Extracellular matrix components can be divided into 2 subclasses, specifically fiber-forming and interfibrillary molecules. Laminins, elastin, fibronectins and certain collagen types are typical fiber-forming ECM molecules, whereas the glycoproteins and proteoglycans are generally regarded as interfibrillary ECM molecules (Frantz et al., 2010). The molecular components of the ECM are subject to numerous post-translational modifications (Kassianidou et al., 2019) and by means of these biochemical and physical characteristics, the ECM creates the mechanical and biochemical properties of each organ, such as its elasticity, compressive and tensile strength, and also contributes to protection through a buffering action that supports extracellular water retention and homeostasis (Frantz et al., 2010). The protective, biomechanical, biochemical and organizational properties of the ECM can vary from tissue to tissue (e.g. lungs versus bone) and even within one tissue (e.g. renal medulla versus renal cortex) as well as from one physiological state to another (cancerous versus normal) (Jarvelainen et al., 2009).

1.3 Collagen structure and physiology

1.3.1 Collagen

Collagens are extracellular matrix proteins that are vital in supporting the structures of many tissues in the mammalian body (Myllyharju and Kivirikko, 2004). They are present in almost all tissues and organs of mammals and constitute between 25-30% of the mammalian body protein content, making it the most abundant protein in mammals (Langrock and Hoffmann, 2012; Bailey and Light, 1989). They are key protein components of tissues of cartilage, teeth, tendons, bones, skin, muscle connective tissues and blood vessels (Fratzl, 2008). Collagens have been found to play important roles in pathways and processes such as cell and muscle morphogenesis, cell signaling mediation, chemotaxis and even wound healing in metazoans (Myllyharju and Kivirikko, 2004; Gjaltema and Bank, 2017). All collagen molecules regardless of their types exhibit a repeating Gly-Xaa-Yaa motif (Exposito et al., 2010) in which the Xaa and Yaa positions can be any amino acid except glycine and are usually occupied by proline and 4-hydroxyprolines respectively (Bella et al., 1995). This highly ordered structure of collagen results in its characteristic inextensibility and rigidity (Parvizi and Kim, 2010). The combination of hydroxyproline, proline, and glycine accounts for approximately 57% of the total amino acid makeup of collagen (Li and Wu, 2018).

1.3.1.1 Hydroxyproline

Hydroxyproline is an amino acid post-translationally derived from the hydroxylation of proline by 4-prolyl hydroxylase (Cundy et al., 2014) with ascorbic acid being its cofactor (Stoilov et al., 2018). At the Y-position, it forms hydrogen bonds with α chains within the triple helix thereby stabilizing the trimeric structure. Hydroxyproline is not exclusive to collagen as it is also found in elastin (Schmelzer et al., 2005), it uniquely constitutes approximately 14% of collagen's overall imino and amino acid content (Neuman and Logan, 1950). It is therefore quantified as a marker amino acid in collagen assays (Stoilov et al., 2018).

1.3.2 Collagen nomenclature

Roman numerals are used to number collagens in the sequence of their discovery (Myllyharju and Kivirikko, 2004). Collagen molecules are composed of 3 left-handed alpha (α) chains (polypeptide chains) identified with Arabic numerals. The type of collagen depends on whether its component molecules are genetically distinct (heterotrimeric) or not (homotrimeric) (Gjaltema and Bank, 2017); that is whether different genes express them or they are expressed by a single gene (see Table 1.1).

This nomenclature identifies the individual α chains of the collagen molecule: $\alpha_n(N)_p$, where n is the identifying number of the α chain, N is the roman numeral that indicates the collagen type and p is the identifier for the polypeptide chain (Li and Wu, 2018; Hulmes, 2018). Thus, $\alpha_1(II)_3$ denotes a homotrimer of type II collagen consisting of 3 α1 chains. The genes that encode collagen alpha chains are prefixed by the letters COL, then the collagen type, followed by the letter A-which means alpha chain and lastly the chain number (Table 1.1). For example, *COL1A1* is the gene coding type 1 collagen alpha 1 chain while *COL1A2* is the gene coding for type 1 collagen alpha 2 chains.

1.3.3 Types of collagen

Two main categories for grouping collagen types are fibrillar and non-fibrillar collagens (Table 1.1).

1.3.3.1 Fibrillar collagens

Fibril-forming collagens are the most abundant collagen types comprising about 90% of the total collagens (Gelse et al., 2003). These collagens provide support, tensile and mechanical strength to tissues and organs like skeletal muscles, skin, ligaments, and tendons in the mammalian body (Kaushal et al., 2014). The regions of the gene that encode their triple helical chains have almost identical exon and intron structures for all mammalian fibrillar collagen genes (Sutmuller et al., 1997) which may indicate common evolutionary pressures and ancestry at the level of the gene (Takahara et al., 1995). Collagens molecules in this category tend to be staggered (quarter-staggered) with respect to neighboring molecules by integral multiples of D, where $D=234\pm1$ amino acid residues or 67nm (Hulmes et al., 1973; Meet et al., 1979; Hulmes, 2008) known as the Hodge-Petruska fibrillar collagen model (Petruska and Hodge, 1964) resulting in the banded appearance of collagen fibrils (Kaushal et al., 2014) (Figure 1.2). Collagens types forming quarter staggered fibrillar structures include collagen types I, II, III, V, XI, XXIV, and XXVII (Table 1.1). This structure provides fibrillar collagen with its rope-like structure, conferring substantial strength to connective tissues in which it is found.

1.3.3.1.1 Some fibrillar collagens in skeletal muscles

1.3.3.1.1.1 Collagen type I

Type I collagen is the most abundant and widely distributed fibrillar collagen in mammalian species, and it provides strength and stability to a wide array of tissues (Fratzl, 2008; Kaushal et al., 2014). Its precursor, type I procollagen is synthesized in the rough endoplasmic reticulum by the combination of 1 proα2(I) peptide chain and two proα1(I) to form a triple helix with these α chains initially interacting at their carboxyl-terminal propeptides (Cundy et al., 2014). It constitutes about 90% of the protein in the bone matrix (Cundy et al., 2004; Gelse et al., 2003) and it is also in tissues of the vasculature, lungs, skin, tendons, cornea (Humes, 2008). Thomas et al. (2000) reported significant decreases in collagen type I and III mRNA expression with increasing age in mice left ventricle. This observation implies that most likely, it is not the synthesis of new collagen molecules that form heat stable crosslinks but the transformation of existing heat labile ones. Studies by Light and Champion (1984) showed that type I collagen is the major component of the epimysium and perimysium of skeletal muscles where it supports the structural integrity of the muscle and thus an important component for muscle physiology.

1.3.3.1.1.2 Collagen type III

This collagen type along with type 1 collagen forms a significant component of the interstitial matrix (Nielsen and Karsdal, 2016). Collagen type III was found to be a minor component of the epimysium and perimysium (Light and Champion, 1984). Apart from its role in structural support, it also acts as a ligand for numerous proteins including von Willebrand factor, G protein-coupled receptor-56 and integrin $\alpha2\beta1$ (Nielsen and Karsdal, 2016). It can also be found in comparatively elastic mammalian tissues like the lungs, blood vessels and the skin of an embryo (Hulmes, 2008). Fugii et al. (1976) found lysinonorleucine to be the predominant crosslink in fibrils of collagen type III while collagen type I mainly formed hydroxylysinonorleucine crosslinks. Shuttleworth and Forrest (1975) observed much higher collagen type III-specific activity than collagen type I in guinea pig fetal dermal tissues although it declined dramatically with increasing fetal age until the specific activity of type I collagen surpassed that of Type III at day 70 of gestation. Based on these observations, they concluded that maximum synthesis of collagen type III occurs at the fetal stage.

1.3.3.1.1.3 Collagen type V

This collagen type is widely distributed in various tissues of the body and is critical to the formation of collagen type I and III tissue-specific matrices (fibrillary formation) (Leeming and Karsdal, 2016). Indeed, Light and Champion (1984) found traces of this collagen type in the perimysium. It supports the integrity of interstitial muscle matrices, corneal stroma, and bone matrices. It forms heterotypic fibrils with type 1 collagen especially in the cornea (Birk et al., 1988). Birk et al. (1986) have chronicled a relationship between type V and type I in which quantitatively increasing type V collagen ratio relative to type I decreased the ultimate collagen fibril diameter in heterotypic corneal fibrils. The relationship between type I and V collagens illustrates that some collagens, like type V, exist in muscle to cooperatively modify the quaternary structure of other collagens.

1.3.3.2 Non-fibrillar Collagens

Non-fibrillar collagens are predominantly lattice-forming collagens which tend to be important structural components of all basement membranes like Type IV collagen (Ricard-Blum, 2011). Their triple helical chains are of varying lengths, interrupted by non-helical sections (Kaushal et al., 2014). This category of collagen includes collagens with multiple triple helical domains with interruptions (multiplexins)(Types XV and XVIII), basement membrane collagens (Types XIII, XVII, XXIII, and XXV), network collagens (Types IV, VIII, and X), and fibril-associated collagens with interrupted triple helices (Types IX, XII, XIV, XVI, XIX, XX, XXI and XXII)(Ricard-Blum, 2011).

1.3.3.2.1 Some non-fibrillar collagens in skeletal muscles

1.3.3.2.1.1 Collagen type IV

This structural collagen is regarded as the collagen type most vital to the integrity of muscle fiber basement membranes (Sand et al., 2016). It possesses several discontinuities in its Gly-Xaa-Yaa motifs due to the presence of non-collagenous sections (Dolz et al., 1988; Hulmes, 2008). Collagen type IV exists in all known metazoans (Sundaramoorthy et al., 2002) especially in their glomerular basement membranes (Hulmes, 2008). The C-terminal non-collagenous domains of type IV collagen prevent angiogenesis (Petitclerc et al., 2000). Expression of this collagen type has been reported (Feru et al., 2016) to decrease with age in some tissues while transforming growth factor beta 1 (TGF-ß1) treatment causes a significant rise in its expression in fibroblasts indicating a possible influence of TGF-ß1 on collagen IV expression and indirectly, basement membrane integrity. Future studies may need to look at the effect of these hormonal treatments on the expression and synthesis of collagen molecules in livestock species as manipulation of these hormones could lead to a lower collagen synthesis to turnover ratio and probably a weakened muscle structure.

1.3.3.1.1.2 Collagen type VI

Tetramers of this collagen type aggregate to form beaded filament structures in most extracellular matrices as it forms microfibrillar networks between the interstitial matrix and basement membrane interfaces (Sun and Karsdal, 2016). In humans, mutations in its alpha chain coding genes lead to muscular defects like Bethlem myopathy and Ullrich disease (Lampe and Bushley, 2005). Bonaldo et al. (1998) in their study of the role of collagen VI in muscle fiber integrity found that *COL6A1* gene knockout mice exhibited pronounced muscle fiber phagocytosis and necrosis as well as fiber diameter variations. These myopathic characteristics suggest that collagen VI is crucial to muscle fiber integrity.

1.3.3.1.1.3 Collagen type XXI

In the extracellular matrix, collagen XXI acts as molecular bridges by enhancing protein-protein interactions using their non-collagen N-terminal domains (Kehlet and Karsdal, 2016). The marked expression of *COL21A1* in smooth muscle cells of the aorta after introducing platelet-derived growth factor led Cho and Li (2002) to suggest that it may be involved in extracellular matrix arrangement during formation of blood vessels. Furthermore, its co-expression with type 1 collagen in skeletal muscles may play an important role in interstitial collagen fibril organization (Fitzgerald and Bateman, 2001) and thus an important collagen for extracellular matrix integrity.

1.3.4 Collagen biosynthesis

All proteins belonging to the collagen superfamily are secretory proteins that are synthesized on bound ribosomes (protein synthesis site in cells), secreted into the endoplasmic reticulum lumen for post-translational modifications, transported to the Golgi apparatus for further modifications and finally secreted into the extracellular space (Myllaharju, 2005; Koide and Nagata, 2005; Cundy et al., 2014). Figures 1.3 and 1.4 depict the steps involved in collagen synthesis and subsequent post-translational modifications.

1.3.4.1 Ribosomal stage

The genes coding for their amino acid sequences essentially control the basic structure/template of collagens (Di Pasquale, 1997). In the ribosome, triplet codons for particular amino acids on the mRNA are recognized and read by the anti-codon on the cognate amino-acyl tRNA (Zaher and Green, 2009). This process occurs at the 80S when the 40S and 60S subunits combine to initiate translation. Uncharged amino acids, at the onset, interact with Mg^{2+} and ATP forming an amino acid adenylate (enzyme bound) catalyzed by amino acyl-tRNA synthetase (Coulson, 1994). This aminoacylation guarantees that only matching amino acids bind to the tRNA's. A complex composed of amino-acyl tRNA, guanosine triphosphate and eEF1A elongation factor is conveyed to the aminoacyl site. This ternary complex interacts with peptidyl tRNA at the peptidyl site, elongating the forming polypeptides (Zaher and Green, 2009). Synthesis of the nascent polypeptide is terminated when a stop codon at the Aminoacyl site is detected by eukaryotic translation termination factor 1.

In summary, polysomes control the inclusion of amino acyl groups to the increasing peptidyl tRNA forming peptide bonds through condensation reactions (Coulson, 1994). Pre-procollagen, a protein precursor, translated from mRNAs on the ribosomes is formed.

1.3.4.2 Endoplasmic reticulum stage

Pre-procollagen, a newly formed polypeptide chain, is synthesized with a hydrophobic leader peptide that enhances the binding of ribosomes to the endoplasmic reticulum and directs the lengthening polypeptide chain (pre-procollagen) into the lumen of the endoplasmic reticulum (Kaushal et al., 2014). Thus, the polypeptide chains undergo co-translational translocation across the endoplasmic reticulum lumen (Bullied et al. 1997). Initiation of post-translational modifications of pre-procollagen occurs upon cleaving of the leader peptide in the endoplasmic reticulum coupled with the addition of hydroxyl groups to lysine and proline residues (Kaushal et al., 2014).

Proline residues at the Y-position are mostly modified to 4-hydroxyproline by prolyl-4-hydroxylase (Cundy et al., 2004). When proline residues are not fully hydroxylated, collagen molecules tend to have comparatively lower thermal stability as well as abnormal assemblage (Gjaltema and Bank, 2017) indicating the importance of this modification in the stability of the whole structure. Lysyl hydroxylase catalyzes the conversion of lysine residues into 5-hydroxylysine on the individual α chains of a procollagen molecule (Gjaltema and Bank, 2017). Proline residues in the X-positions convert to 3-hydroxyproline catalyzed by prolyl-3-hydroxylases (Koide and Nagata, 2005). Prolyl-4-hydroxylases, lysyl hydroxylases, and prolyl-3-hydroxylases belong to the alpha-ketoglutarate-dependent hydroxylase enzyme family and thus require oxygen, vitamin C (ascorbate), 2-oxoglutarate and iron (Fe^{2+}) to perform their functions (Gjaltema and Bank, 2017). The hydroxylation of these residues is a necessary modification leading towards the formation of intermolecular crosslinks that are stable.

During the actual triple helix formation, the alpha chain association is initiated at the carboxyl (C)-terminal propeptide propagating the triple helix formation in a zipper-like folding to the amino (N)-termini (Engel and Prockop, 1991). The formation of the triple helix is completely driven by the initial association of the alpha chains through their C-terminal poly-peptides, as Bullied et al. (1997) found that helix formation was not initiated among monomeric chains lacking the carboxyl-terminal propeptides.

Proper trimerization and folding of collagen are achieved through the assistance of various enzymes (Koide and Nagata, 2005). Involved enzymes include protein-disulfide isomerase, which catalyzes the formation of inter and intrachain disulfide bonds at the carboxyl-terminal region, allowing for the folding and association of peptide chains into a triple helical structure (Okumura et al., 2015; Cundy et al., 2014). Prolyl peptidyl cis-trans isomerase B accelerates the folding around prolyl residues by catalyzing isomerization of cis-peptide bonds in proα-chains into trans-peptide bonds (Cundy et al., 2014). Lysyl hydroxylases-2 aids the hydroxylation of lysine residues at the exterior of the helix (telopeptides) to 5-hydroxylysine. Some lysine residues in the Y-position inside the triple helical domain undergo hydroxylation catalyzed by the enzyme lysyl hydroxylase-1. Galactosyltransferase catalyzes the occurrence of O-linked glycosylation by adding galactosyl residues to hydroxylysine. Glucose groups are further added to the galactosyl hydroxylysine to form a disaccharide catalyzed by glucosyltransferase. Glycosylation occurs only on non-collagenous domains by these enzymes (Kaushal et al., 2014). In the non-fibrillar domains, oligosaccharides are added (N-linked glycosylation) on specific asparagine residues. Non-fibrillar collagens tend to be more glycosylated compared to their fibrillar counterparts most likely due to the higher occurrence of non-helical domains in them. These hydroxylated residues are vital in the formation of covalent crosslinks and subsequent thermal stability (Gjatema and Bank, 2017; Cundy et al., 2014).

The multiple enzymes involved mean that the formation of collagen structures is a metabolically intensive process, with ample potential for error. As a result, chaperone proteins are essential in the processes leading to collagen formation (Koide and Nagata, 2005). These include the heat shock protein 47 (HSP 47), a glycoprotein found to aid triple helix propagation by binding procollagen and to prevent collagen aggregation in the endoplasmic reticulum (Nagata and

Yamada, 1986). FK-binding protein 65 (FKBP 65) is a chaperone that has been found to be involved in procollagen synthesis and regulation (Knüppel et al., 2018) and mutation in this protein has been reported to cause a decline in extracellular matrix rigidity (Staab-Weijnitz et al., 2015).

1.3.4.3 Golgi apparatus stage

After triple helix formation in the rough endoplasmic reticulum, the procollagen molecule is transported through the Golgi apparatus (Koide and Nagata, 2005). Here, it undergoes packaging into cylindrical aggregates in membrane-bound secretory organelles (Myllyharju, 2005). At this stage, the initial formation of fibrils occurs in the case of fibril-forming collagens (Cundy et al., 2014). These secretory organelles are then conveyed into the extracellular space via exocytosis. During the secretion of these procollagen molecules, further modifications occur as specific C- and N- terminal procollagen proteinases cleave off the non-helical domains of the molecule (Prockop et al., 1998). Disintegrin and metalloproteinase with thrombospondin motifs 2 (ADAMTS-2), also known as procollagen N-proteinase, cleave the N-terminal propeptides while bone morphogenetic protein 1 (BMP 1) also called procollagen C-proteinase cleaves the C-terminal propeptides (Prockop et al., 1998). The resulting molecule is termed tropocollagen.

1.3.4.4 Extracellular stage

In the extracellular space, tropocollagen trimers are assembled into collagen fibers and fibrils. Intermolecular aldehyde-derived crosslinks stabilize these structures. Also, oxidative deamination of the amino groups from some hydroxylysine and lysine residues side chains, catalyzed by lysyl oxidase results in the production of hydroxyallysine and allysine (reactive aldehyde derivatives) (Fujii et al., 1976). Subsequent formation of aldol condensation products by these aldehyde groups results in crosslinks between and within the collagen molecules. Imine (Schiff base) crosslinks may also be formed when these aldehyde groups react with amino groups from unoxidized hydroxylysine and lysine residues. Stable cross-links like lysinonorleucine may be formed from the rearrangement, reduction or dehydration of the above products. Other non-reducible cross-links include lyslypyridinoline and hydroxylysylpyridinoline. Lysylpyridinoline crosslinks are composed of 2-hydroxyallysine residues in the telopeptide section and a specific lysine residue in the helical domain while hydroxylysylpyridinoline is made from 2 hydroxyallysine residues in the telopeptide region and a specific 5-hydroxylysine in the triple helical domain (Cundy et al., 2014). Research on the organic compound ß-aminopropionitrile, which inhibits the activity of lysyl oxidase, strongly suggests that the formation of collagen crosslinks is important for tissue strength and mechanical properties as a significant reduction in pyridinoline cross-link content and bone strength was observed after treating mice with ß-aminopropionitrile (McNerny et al., 2015). Thus, reducibility and density of collagen crosslinks likely affect meat toughness. Ehrlich chromogen is another crosslink proposed by Scott et al. (1983). It is a trifunctional pyrrolic crosslink derived from a Knorr reaction between amino-ketones to produce pyrroles (Scott et al., 1981).

1.4 Pork quality

1.4.1 Definition of pork quality

Pork quality is dictated mainly by muscle metabolism peri- and post-mortem and is dependent on a pig’s genetics and environmental factors (Lebret, 2008; Enfält et al., 1997). Some of these environmental factors include management practices, animal nutrition, slaughter practices and carcass management (Salas and Mingala, 2017). Pork quality is defined by Hoffman (1973) as encompassing all the toxicological, technological, food physiological and sensorial attributes of pork (Figure 1.5). A similar definition by Ciobanu et al. (2011) described pork quality as consisting of a class of sensorial and meat processing traits critical for competition and profit-making by the pork industry in the ever-dynamic food sector. Sensorial traits were explained to include eating quality and appearance as assessed by sensory panelists while meat processing traits included cooking loss, water-holding capacity, color, and firmness. Further, a typical meat scientist according to Bray (1966) will define the quality of fresh meat to include the components/aspects linked to the palatability of cured and fresh meat products as well as the associated financial losses incurred during its processing and subsequent distribution.

From the above definitions, it is clear that different definitions exist in the pork industry to describe quality. However, the one that should carry the most weight is that one given by consumers. The general view on meat quality of consumers is summed up as meat products that are wholesome, safe, nutritious, aesthetically pleasing, worth its cost and produced with procedures that are morally admissible (Eikenboom, 1983 as cited by Smulders, 1986). The perceptible quality factors are especially of economic significance as consumers experience these themselves (Mir et al., 2017).

1.4.1.1 Meat quality versus carcass quality

As is often the case, people tend to confuse the term carcass quality with meat quality. However, there are some distinctions between those two terms (Smulders, 1986). Carcass quality usually subsumes factors that critically affect the market price of carcasses, and some of these factors are carcass fat cover, bone to meat ratio and carcass weight (Smulders, 1986). In most countries, carcass grading policies, pricing, and procedures are designed in such a way as to allow carcass quality characteristics/attributes to, for the most part, harmonize with an improved meat quality derived from the carcass (Smulders, 1986). However, there are numerous factors affecting meat quality and these determinants justify the distinction between carcass and meat quality.

Different players in the food sector such as consumers, microbiologists, nutritionists, veterinarians, and meat technologist, at times, append similar weights to some subcomponents of meat quality. However, now and then, their interests conflict (Smulders, 1986). A classic example is that of a dark-cutting (dark, firm and dry) meat. The microbiologist will consider such meat as a possible hazard due to its unusually high pH; however, the meat technologist or processor, realizing that such high pH will likely equate to outstanding water holding capacity will see such meat as particularly suitable for certain sausage types.

1.5 Eating quality

A major aim of the current pork industry is to offer end-products that will achieve consumer satisfaction at equitable costs (Drescher et al., 2012). From their principal component analysis, Dransfield et al. (1984) reported that overall acceptability of bovine longissimus muscle steaks was determined primarily by juiciness, flavor, and tenderness. Similarly, eating quality attributes of pork are described by consumers with respect to its juiciness, tenderness, and flavor (Aaslyng et al. 2003). It is important therefore to understand how the characteristics of pork affect pork juiciness, tenderness and flavor.

1.5.1 Juiciness

Juiciness, a subjective sensory trait (Warner, 2017) is one of the most significant factors influencing meat palatability (Tannor et al., 1943). It is the sensation of lubrication and wetness (moisture) experienced during mastication of meat (Warner, 2017). Thus, it provides an indication of the amount and level of moisture in meat that is released during chewing (Heymann et al., 1990). Juiciness of meat can be divided into two aspects: the sensation of wetness perceived during initial mastication due to the expression of meat fluids; and the perceived juiciness experienced during sustained mastication. The latter aspect may be related to the stimulating influence of muscle fats on salivation (Winger and Hagyard, 1994; Aaslyng et al., 2003).

Well-marbled pork gives a better impression of juiciness and tenderness than pork devoid of marbling (Thompson, 2004). This could be due to the ECM remodeling theory proposed by Nishimura (2010) in which deposition of fat in the perimysium results in a remodeling of the extracellular matrix leading changes in the mechanical properties (weakening) of the intramuscular connective tissue. Fernandez et al. (1999) found that rising levels of intramuscular fat were significantly linked to juiciness in porcine Longissimus muscles. Kempster et al. (1986) made similar observations, although in their study the level of leanness did not affect overall product acceptability. These studies indicated that there is an intimate relationship between intramuscular fat content and juiciness in meat. Wood et al. (2004) found that feeding intact male pigs low protein diets of about 16% crude protein content with higher lysine to energy ratio resulted in a much juicier and tender longissimus muscle compared to a high protein diet of 20% crude protein and these results showed that certain quality traits can be manipulated through animal nutrition.

Swine breed has also been shown to affect pork sensory quality. Cameron et al. (1990) in comparing the British Landrace with Duroc found that pork from Durocs had higher scores for juiciness than Landrace and this was subsequently attributed to the greater levels of intramuscular fat in the Duroc pork compared to that of the Landrace. Ventanas et al. (2007) also reported that purebred Iberian pigs had higher scores for juiciness than Duroc × Iberian pigs in their study on dry-cured loins. Serra et al. (1998) found a positive correlation between intramuscular fat percent and type I muscles fibers. In that study, Serra et al. (1998) compared quality and histochemical characteristics between Landrace and Iberian pigs and found the latter to have twice the backfat depth and 5 times the intramuscular fat percent and a significantly higher proportion of oxidative type I fibers. Similar results were obtained by Lee et al. (2012) as their results showed that breeds with higher fat content like Berkshires and Duroc also had higher Type I and lower Type IIB muscle fibers compared to the Landrace and Yorkshire who had comparative lower fat content. Thus, a plausible underlying driving factor for these breed differences in juiciness is most likely muscle fibre type (oxidative vs glycolytic). Interestingly, this trend may not be species specific as it has also been reported in Hanwoo beef steers by Joo et al. (2017). In their study, they found a strong positive correlation between intramuscular fat content and the proportions of Type I muscle fibers but a negative correlation of similar magnitude with the proportion of Type IIB muscle fibers.

A relationship between ultimate pH and juiciness has also been established by Eikelenboom et al. (1996), who reported a positive correlation between these traits and subsequently suggested that selection of carcasses for juiciness should be based on ultimate pH. Jonsall et al. (2001) reported juicier pork from pigs reared indoors compared outdoors which may have been due to the outdoor pigs requiring more energy for locomotion and maintaining body temperature thus resulting in less fat deposition. Channon et al. (2016) reported higher juiciness scores for castrates compared to intact male pigs. This is not surprising as castrates are known to have a higher propensity for fat deposition (Bonneau, 1998). The presence or absence of testosterone is the main difference between intact male pigs and castrates. Indeed, low testosterone levels have been associated with metabolic syndrome and obesity (Wang et al., 2011). Wang et al. (2017)

speculated that the *MARK4* gene might play a vital role in obesity as their results showed that fat accretion in castrates may be regulated by ssc-miR-7134-3p by acting as a translational inhibitor of *MARK4*. Thus, castrates had lower levels of ssc-miR-7134-3p and increased MARK4 protein levels in their fat tissues than intact males. Muscle fiber type may also affect juiciness, as Shen et al. (2005) found that pork with proportionally more glycolytic muscle fibers had a reduced pH and light colour, which is associated with pale, soft and exudative pork (Lee et al., 2012).

End-point temperature has also been found to significantly influence juiciness ratings, as higher juiciness ratings have been reported (Channon et al., 2016) for pork cooked to an internal end-point temperature of 70℃ relative to those cooked to 75℃. This is probably because with increasing temperature comes a concomitant increase in loss of fluids and volatile fatty acids which may decrease the sensation of juiciness during mastication. Sheard et al. (1999) reported significantly improved juiciness in polyphosphate-injected pork loins. This is probably because phosphates are known to increase meat pH and thus the water holding capacity of meat (Hamm, 1961). All the above studies show that animal genetics, management practices and processing techniques can be manipulated to affect meat juiciness.

1.5.2 Tenderness

Tenderness is considered the most important eating quality trait influencing consumer satisfaction and acceptance (Suman, 2012; Williams., 1986). It can be defined as the ease with which meat fibers are cut through by the teeth during chewing (Coggins, 2012), thus simulating the effort required to masticate. In general, three methods have been used to evaluate the differences in meat tenderness. The first method is sensory evaluation in which trained panelists are used to describe the meat product of interest under standardized conditions. Another method employed by some researchers to evaluate tenderness is chemical analysis through the determination of elastin and collagen contents of meat samples. A third method widely accepted in most sectors in the food industry is the mechanical method, that is, an instrumental measurement which assesses the shear force strength or resistance to shearing of a meat product (Bratzler, 1930). Dissatisfaction among consumers could arise due to variations in the tenderness of meat products (Mane et al., 2014). As illustrated in Figure 1.6 numerous factors affect pork tenderness. Some of these factors are highlighted below. The two most important groups of proteins determining tenderness are connective tissue proteins and myofibrillar proteins (Mane et al., 2014; Bouton et al., 1974).

In cooked meats (Purslow, 2018), connective tissues are thought to contribute to an immutable background toughness, although they are still implicated in muscle to muscle and animal to animal variation while myofibrillar contraction state influences the sensation of toughness for the most part (Bouton et al., 1974; Huff-Lonergan et al., 2010; Sikes et al., 2010). The statement about the immutable background role of collagen is still subject to some debate as discussed later in section 1.5.5.

The mean adhesion value of meat cooked to a temperature of 50°C according to Bouton et al. (1974) was approximately five times that cooked at 90°C for 1hr. Because these values represent the strength of connective tissues among the meat fibers, these results suggest a major influence of connective tissues at low temperatures. Williams et al. (1986) reported a rise in Z-disc fragmentation and a decrease in sarcomere length in poultry breast muscle cooked to an internal temperature of 80°C. They further observed during their sensory tests that samples with longer sarcomere lengths scored as more tender, adding to the well-established effect of sarcomere length on meat toughness. Feldhusen and Kuhne, (1992) observed an increase in sarcomere length and tenderness of pork loins after aging for two days. Channon et al. (2004) further looked at a greater period of 7 days with vacuum bags and found that pork loins aged for that length of time were significantly more tender than those aged for two days. Wood et al. (1996) also reported an increase in myofibrillar fragmentation index with increasing aging time. These results suggest that as aging period increases, so too does tenderness probably due to an increase in proteolytic enzyme activity.

Guzek et al. (2016) reported no significant differences in Longissimus lumborum shear force values and sarcomere lengths for crossbred Polish Landrace× Duroc and purebred Landrace pigs. Wood et al. (1996) also reported no difference in tenderness between the Duroc and Large White pigs. These results partially question the influence of breed on these pork quality traits. Carlson et al. (2017) implicated proteolytic degradation and lipid content in the significant variations they observed in their instrumental meat tenderness measurements, as the groups of samples determined as tender tended to have high lipid and marbling scores as well as significantly greater degradation of filamin, troponin, and desmin. Wheeler et al. (2000) stated that enzymatic proteolysis, sarcomere length, variations in collagen content and the extent of their interactions dictates individual pork muscle tenderness.

1.5.3 Flavor

For us to generate the numerous perceptual responses of food during mastication, numerous chemicals are detected and then turned into nerve impulses (Reineccius, 2016). Flavor according to Lawrie (1966) is essentially a complex sensation experienced by humans that involves taste, pH, temperature, texture, and odor. It is regarded as one of the factors affecting consumer purchasing decisions (Spanier et al., 2004).

Flavor formation and subsequent deterioration in meat products are said to be a process that is continuous with respect to the formation and subsequent deterioration of some desirable flavor compounds as well as the development of some off-flavor components (Spanier et al., 1992). Formation of these flavor generating components has been reported to be correlated with some factors like end-point cooking temperature, post cooking storage and aging period postmortem (Yang et al., 2016; Cambero et al., 1992; Spanier et al., 2004). Factors influencing pork flavor are illustrated in Figure 1.7 and indicate the complexity of flavor development.

Some descriptors used by sensory analysts to describe pork flavor include metallic, serum, musty, boar odor, bloody, liver-like, porky, piggy, cardboard, rancid, briny, fatty and browned (Hayes, 2010). More than 1,000 volatile compounds that dictate aroma characteristics and meat flavor have been isolated from cooked meats (Mottram, 1994). Maillard reactions between some reducing sugars and amino acids result in the formation of aroma volatiles during cooking (Mottram, 1994). This discovery was originally made by Morton et al. (1960) after noticing that at elevated temperatures, reacting cysteine with pentose monosaccharides like ribose in the presence of water led to the production of meat flavors and the author subsequently patented this discovery. Some other reactions that may occur during cooking of meat and which could ultimately result in flavor development are caramelization of some carbohydrates, thiamine and ribonucleotide degradation, peptides and amino acids pyrolysis, and lipid degradation (MacLeod and Seyyedain-Ardebili, 1981).

Hornstein and Crowe (1960) in their research on pork and beef flavor reported that odor characteristics of heated lean pork and beef aqueous extracts were identical as sensory panelist could not differentiate the meats of those two species. Further, they observed a striking resemblance in the spectrophotometric and gas chromatographic behaviors of their compound isolates. However, flavor difference existed in their heated fat portions, producing species-specific flavors. Indeed, Fernandez et al. (1999) found that flavor scores increased with increasing intramuscular fat content. Wood et al. (1996) reported higher flavor intensity ratings for Duroc pigs compared to Large Whites which was not surprising as they also observed higher marbling fat content in the Durocs.

Sheard et al. (1999) found that injection of polyphosphates in porcine longissimus muscle reduced flavor intensity. This is not surprising as these polyphosphates are known to have water-binding properties and therefore may increase the water ratio of the muscle leading to a decrease in the concentrations of flavor compounds. It was also not surprising that after heating their samples to an internal temperature of 80℃, Sheard et al. (1999) recorded an increase in flavor intensity probably because evaporation of moisture might have caused an increase in flavor compound concentration suggesting a possible negative relationship between increasing moisture content and flavor.

1.5.4 Intramuscular fat and pork eating quality

Pork intramuscular fat, in general, has been known to influence the three cardinal eating quality traits, specifically juiciness, tenderness, and flavor (Smith and Carpenter, 1974). The notion that fat deposition improves the worth of meat has been recognized since the beginning of written history (Smith and Carpenter, 1974). This belief that fatness is positively correlated with palatability and eating quality of meat products led famous 18th-century British animal breeding pioneers like Robert Bakewell to improve a number of livestock species during the agricultural revolution of the mid-18th century (Philips, 2001). For instance, Robert Bakewell transformed the Leicestershire sheep, a previously heavily boned breed with little disposition to fatten into a fast fattening, fine-boned breed also known as the Bakewell Leicester (Bulliet, 2005). It may however be worth point out that during that period, many workers expended lots of energy on tasks presently performed by machines and as fat has comparatively larger amounts of stored energy than lean, the meat of those times supplied a significant proportion of their daily energy requirements (Swatland, 1994).

Hall (1910) observed that marbling, in addition to its contribution to juiciness and flavor, also increased meat tenderness, through a reduction in connective tissue elasticity as a result of the fat deposition in it. Nishimura et al. (1999) studied the relationship between marbling and beef tenderness in Japanese black cattle, and these authors reported that shear force values obtained from the Longissimus lumborum muscle increased by about 50N between 9 to 20 months of age but saw a reduction of about 45N from 20 months to 32 months of age. Interestingly, this is the final fattening period of those animals. They, therefore, concluded that increased fat deposition might increase affect tenderness by altering intramuscular connective tissue structures in breeds with predispositions to increased marbling.

1.5.5 Collagen and pork eating quality

Light et al. (1985) proposed two theories of the impact of collagen on meat toughness and texture. Firstly, they proposed that shrinkage of collagen fibers in the connective tissues results in muscle bundle compression and moisture loss which ultimately affects texture. Secondly, they proposed that the amount of insoluble cross-linked collagen which could offer some resistance to shear force could also affect meat toughness. Researchers have identified two major consequences of temperature (heat) on collagen characteristics intimately linked to the theories proposed by Light et al. (1985) as these effects can significantly affect cooked meat texture. Firstly, at approximately 65°C (shrinkage temperature of mammalian collagen), collagen fibers undergo significant denaturation resulting in the collapse of its structure, leading to shrinkage by as much as one fourth its original length (Bailey and Light, 1989) and this ultimately results in toughening of the meat (Voyle, 1979). Secondly, most collagen fibers solubilize (Figure 1.8) at temperatures around 80℃. However, the degree of solubilization is dependent upon the proportions of heat resistant intramolecular and intermolecular crosslinking (Hill, 1966) resulting in lower intrafibrillar water content and this decreased hydration leads to an increase in thermal stability (Miles et al., 2005). Research by Purslow et al. (2016) however suggested that collagen fiber shrinkage may not be the cause of fluid loses in cooked meat. After comparing the dimensional variations in muscles with intact perimysium and endomysium with those with only endomysium and those without connective tissues, they attributed transverse shrinkage at 50-65℃ to myosin denaturation while actin denaturation caused longitudinal shrinkage at 70-75℃. However, comparative analysis of fluid or weight loss between whole meat blocks and myofibrils devoid of connective tissue was not provided by Purslow et al. (2016); this information however would have been very helpful for drawing concrete conclusions. Furthermore, Purslow et al. (2016) premised the hypothesis of their study on research by Tornberg (2005) who compared cooking loss (%) between whole meat, hamburger and emulsion-type sausages. It would have been more informative for Purslow et al. (2016) to indicate that for all the temperatures examined by Tornberg (2005), whole meat had the highest mean cooking loss (%) of the 3 products and it was especially significant at 65℃, the temperature at which collagen fiber shrinkage occurs. In fact, addition of salt (0.4 and 4% for the hamburger and emulsion-type sausage respectively) and comminution of meat leads to meat protein extraction which form protein gel networks upon heat treatment, which is what would be expected to occur in emulsion-type sausages and to an extent, hamburger patties and thus one would expect water holding capacity of hamburgers to be higher than that of whole meat. The evidence suggests that fluid losses may be driven by connective tissue shrinkage up to 65℃ above which shrinkage of muscle proteins dominates, as connective tissue fibers will start gelatinizing at higher temperatures. Future studies should look at whether the water released is bound or loose by comparing the shrinkage of connective tissue-bound muscle fibers with muscle fibers devoid of connective tissue when heated.

There is disagreement on the effect of the presence and level of collagen crosslinking on cooked meat texture. Avery et al. (1996) concluded that perimysial collagen crosslinks were not related to cooked meat texture obtained either subjectively or objectively. Ngapo et al. (2002) also found a weak and insignificant relationship between crosslink amounts and shear force values of cooked meat. In contrast, researchers like Jeremiah et al. (2003) reported that the amount of insoluble collagen negatively affected meat texture. Dransfield (1997) also chronicled a relationship between muscle toughness and total collagen content especially at lower temperatures (60℃ for 20 mins).

1.5.5.1 Animal age

Irrespective of species and muscle type, the amount of heat-soluble, reducible collagen crosslinks decreases with increasing age (Figure 1.9) (Shimokomaki et al., 1972); implying that these reducible cross-links may be intermediates which with time most likely become stabilized during the crosslinking (Bailey and Shimokomaki, 1971). Indeed, Goldspink et al. (1994) reported an age-induced decline in collagen expression in skeletal muscles and Khorramiza et al. (1999) further reported an increase in collagenase mRNA expression in older fibroblasts.

A greater amount of collagen is solubilized in cooked meat from young animals compared to matured ones, and this, according to Hill (1966) is most likely a major contributing factor to the comparatively increased sensation of tenderness experienced during mastication of meat products from young animals. The decrease in solubility that occurs with increasing age (Figure 1.9) is most likely due to the decline in new collagen synthesis, thus lending time for the heat-soluble crosslinks to stabilize and convert into matured heat-stable crosslinks (Shimokomaki et al., 1972). Hill (1966) reported approximately five times more soluble collagen percent in young hogs compared to old boars and sows although the hogs had a greater percentage of total collagen in muscle. Hill (1966) attributed the comparatively higher total collagen content in young animals versus old ones to muscles not being fully developed at young ages. Shimokomaki et al. (1972) further implicated rapid growth rate during the formative months and therefore the presence of more intermediate heat labile crosslinks. This conflicts with the findings of Berge et al. (1997) who found significant positive correlations between crosslink concentrations and total collagen in their study of the crosslink profile of the semitendinosus and longissimus muscles in three bovine breeds types (Angus × Hereford, Piedmontese × Hereford, pure Brahman). It is therefore contentious for Shimokomaki et al. (1972) to suggest that it is the ratio of heat resistant to heat labile intermolecular crosslinks and not total collagen that is of prime importance.

1.5.5.2 Muscle Location

Intramuscular connective tissues as has been previously elucidated, supports the structural integrity of muscles. They comprise about 2-10% of skeletal muscles on a dry weight basis (Bendall, 1967) and the more active a muscle is, the more connective tissues and mature crosslinks it tends to possess (Provost et al., 2016). In addition, muscles with immediate or close anatomical connections with various skeletal structures tend to possess more connective tissue amount than those further away (Mackenzie, 1919). By way of some research studies supporting the above statements, Kim et al. (1967) found significantly higher amounts of collagen nitrogen in the biceps femoris compared to the longissimus dorsi. Furthermore, their trained sensory panelists rated the longissimus muscle as softer with comparatively lower connective tissue content compared to the bicep femoris. Torrescano et al. (2003) in their study of 14 muscles from Swiss Brown bulls found that the psoas major had the lowest total collagen content (0.31±0.04 mg hydroxyproline/g wet tissue) and insoluble collagen concentration (0.18±0.01 mg hydroxyproline/g wet tissue) while the infraspinatus had the highest total and insoluble collagen contents: 0.98±0.05 mg hydroxyproline/g wet tissue and 0.76±0.08 mg hydroxyproline/g wet tissue respectively. Light et al. (1985) also found that tougher bovine muscles like the gastrocnemius and sternomandibularis tended to have greater fractions of perimysium, epimysium and total collagen in comparison with more tender cuts like the longissimus dorsi and psoas major. Based on these observations, one can conclude that intramuscular connective tissues characteristics influence textural incongruities observed between tough and tender muscles and ultimately meat tenderness.

1.5.5.3 Breed and species

Gonzalez et al. (2014) studied in cattle the influence of Brahman genetics on tenderness and mRNA expression of the genes for cystatin C (*CST3*), lysyl oxidase (*LOX*) and bone morphogenetic protein 1 (*BMP1*), and their association with meat quality and collagen intermolecular crosslink formation. They found that cattle with 50% Brahman genetics and purebred Brahmans produced higher Warner Bratlzer shear force values and had higher expression of *CST3* and *LOX* at weaning compared to the Angus and Brangus cattle. They therefore concluded that meat tenderness is influenced by the activities of collagen crosslinking enzymes in young animals. Hill (1966) found young hogs and old sows to possess more soluble and total collagen than calves and cows as well as lamb and ewes, and the inclusion of the percent insoluble collagen in that work would have been more informative. Porcine longissimus muscle intramuscular connective tissue had the lowest thermal shrinkage temperature (60.2℃ ±0.4) compared to ovine (63.0℃ ±0.7) and bovines (63.0℃ ±0.4) (McClain et al., 1971) indicating that connective tissue from swine may be more heat labile compared to the other livestock breeds.

Research by Dunner et al. (2013) with 15 European cattle breeds on genes associated by meat quality traits found single nucleotide polymorphisms (SNPs) in the aralkyamine N-acetyltransferase (*AANAT*) gene that were significantly associated with total collagen. These authors also found that SNPs in the matrix metalloproteinase-1 (*MMP-1*) gene were associated with m-calpain activity in the muscle. Taye et al. (2017) studied candidate genes related to meat quality in Ankole cattle and identified *COL9A2* influenced meat tenderness. Also, genome wide association studies (GWAS) by Castro et al. (2017) obtained 46 SNPs associated with tenderness in polled Nellore cattle. These studies shed light on the biological mechanisms influencing tenderness in various cattle breeds; however, the same cannot be said for swine breeds especially with respect to genetic parameters for collagen characteristics and their genetic architecture.

1.6 Major Genes affecting pork quality

A major gene is defined as a single gene with a detectable and pronounced effect or influence on the phenotypic expression of a quantitative trait (Bouchard et al., 1997). The halothane and Rendement Napole genes are major genes identified as influencing pork eating quality as well as carcass quality (Salas and Mingala, 2017; Apple and Yancey, 2013).

1.6.1 Halothane gene

Recognition of porcine stress syndrome susceptible pigs was made possible largely by the halothane gene discovery (Fujii et al., 1991; Salas and Mingala, 2017). Eikenkelenboom and Minkema (1974) observed that when exposed to the halothane gas, pigs that were stress susceptible died and subsequently produced a pale, soft and exudative meat.

With knowledge of the halothane gene's inheritance, pigs can be placed into three possible genotypes, namely: normal/halothane-negative (Hal^{NN}), heterozygote/halothane-carrier (Hal^{Nn}) and mutant/halothane positive (Hal^{nn}) (Apple and Yancey, 2013). When exposed to pre-slaughter stress, muscles from pigs of the Hal^{nn} genotype (halothane positive pigs) are more likely to produce a pale, soft and exudative meat due to an atypical metabolism of lactic acid resulting in a dramatic drop in pH while the muscle is still warm, leading to the denaturation of some muscle proteins (Salas and Mingala, 2017). This denaturation of muscle proteins inevitably leads to the low water holding capacity evident in PSE pork (Bowker et al., 2000).

The porcine halothane locus is composed of 2 alleles, Hal^{n}- the recessive allele and Hal^{N}-normal allele located at the 6p11-q21 region of chromosome 6 (Fujii et al., 1991). Fujji et al. (1991) found that a single mutation (position 1843) in the gene encoding for ryanodine receptor ($RYR1$) in the calcium release channel of the sarcoplasmic reticulum was linked to porcine stress syndrome in some lean swine breeds. At the time of muscle contraction or relaxation, ryanodine receptor proteins on the sarcoplasmic reticulum membrane surface regulate calcium release rate or uptake (Apple and Yancey, 2013). Pigs with the recessive genotype (Hal^{nn}) have defective ryanodine receptors which results in an uncontrolled Ca^{2+} release and an inability to sequester Ca^{2+} in the sarcoplasmic reticulum after contraction of a muscle (Salas and Mingala, 2017;

Apple and Yancey, 2013). This high Ca^{2+}concentration in the muscle results in a rapid postmortem metabolism which, at high muscle temperatures, leads to denaturation of some muscle proteins, resulting in increased moisture losses and subsequently, an increased occurrence of pale, soft and exudative pork in susceptible pigs (Apple and Yancey, 2013). Zhang et al. (1992) reported that the halothane locus explained about 20-30% of the overall meat quality variation in swine populations.

Apple et al. (2002) after randomly assigning homozygote halothane negative and heterozygote carriers to diets containing varying levels of magnesium mica, found that halothane carriers produced significantly heavier and leaner carcasses than halothane negative individuals. Further, a higher proportion of carcasses having color scores indicative of the pale, soft and exudative defect came from these carriers. Fernandez et al. (2002) found the longissimus muscle of halothane positive pigs to have higher L^* and drip loss values than the other 2 genotypes. Their subjective sensory test also revealed a lower color score (lighter color) for halothane positive pigs, but a higher rating for tenderness was observed in the halothane negative pigs. Fisher et al. (2000), studying 60 crossbred Landrace × Large White pigs composed of the three halothane genotypes, found that halothane positive pigs had less mean fat (at the 2^{nd}-3^{rd} last rib), larger mean loin eye area and depth, longer carcasses and higher mean lean percent than halothane negative genotypes. This result is similar to the findings of Aalhus et al. (1991) who also observed a higher lean percent in halothane positive pig carcasses.

1.6.2 Rendement Napole gene

Another major gene with significant influences on pig carcass and meat quality is the Rendenment Napole gene also called the *protein kinase AMP-activated non-catalytic subunit gamma 3* (*PRKAG3*) gene located on chromosome SSC 15 (Monin and Sante-Lhoutellier, 2014).

The $\gamma3$ isoform of *adenosine monophosphate activated protein kinase* (*AMPK*), which is highly expressed in skeletal muscles (Cheung et al., 2000; Mahlapuu et al., 2004), is encoded by $PRKAG3$ (Ryan et al., 2012). Mahlapuu et al. (2004) found a significant correlation between the protein expression of $\gamma3$ isoforms and its mRNA expression in mice and rat gastrocnemius muscles. They further found that the $\gamma3$ isoform tended to associate with $\alpha2$ and $\beta2$ isoforms to form $\alpha2\beta2\gamma3$ complexes, the main AMPK heterotrimer in most skeletal muscles especially white muscles. The AMPK enzyme is an energy sensing enzyme vital in the regulation of numerous pathways including glycogen metabolism (Monin and Sante-Lhoutellier, 2014; Winder, 2001). A mutation that occurs on $PRKAG3$ in which guanine is substituted with adenine resulting in a non-conservative substitution to glutamine from arginine has been reported to be the driving force behind the low ultimate pH or acid pork characteristic of homozygous dominant RN^- genotypes (Milan et al., 2000).

The RN^- allele has proven to be of appreciable economical relevance to the swine industry due to its detrimental impact on yield after processing (Milan et al., 2000). Le Roy et al. (1990) first tested the hypothesis that the presence of a major gene locus significantly influencing the Napole technological yield trait- a measure of product yield after curing and subsequent cooking (England et al., 2017)- using segregation analysis in the semimembranosus of pigs resistant to porcine stress syndrome. They indeed found a major locus comprising of 2 alleles and these are: RN^-, a completely dominant allele with detrimental effects on Napole Yield; and rn^+, a normal recessive allele. Research by Monin and Sellier (1985) had earlier revealed the influence of the RN^- gene on pork quality in Hampshire pigs, which they described as the Hampshire type/effect. In their study, three swine breeds were used: Large White, Pietrain (halothane positive) and Hampshire. They found that although pH values 1hr post slaughter were the same between the Hampshire and Large white, a lower ultimate pH was recorded for the Hampshire pigs, which they suggested was most likely due to an extremely high glycolytic potential in the Hampshire pigs. Estrade and Monin (1993) found that pigs with RN^- mutation had as high as a 70% rise in glycolytic potential/glycogen content in their longissimus muscles compared to rn^+ pigs. This increase in glycolytic potential leads to increased lactate production at the time of postmortem glycolysis, leading to a low ultimate pH (Monin and Sante-Lhoutellier, 2014) which leads to a reduction in water holding capacity of meat from RN^- genotypes. In fact, this low ultimate pH is not the only cause of reduced water holding capacity in these meats as the high glycogen content also influences water holding capacity. The water binding potential of glycogen is approximately the same as that of proteins (Lebret et al., 1999), however, during post slaughter glycolysis or meat processing, glycogen is depleted, leading to the release of water bound to it, which is subsequently lost during cooking, resulting in the lower product yields observed in RN^- genotypes (Lebret et al., 1999).

The RN^- gene is primarily found in swine populations with Hampshire ancestry (Moeller et al., 2003). Its allele frequency in the United States (US) Hampshire populations has been found to be 0.63 (Miller et al., 2000). Considering the propensity of the RN^- genotype to produce poor quality pork, this high frequency was problematic as Hampshire pigs were widely utilized as terminal sires in the US. The Canadian Centre for Swine Improvement (CCSI) in conjunction with 11 artificial insemination centers and the Center for Food Research and Development (CFRD) reported a net loss of $12 per hog for those carrying the RN^- gene. Further, CCSI (2001) reported on a research study at the Lacombe Research Centre in which 25% of pork chops obtained from various retail stores in Alberta had abnormally high glycolytic potential suggesting they were likely RN^- gene carriers. Enfalt et al. (1997a) found that RN^- allele carriers had significantly greater average daily gain, lean percent and hind leg muscles than non-carriers, but lower Napole yield, ultimate pH, and crude protein, and higher drip loss, ash and glycolytic potential. Thus, the influence of the RN^- allele may not be restricted to meat quality traits alone but might affect carcass traits and even proximate composition. Estrade and Monin (1993) also found a 10% reduction in protein content in the Longissimus muscle of RN^- pigs compared to their normal counterparts. Lebret et al (1999) found no difference in hydroxyproline content (mg/g) between the three *RN* genotypes. Enfalt et al. (1997b) looked at breed differences and found RN^- carriers to produce leaner carcasses compared to the Swedish Landrace and purebred Yorkshire breeds.

Both RN^- and Hal^{nn} have been reduced to non-significance in the Canadian swine populations through removal of the Hampshire breed from breeding programs and coordinated testing and removal of *Hal* positive boars and sows from nucleus breeding herds (Mathur and Liu, 2003, https://www.ccsi.ca/Reports/Reports_2003/nsif_CCSI.pdf). Vigilance is still required by the pork industry, however, as Nonneman et al. (2012) identified a novel stress syndrome in pigs characterized by cardiac abnormalities which under stressful conditions can result in death. The dystrophin gene was found to be significantly associated with this syndrome. This stress susceptibility was found to be due to an arginine to tryptophan polymorphism in exon 41 of dystrophin gene. Affected animals tended to have elevated plasma creatine phosphokinase (CPK) levels (Nonneman et al., 2012).

1.7 Other genes affecting pork quality

A number of genes with convincing association to pork quality have been found by various researchers. Ciobanu et al. (2004) reported a quantitative trait locus mapped to the SSC 2 region where the *calpastatin* (*CAST*) gene is found that was significantly associated with eating quality traits like tenderness and juiciness. Calpastatin is a specific inhibitor of calcium-dependent cysteine proteases. These proteases are known to play important roles in the tenderization of meat through degradation of muscle proteins postmortem. Gerbens et al. (1998) studied the association of the *adipocyte fatty acid binding protein* (*A-FABP*) gene with pork quality traits and their results showed that the *A-FABP* locus on SSC4 is associated with the regulation of intramuscular fat (IMF) deposition in pigs. Gerbens et al. (1999) also found increased intramuscular fat content and backfat thickness to be associated with identical heart *fatty acid binding protein restriction fragment length* polymorphism genotypes (*RFLP*) on SSC6 in halothane negative Duroc pigs. Kim et al. (2004a) examined the porcine *Delta-like non-canonical notch ligand* (*DLK-1*) *gene trap locus 2* (*GLT 2*) region in Yorkshire and Berkshire pigs to assess whether the callipyge polar over-dominance was present in those breeds. They found that F2 progeny with a maternally transmitted allele 1 and a paternally derived allele 2 had greater lean percent and lower backfat thickness. This form of overdominance is described as polar because the phenotypic expression of the heterozygote is more common than the other homozygote genotypes on the same locus (Noelle et al., 1996). Parental imprinting is closely related to this form of overdominance as only one parental allele is expressed in the progeny (Oczkowicz, 2009). This form of overdominance was first reported in sheep after continuous selection for increased muscling resulted in a ram lamb (named Solid Gold) being born with pronounced muscularity in the rump and upper hind legs. It was saved for future mating and descendants of this ram are known as callipyge (Greek for “beautiful buttocks”). The genomic location of the gene influencing this form of muscular hypertrophy has been mapped to the distal end of chromosome 18 (Murphy et al., 2006).

Kim et al. (2004b) reported a potential association of the *porcine agouti signaling protein (ASIP)* gene, mapped to SSC17q21 to be having an effect on fat accretion and growth. These results suggest that there may be numerous genes with small additive effects on quality. However, to the author's knowledge, there have been no reports on genetic correlations of Warner-Bratzler shear force measures with soluble and insoluble collagen concentrations. An understanding of this relationship will enrich our knowledge of connective tissue characteristic and determine if selection for collagen traits is possible.

Cameron (1990) reported that traits like pork flavor, flavor-liking, and abnormal flavor were low to moderately heritable (0.16-0.31). Cameron (1990) further found a strong positive genetic correlation between pork flavor and intermuscular fat weight (0.60) and subcutaneous fat weight (0.85), thus selecting for these two traits over time may lead to increased pork flavor. Jonsall et al. (2001) reported that ham from carriers of RN^- gene had higher scores for odor intensity than non-carriers, insinuating a possible influence of major genes on this trait, although further research may be needed to substantiate this observation.

1.8 Heritability estimates of some pork quality traits

Information on the heritabilities of meat quality traits provides tremendous insights on the most probable response to selection (Mateescu, 2015). Most pork quality traits typically are low to moderately heritable, as the heritabilities reported for these traits in this current review usually lay within the bounds of 0.10-0.35. Mateescu (2015) also reported low to moderate means in a review on the heritability estimates of beef quality (physicochemical) quality traits ranging between 0.02-0.47. Also, Safari et al. (2005) reported low to moderate heritabilities for meat traits in sheep, ranging from 0.04 to 0.35. Mir et al. (2017) however observed higher heritability estimates for poultry, which had moderate to high heritabilities for quality traits between 0.35 and 0.81.

Table 1.2 presents a summary of the heritabilities of some selected pork and eating quality traits. Ciobanu et al. (2011) reported that in the category of sensory traits, traits like tenderness (measured either subjectively or through instrumental determinations) were more heritable than traits like juiciness and flavor. Similar observations were made during the scan of the literature for this current review (Table 1.2). Technological traits like color and shear force value were more heritable than pH and cooking loss (Table 1.2). The results from the papers reviewed suggest that improvements in meat quality traits like tenderness (Miar et al 2014), water holding capacity and intramuscular fat are likely with genetic selection. Suzuki et al. (1995) and Hovenier et al. (1993) reported low-moderate heritability estimates for total collagen which suggests that improvements can be made in this trait over time.

1.9 Genetic relationships among some pork quality traits

Genetic correlation between two traits is basically a measure of the influence of pleiotropic genes on those traits and thus, estimates the strength and direction of the relationship between the breeding values of two traits under consideration while phenotypic correlations measure the strength of the relationship between performance/phenotypes of two traits under consideration (Bourdon, 1995).

Hovenier et al. (1993) reported a high negative phenotypic correlation (-0.51) between sensory panelist assessment of tenderness and Warner-Bratzler shear force values and subsequently recommended the use of shear force values to predict pork tenderness and possibly as an index trait since the genetic correlation between those traits were also high (-0.71) (table 1.3). Further, they found an almost non-existent (0.01) phenotypic correlation between collagen value and subjective tenderness and a very weak phenotypic relationship with Warner-Bratlzer shear force values, indicating that collagen value may not be a good indicator of these two traits (Table 1.4). However, given the sparseness of the information provided on how collagen determinations were made, and the fact that determinations of the amounts of soluble and insoluble collagen were apparently not made, further research is warranted in this regard.

1.10 Conclusions and overall hypotheses

Although heritability and genetic relationships between total collagen and some carcass and meat quality traits have been reported by Suzuki et al. (2005), no literature examining the heritability of collagen heat solubility was noted. Therefore, this thesis, will examine genetic and phenotypic relationships between total, insoluble and soluble collagen and pork quality as no studies have looked at these two traits especially in Canadian swine populations. Specifically, this thesis will test the hypotheses that 1) pork intramuscular collagen characteristics are heritable, and 2) are related to Warner-Bratzler shear force and other meat quality traits. The influence of collagen content on pork texture is not yet well understood and, in light of the competition between pork products and other meat products, there is a need to estimate the heritabilities and genetic relationships of pork collagen characteristics.

The objectives of this thesis were then to:

1) To estimate the heritabilities and genetic and phenotypic correlations of total, heat-soluble and heat-insoluble collagen from pork intramuscular tissue and compare them to those of other meat quality characteristics;

2) To examine regression equations considering total, heat-soluble and heaet-insoluble collagen that describe pork quality indicators; and

3) To examine how intramuscular pH, fat, muscle lightness, and Warner-Bratzler shear force relate to each other and other pork quality attributes.

1.11 Tables

Table 1.1: Classification of collagen with their tissue distributions and their chromosomal locations

Collagen Category	Structures formed/ collagen sub-family	Members/ collagen type	Molecular/alpha chain composition	Location/tissue distribution	Alpha chain coding genes (gene location) †	Chromosome number-Sus scrofa	NCBI Gene ID Homo sapiens	NCBI Gene ID (Sus scrofa)	Trimer composition
Fibrillar	Quarter staggered fibrils	I[1-4,7]	$[\alpha1(I)]_2\alpha2(I)$	Skin, bone, ligaments, striated muscles, most connective tissues,	*COL1A1* (17q21.3) *COL1A2*(7q21.3)	12 9	1277 1278	100738123 100626716	Hetero-trimer
		II[8, 10]	$\alpha1(II)]_3$	vitreous humor, cartilage	*COL2A1* (12q13.11)	2	1280	397323	Homo-trimer
		III[6]	$[\alpha1(III)]_3$	Striated muscles, reticular fibers of most tissues,	*COL3A1* (2q31)	15	1281	100152001	Homo-trimer
		V[3]	$[\alpha1(V)]_2\alpha2(V)$ $[\alpha1(V)]_3$	Skeletal muscle, skin, heart, bone	*COL5A1* (9q34.3) *COL5A2* (2q32.2) *COL5A3* (19p13.2)	1 15 2	1289 1290 50509	397533 397532 397531	Hetero-trimer or homo-trimer
		XI[3, 9]	$\alpha1(XI)\alpha2(XI)\alpha3(XI)$	Cartilage	*COL11A1* (1p21.1) *COL11A2* (6p21.32) *COL11A3/COL2A1* (12q13.11)	4 7 -	1301 1302 1280	397175 100520915 -	Hetero-trimer
		XXIV[7, 11]	$[\alpha1(XXIV)]_3$	Nascent bones, cornea	*COL24A1* (1p22.3)	4	255631	102157845	Homo-trimer
		XXVII[3, 7, 12]	$[\alpha(XXVII)]_3$	Cartilage, ear, eye	*COL27A1* (9q32)	1	85301	102159686	Homo-trimer
Non-	Basemen	IV[3, 13, 14]	$[\alpha1(IV)]_2\alpha2(IV)$	Basement	*COL4A1*	11	1282	1005153	Hetero-

fibrillar	t membranes		$\alpha1-\alpha6$	membranes of tissues	(13q34) *COL4A2* (13q34) *COL4A3* (2q36.3) *COL4A4* (2q36.3) *COL4A5* (Xq22.3) *COL4A6* (Xq22.3)	11 15 15 X X	1284 1285 1286 1287 1288	36 100153454 100621504 100621403 100737091 100620724	trimer
	Short chain (hexagonal lattices)	VIII [15]	$[\alpha1(VIII)]_2\alpha2(VIII)$	Descemet's membrane, striated muscles, endothelial cells	*COL8A1* (3q12.1) *COL8A2* (1p34.3)	13 6	1295 1296	397430 100525585	Hetero-trimer
		X[3, 16]	$[\alpha3(X)]_3$	Growth plate cartilage	*COL10A1* (6q22.1)	1	1300	448809	Homo-trimer
	Beaded filaments	VI [7, 17]	$\alpha1(VI)\alpha2(VI)\alpha3(VI)$	Skeletal muscles, cornea, most connective tissues	*COL6A1* (21q22.3) *COL6A2* (21q22.3) *COL6A3* (2q37.3)	13 - 15	1291 1292 1293	100623720 100101552 100101551	Hetero-trimer
	Fibril-associated collagens with interrupted triple helices (FACITs)	IX [18]	$\alpha1(IX)\alpha2(IX)\alpha3(IX)$	Cornea, cartilage	*COL9A1* (6q13) *COL9A2* (1p34.2)	1 6	1297 1298	100155319 100621911	Hetero-trimer
		XX [5, 19]	$[\alpha1(XX)]_3$	Skin, tendon, cartilage	*COL20A1* (20q13.33)	17	57642	110257377	Homo-trimer
		XXI[3, 24]	$[\alpha1(XXI)]_3$	Blood vessel walls Skeletal muscle, heart, stomach	*COL21A1* (6p12.1)	7	81578	100523618	Homo-trimer
		XII[6, 26]	$[\alpha1(XII)]_3$	Skeletal muscle, endothelial cells, tendons	*COL12A1* (6q13-q14.1)	1	1303	100156689	Homo-trimer

	XXII [5]	$[\alpha 1(XXII)]_3$	Myotendinous junctions of skeletal	*COL22A1* (8q24.23-q24.3)	4	169044	100519955	Homo-trimer
	XIV [6]	$[\alpha 1(XIV)]_3$	Tendon, liver, skin	*COL9A1* (6q13)	1	12839	100155319	Homo-trimer
	XVI [6,7]	$[\alpha 1(XVI)]_3$	Fibroblast, keratinocytes	*COL16A1* (1p35.2)	6	1307	100737666	Homo-trimer
	XIX [3]	$[\alpha 1(XIX)]_3$	Skeletal muscle, spleen	*COL19A1* (6q13)	1	1310	100512751	Homo-trimer
Anchoring fibrils	VII [2]	$[\alpha 1(VII)]_3$	Skeletal muscle, skin, esophagus	*COL7A1* (3p21.31)	13	1294	100523209	Homo-trimer
Multiple triple helix domains and interruptions (MULTIPLEXINS)	XV [3]	$[\alpha 1(XV)]_3$	Smooth muscle cells, fibroblasts	*COL15A1* (9q22.33)	1	1306	100620394	Homo-trimer
	XVIII[6]	$[\alpha 1(XVIII)]_3$	Liver, lungs	*COL18A1* (21q22.3)	13	80781	100624675	Homo-trimer
Transmembrane collagens	XIII [20]	$[\alpha 1(XIII)]_3$	Endomysium, epidermis, intestine	*COL13A1* (10q22.1)	14	1305	100157199	Homo-trimer
	XVII [21]	$[\alpha 1(XVII)]_3$	Eye, epithelial hemidesmosomes	*COL17A1* (10q24.3)	14	1308	414914	Homo-trimer
	XXIII [5,7]	$[\alpha 1(XXIII)]_3$	Skin, lung, tendon	*COL23A1* (5q35.3)	2	91522	100521775	Homo-trimer
	XXV [23]	$[\alpha 1(XXV)]_3$	Testis, heart	*COL25A1* (4q35)	8	84570	102160320	Homo-trimer
Others	XXVIII [5, 25]	$[\alpha 1(XXVIII)]_3$	Peripheral nerves	*COL28A1* (7p21.3)	9	340267	100510974	Homo-trimer
	XXIX [22, 27]	$[\alpha 1(XXIX)]_3$	Skin, lung	*COL29A1/COL6A5* (3q22.1)	-	256076	-	Homo-trimer
	XXVI [5, 25]	$[\alpha 1(XXVI)]_3$	Testis, ovary	*COL26A1*	3	136227	1005195	Homo-

		(7q22.1)	42	trimer

1-MGC (2002); 2-Sutmuller et al. 1997; 3-Gelse et al. (2003); 4-Henriksen and Karsdal (2016); 5-Myllyharju and Kivirikko (2004); 6-Kovanen (2002); 7- Uhlen et al. (2015); 8-Gudman and Karsdal, (2016); 9-Morris and Bachinger (1987); 10-Keigo et al. (2017); 11-Matsuo et al. (2008); 12- Plumb et al (2011); 13- Sand et al. (2016); 14-Khoshnoodi et al. (2008); 15- Shuttleworth (1997); 16-Gudmann and Karsdal (2016); 17- Cescon et al. (2015); 18-Olsen (1997); 19-Koch et al. (2001); 20-Siebuhr and Karsdal (2016); 21- Li et al. (1993); 22- Wefel et al. (2011); 23-Keld and Karsdal (2016); 24- Fitzgerald and Bateman (2001); 25- Gordon and Haln (2010); 26- Dublet et al. (1989); 27-Söderhäll et al. (2007) †-Homo sapiens.

Table 1. 2**:** Heritability estimates of some meat quality traits

Trait	Heritability (h^2)⊤	Number of estimates	Range
Cooking loss	0.13	5	0.06-0.20
Shear force value	0.25	6	0.04-0.45
Ultimate pH	0.18	11	0.00-0.39
Drip loss	0.17	8	0.08-0.30
Intramuscular fat	0.40	12	0.19-0.67
Minolta L^*	0.26	6	0.16-0.44
Minolta a^*	0.29	2	0.21-0.36
Minolta b^*	0.18	2	0.15-0.20
Tenderness†	0.34	2	0.23-0.45
Juiciness†	0.16	3	0.12-0.19
Overall acceptability†	0.16	1	-
Water holding capacity	0.63	1	-
Pork flavor†	0.28	2	0.13-0.14
Collagen value	0.27	2	0.23-0.30

† obtained through a subjective sensory evaluation with panelists. ⊤- The heritabilities hereby presented were average from the following papers: Allen et al. (1966); Cai et al. (2008); Cameron (1990); DeVries et al. (1994); Cabling et al. (2015); Hovenier et al. (1992); Jensen et al. (1967); Knapp et al. (1997); Larzul et al. (1997); Lo et al. (1992); Mair et al. (2004); Suzuki et al. (2005); Van Wijk et al. (2005); Hovenier et al. (1993).

Table 1. 3**:** Genetic and phenotypic correlations of cooking loss, shear force and intramuscular fat with some meat quality traits

Traits	Cooking loss		Intramuscular fat		Shear force		Authors
	r_g^1	r_p^1	r_g^2	r_p^2	r_g^3	r_p^3	
Subjective tenderness			0.31	0.05	-0.73	-0.40	Cameron (1990)[2], Malmfors and Nilsson (1978)[3]
pH			-0.18	-0.09			Hovenier et al. (1992)[2]
Moisture Content			-0.72	-0.50			Malmfors and Nilsson (1978)[2]
Drip loss	0.66	0.19	-0.59	-0.35			Malmfors and Nilsson (1978)[1], Jensen et al. (1967)[2]
Ether extract				0.70			Jensen et al. (1967)[2]
Water holding capacity			-0.14	-0.25			Jensen et al. (1967)[2]
Lean percent	-0.06	0.10	-0.37	-0.23			De Vries et al. (1994)[1,2]

Table 1. 4: Genetic and phenotypic correlations of total collagen with some pork quality traits

Traits	Total collagen		Author
	r_g	r_p	
Tenderness		0.01	Hovenier et al. (1993)
Intramuscular fat	0.43	0.12	Suzuki et al. (2005)
pH	-0.42	0.03	Suzuki et al. (2005)
Drip loss	-0.09	-0.26	Suzuki et al. (2005)
Cooking loss	-0.64	0.06	Suzuki et al. (2005)
L^*	-0.17	0.18	Suzuki et al. (2005)
a^*	-	0.11	Hovenier et al. (1993)
Shear force value	0.26	-0.10	Suzuki et al. (2005)
Longissimus muscle area	0.19	0.07	Suzuki et al. (2005)
Back fat	-0.35	-0.07	Suzuki et al. (2005)

1.12 Figures

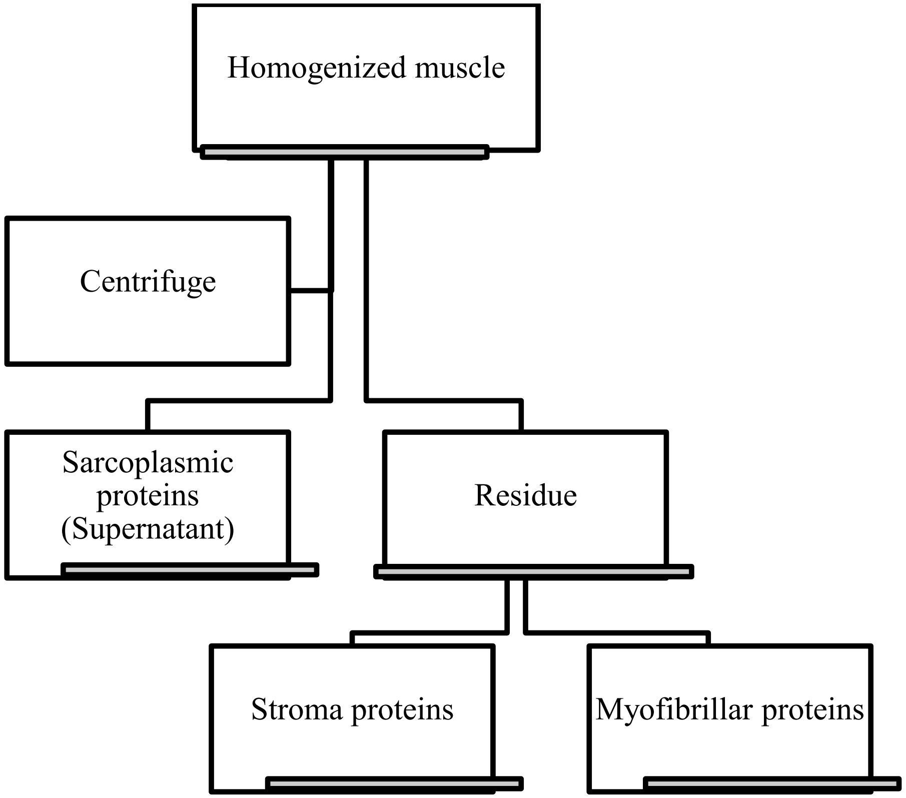

Figure 1. 1: Muscle protein fractionation into its solubility categories. Adapted from Greaser and Guo (2015) with modifications.

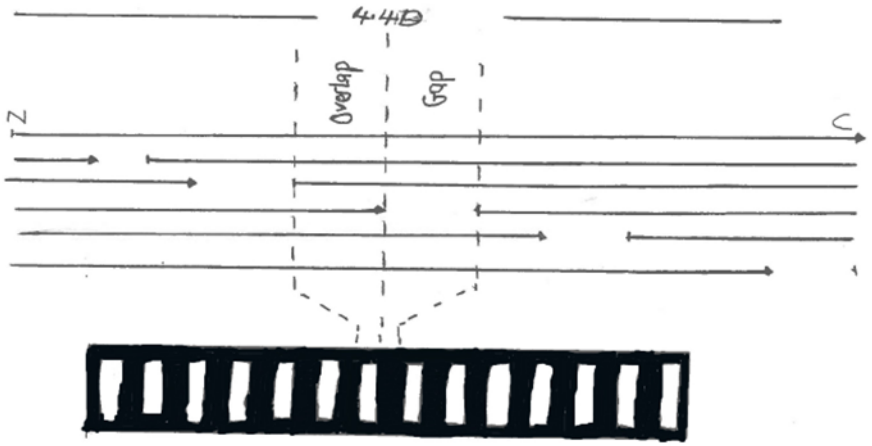

Figure 1. 2: A Schematic representation of the 4.4 D overlap conformation of negatively stained collagen fibers under electron microscope showing the banding patterns.

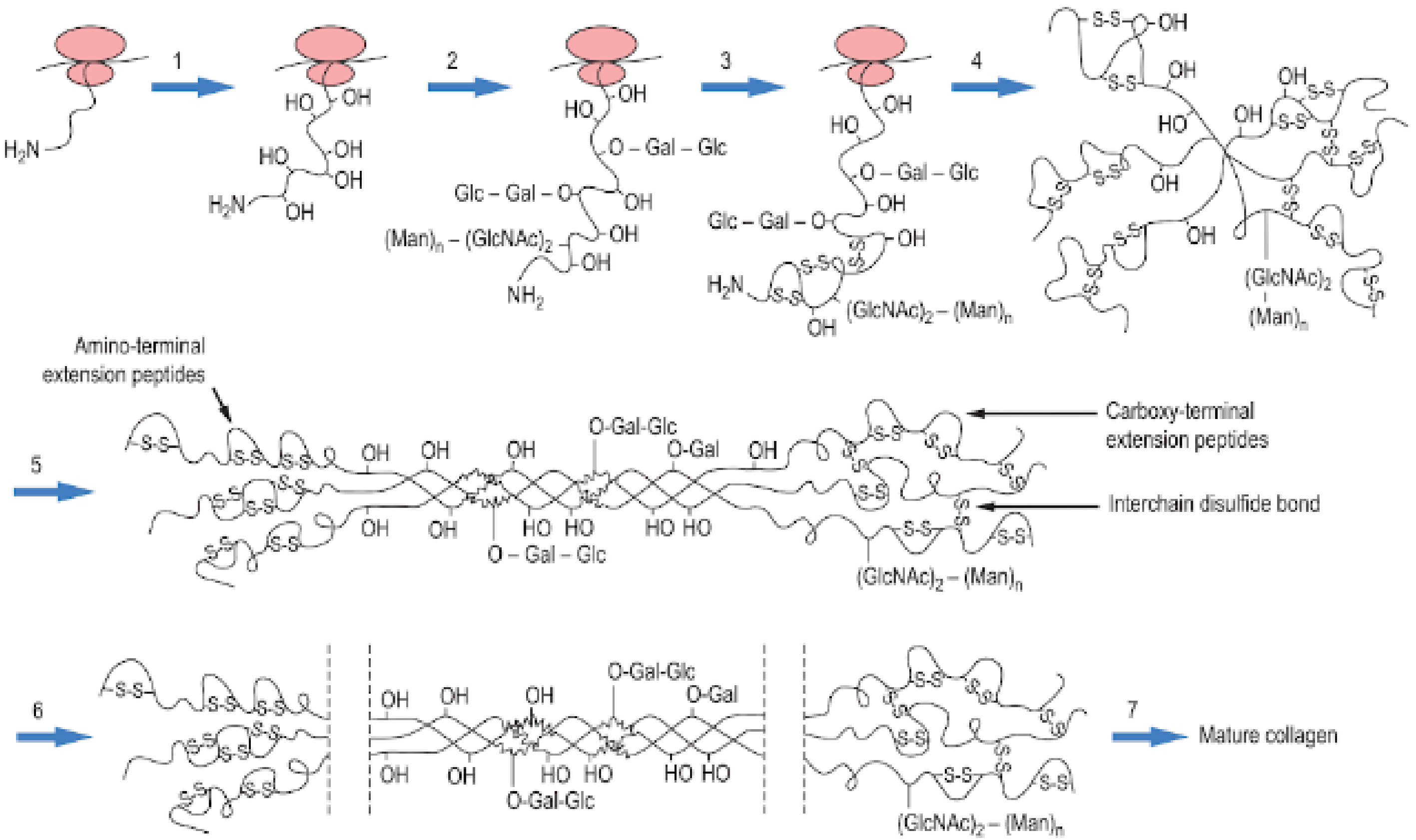

Figure 1. 3: Collagen biosynthesis and post-translational modifications. 1- hydroxylation of lysine and proline residues; 2-addition of N- and O-linked oligosaccharides to alpha chains; 3-intrachain disulfide bonds formation in the N-terminus of the polypeptide chains; 4-interchain disulfide bond formation at the C-terminus aiding in chain alignment; 5- soluble tropocollagen (triple stranded) formation which is subsequently transported to the Golgi vesicles.; 6- removal of C- and N-terminal propeptides after exocytosis; 7- final processing- a lateral association of collagen molecules, crosslink formation and formation of collagen fibers. Where: Glc= glucose; Gal= galactose; Man= mannose and GlcNAc=N-acetylglucosamine. Reproduced from Kaushal et al. (2014) with permission from publishers (copyright 2014 Saunders Elsevier).

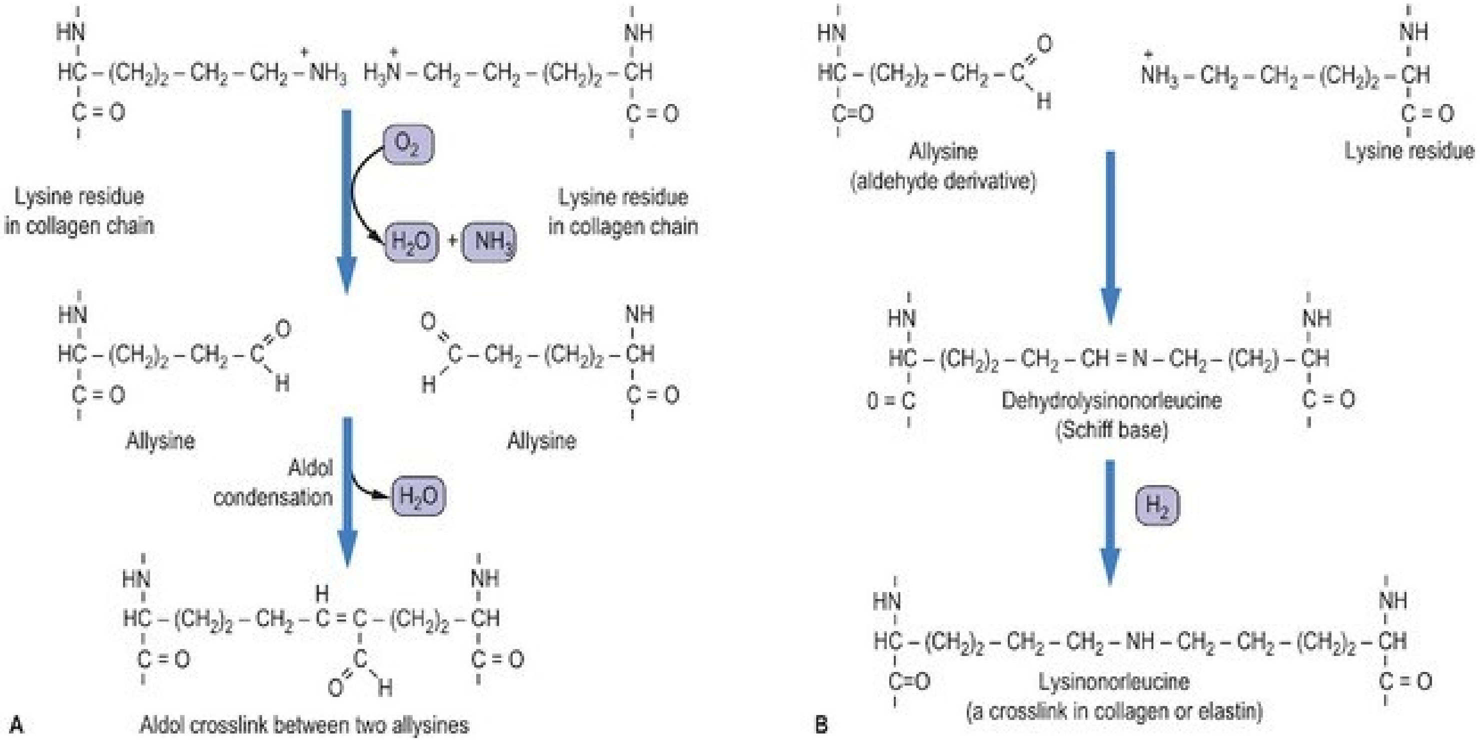

Figure 1. 4: Formation of collagen crosslinks. A-crosslinking by aldol condensation; B-crosslinking by Schiff base intermediates. Reproduced from Kaushal et al. (2014) with permission from publishers (copyright 2014 Saunders Elsevier).

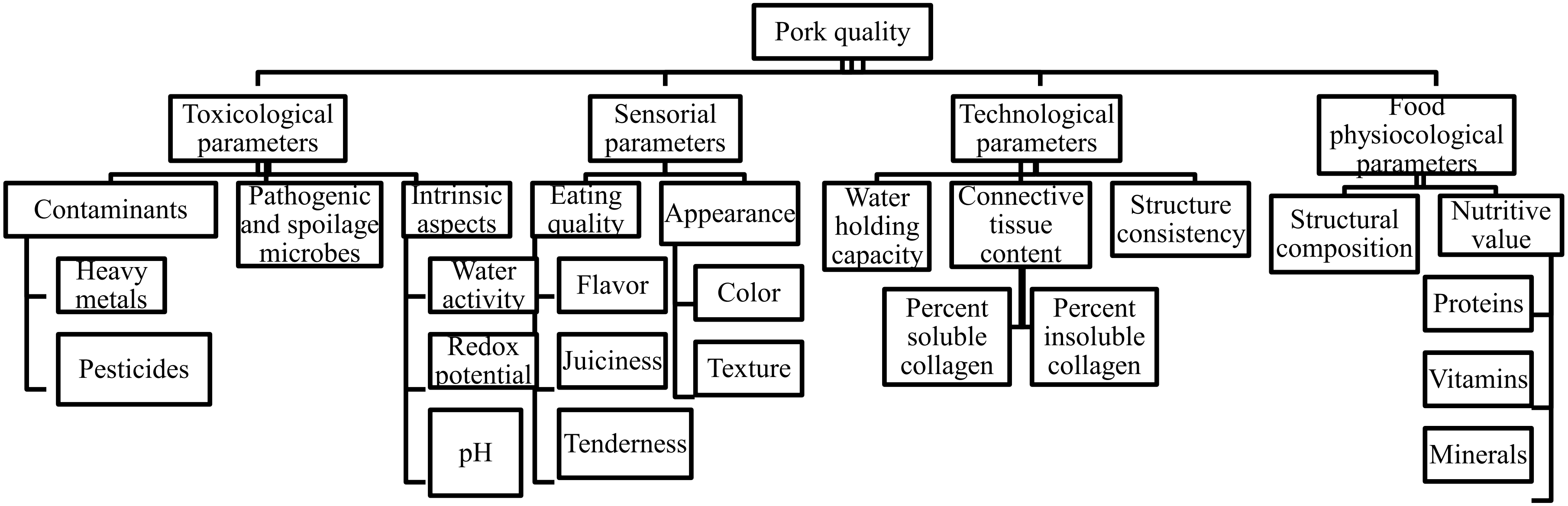

Figure 1. 5 : Major components of pork quality.

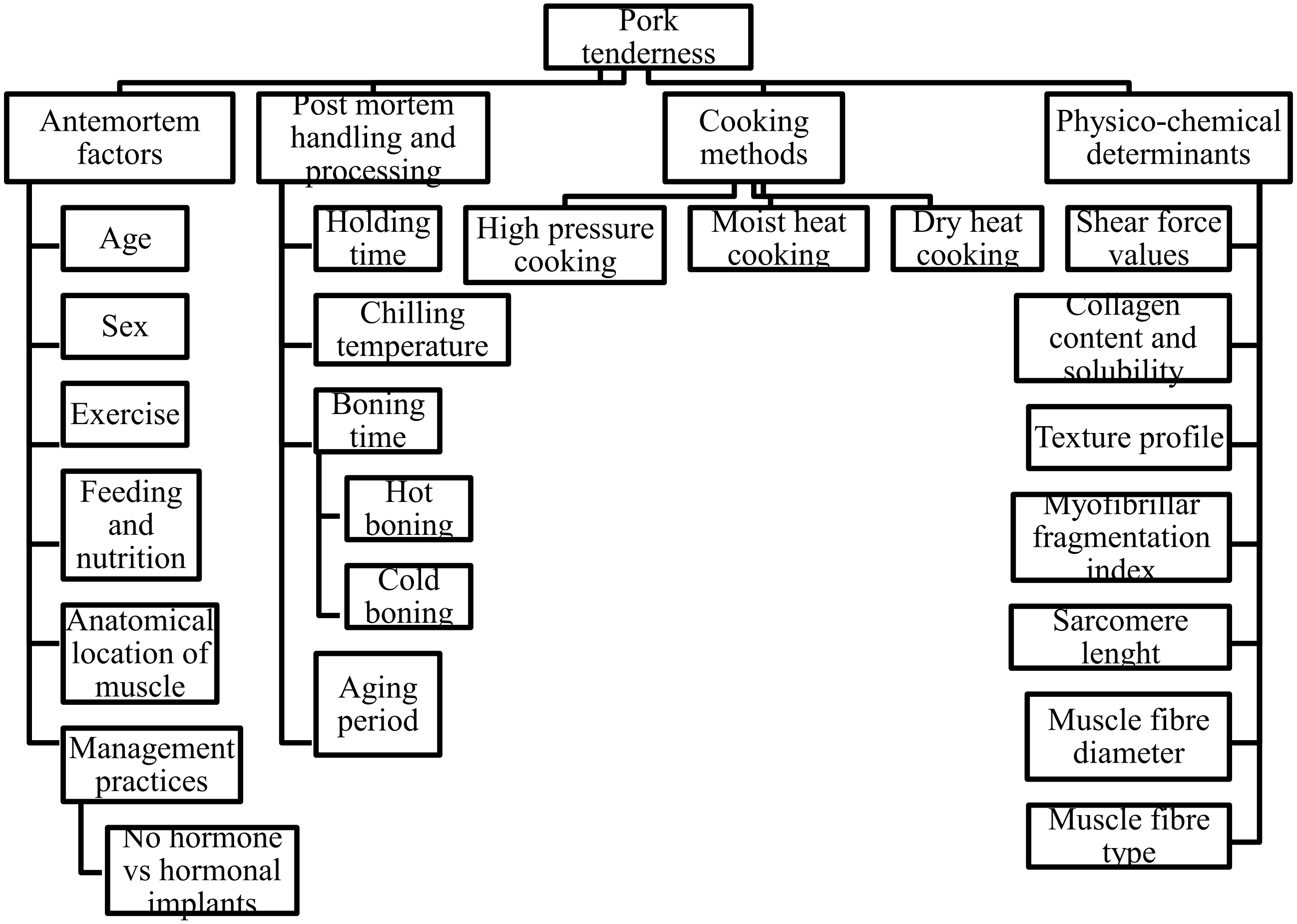

Figure 1. 6: Factors affecting pork tenderness.

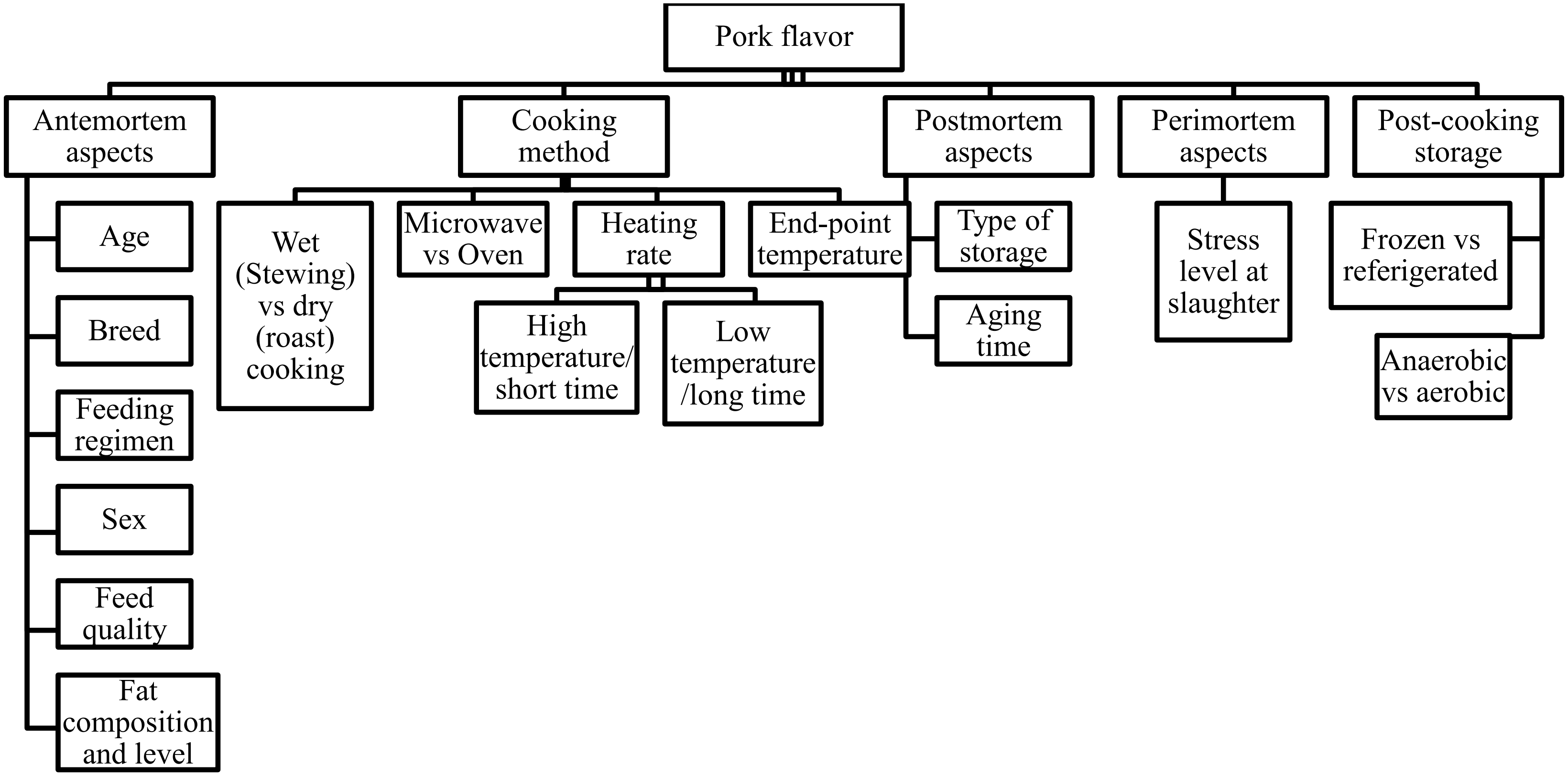

Figure 1. 7: Factors influencing perceived pork flavor

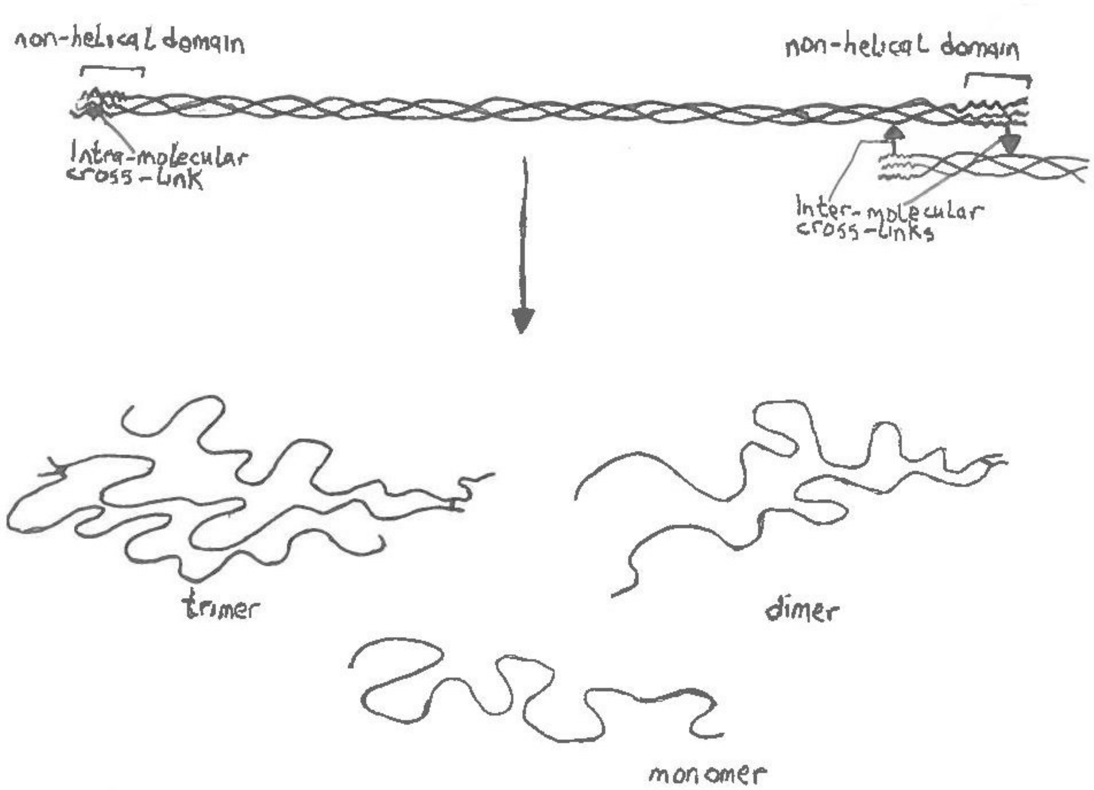

Figure 1. 8: A Schematic representation of collagen denaturation into gelatin upon heat application.

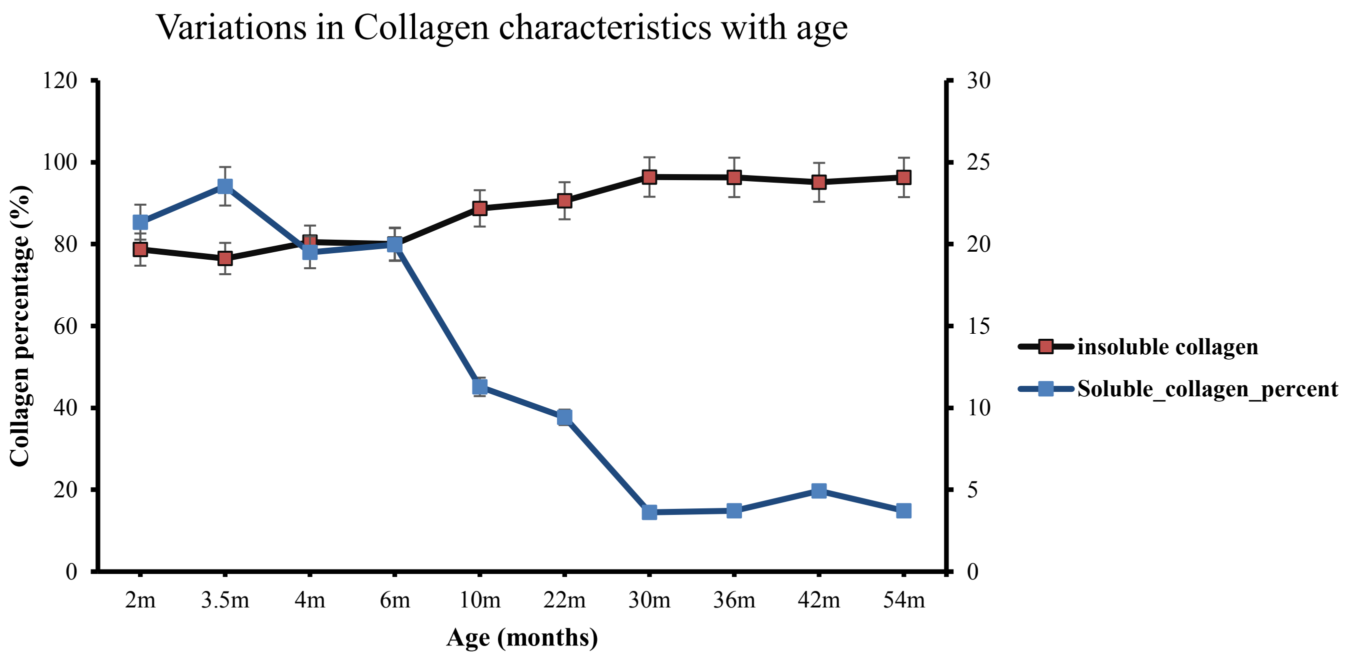

Figure 1. 9: Percent soluble and insoluble collagen after heat treatment at 77°C for 1hr in the sternomandibularis muscles of bovines of different ages showing the decline in collagen solubility with increasing age. Adapted from Hill (1966) with modifications.

1.13 References

Aalhus, J. L., Jones, S. D. M., Robertson, W. M., Tong, A. K. W., and Sather, A. P. (1991). Growth characteristics and carcass composition of pigs with known genotypes for stress susceptibility over a weight range of 70 to 120 kg. Animal Science, 52(2), 347-353. doi:10.1017/S0003356100012873.

Aaslyng, M. D., Bejerholm, C., Ertbjerg, P., Bertram, H. C., and Andersen, H. J. (2003). Cooking loss and juiciness of pork in relation to raw meat quality and cooking procedure. Food Quality and Preference, 14(4), 277-288. doi:10.1016/S0950-3293(02)00086-1.

Aberle, E. D., Etherton, T. D., and Allen, C. E. (1977). Prediction of pork carcass compositions using subcutaneous adipose tissue moisture or lipid concentration. Journal of Animal Science, 45(3), 449-456. doi:10.2527/jas1977.453449x.

Allen, E., Forrest, J. C., Chapman, A. B., First, N., Bray, R. W., and Briskey, E. J. (1966). Phenotypic and genetic associations between porcine muscle properties. Journal of Animal Science, 25(4), 962-966. doi:10.2527/jas1966.254962x.

Apple J.K. and Yancey. J.W.S. (2013). Water-holding capacity of meat. In C.R. Kerth (Ed.), The science of meat quality. John Wiley and Sons. Pp. 119-139.

Apple, J. K., Maxwell, C. V., Stivarius, M. R., Rakes, L. K., and Johnson, Z. B. (2002). Effects of dietary magnesium and halothane genotype on performance and carcass traits of growing-finishing swine. Livestock Production Science, 76(1), 103-113. doi:10.1016/S0301-6226(02)00004-0.

Avery, N. C., Sims, T. J., Warkup, C., and Bailey, A. J. (1996). Collagen cross-linking in porcine m. longissimus lumborum: Absence of a relationship with variation in texture at pork weight. Meat Science, 42(3), 355-369. doi:10.1016/0309-1740(95)00021-6.

Bailey, A. J., and Light, N. D. (1989). Connective tissue in meat and meat products. Elsevier Publishers.

Bailey, A. J., and Shimokomaki, M. S. (1971). Age related changes in the reducible cross-links of collagen. FEBS Letters, 16(2), 86-88. doi:10.1016/0014-5793(71)80338-1.

Bella, J., Brodsky, B., and Berman, H. M. (1995). Hydration structure of a collagen peptide. Structure, 3(9), 893-906. doi:10.1016/S0969-2126(01)00224-6.

Bendall, J. R. (1967). The elastin content of various muscles of beef animals. Journal of the Science of Food and Agriculture, 18(12), 553-558. doi:10.1002/jsfa.2740181201.

Berge, P., Kuypers, R. and Kurth, L. B. (1997). Collagen crosslink profile and meat texture in two beef muscles. In Proceedings 43rd International Congress of Meat Science and Technology (pp. 548-549), 27 July - 1 August, Auckland, New Zealand.

Birk, D. E., Fitch, J. M., and Linsenmayer, T. F. (1986). Organization of collagen types I and V in the embryonic chicken cornea. Investigative Ophthalmology and Visual Science, 27(10), 1470-1477. Retrieved from http://www.iovs.org/cgi/content/abstract/27/10/1470.

Bonaldo, P., Braghetta, P., Zanetti, M., Piccolo, S., Volpin, D., and Bressan, G.M. (1998). Collagen VI deficiency induces early onset myopathy in the mouse: An animal model for bethlem myopathy. Human Molecular Genetics, 7(13), 2135-2140. doi:10.1093/hmg/7.13.2135.

Bonneau, M. (1998). Use of entire males for pig meat in the European union. Meat Science, 49S1, S257-S272. doi:10.1016/S0309-1740(98)00089-8.

Bornstein, P., and Sage, H. (1980). Structurally distinct collagen types. Annual Review of Biochemistry, 49(1), 957-1003. doi:10.1146/annurev.bi.49.070180.004521.

Bosse, M. (2018). A Genomics Perspective on Pig Domestication, Animal Domestication, Fabrice Teletchea, IntechOpen, DOI: 10.5772/intechopen.82646. Available from: https://www.intechopen.com/books/animal-domestication/a-genomics-perspective-on-pig-domestication

Bouchard, C., Malina, R. M., and Pérusse, L. (1997). Understanding the methods. In Malina, R.M and Perusse, L. (Ed.), Genetics of fitness and physical performance. Human Kinetics. Pp. 58-78.

Bourdon, R. M. (1995). Understanding animal breeding. Prentice Hall. Retrieved from http://www.vlebooks.com/vleweb/product/openreader?id=none&isbn=9781292052069&uid=none.

Bouton, P. E., Harris, P. V., Shorthose, W. R., and Ratcliff, D. (1974). Changes in the mechanical properties of veal muscles produced by myofibrillar contraction state, cooking temperature and cooking time. Journal of Food Science, 39(5), 869-875. doi:10.1111/j.1365-2621. 1974.tb07264. x.

Bowker, B. C., Grant, A. L., Forrest, J. C., and Gerrard, D. E. (2000). Muscle metabolism and PSE pork. Proceedings of the American Society of Animal Science, 79(E-Suppl_1), 1-8. doi:10.2527/jas.00.079ES1001c.

Bray, R. W. (1966). Pork quality-definition, characteristics, and significance. Journal of Animal Science, 25(3), 839-842. doi:10.2527/jas1966.253839x.

Brocks, L., Klont, R. E., Buist, W., de Greef, K., Tieman, M., and Engel, B. (2000). The effects of selection of pigs on growth rate vs leanness on histochemical characteristics of different muscles. Journal of Animal Science, 78(5), 1247-1254. doi:10.2527/2000.7851247x

Bulleid, N. J., Dalley, J. A., and Lees, J. F. (1997). The C-propeptide domain of procollagen can be replaced with a transmembrane domain without affecting trimer formation or collagen triple helix folding during biosynthesis. The EMBO Journal, 16(22), 6694-6701. doi:10.1093/emboj/16.22.6694.

Bulliet, R. W., (2005). Post domesticity our lives with animals. Hunters, herders, and hamburgers: The past and future of human-animal relationships (pp. 1-36) Columbia University Press. doi:10.7312/bull13076 Retrieved from https://www.jstor.org/stable/10.7312/bull13076.

Cabling, M. M., Kang, H. S., Lopez, B. M., Jang, M., Kim, H. S., Nam, K. C., Choi, J. G., and Seo, K. S. (2015). Estimation of genetic associations between production and meat quality traits in Duroc pigs. Asian-Australasian Journal of Animal Sciences, 28(8), 1061-1065. doi:10.5713/ajas.14.0783.

Cai, W., Casey, D. S., and Dekkers, J. C. M. (2008). Selection response and genetic parameters for residual feed intake in Yorkshire swine. Journal of Animal Science, 86(2), 287-298. doi:10.2527/jas.2007-0396.

Cambero, M. I., Seuss, I., and Honikel, K. O. (1992). Flavor compounds of beef broth as affected by cooking temperature. Journal of Food Science, 57(6), 1285-1290. doi:10.1111/j.1365-2621. 1992.tb06838. x.

Cameron, N. D. (1990). Genetic and phenotypic parameters for carcass traits, meat and eating quality traits in pigs. Livestock Production Science. 26(2), 119-135. doi:10.1016/0301-6226(90)90061-A.

Cameron, N. D., Warriss, P. D., Porter, S. J., and Enser, M. B. (1990). Comparison of Duroc and British Landrace pigs for meat a and eating quality. Meat Science. 27(3), 227-247. doi:10.1016/0309-1740(90)90053-9.

Canadian Centre for Swine Improvement Inc. CCSI (2001). Annual report 2001/02. pp 1-31.

Carlson, K. B., Prusa, K. J., Fedler, C. A., Steadham, E. M., Outhouse, A. C., King, D. A., Huff-Lonergan E., and Lonergan, S. M. (2017). Postmortem protein degradation is a key contributor to fresh pork loin tenderness. Journal of Animal Science, 95(4), 1574-1586. doi:10.2527/jas2016.1032.

Castro, L. M., Rosa, G. J. M., Lopes, F. B., Regitano, L. C. A., Rosa, A. J. M., and Magnabosco, C. U. (2017). Genomewide association mapping and pathway analysis of meat tenderness in polled nellore cattle. Journal of Animal Science, 95(5), 1945. doi:10.2527/jas2016.1348.

Cescon, M., Gattazzo, F., Chen, P., and Bonaldo, P. (2015). Collagen VI at a glance. Journal of Cell Science, 128(19), 3525-3531. doi:10.1242/jcs.169748.

Channon, H. A., D'Souza, D. N., and Dunshea, F. R. (2016). Developing a cuts-based system to improve consumer acceptability of pork: Impact of gender, ageing period, endpoint temperature and cooking method. Meat Science, 121, 216-227. doi: 10.1016/j.meatsci.2016.06.011.

Cheung, P. C., Salt, I. P., Davies, S. P., Hardie, D. G., and Carling, D. (2000). Characterization of AMP-activated protein kinase gamma-subunit isoforms and their role in AMP binding. The Biochemical Journal, 346 Pt 3(3), 659-669. doi:3460659.

Chou, M., and Li, H. (2002). Genomic organization and characterization of the human type XXI collagen (COL21A1) gene. Genomics, 79(3), 395-401. doi:10.1006/geno.2002.6712.

Ciobanu, D. C., Bastiaansen, J. W. M., Lonergan, S. M., Thomsen, H., Dekkers, J. C. M., Plastow, G. S., and Rothschild, M. F. (2004). New alleles in calpastatin gene are associated with meat quality traits in pigs. Journal of Animal Science, 82(10), 2829. Retrieved from http://jas.fass.org/cgi/content/abstract/82/10/2829

Ciobanu, D. C., Lonergan, S. M., and Huff-Lonergan, E. J. (2011). Genetics of meat quality and carcass traits. The genetics of the pig (pp. 355-389) CABI. doi:10.1079/9781845937560.0355. Retrieved from: http://www.cabi.org/cabebooks/ebook/20113037220.

Cockett, N. E., Jackson, S. P., Shay, T. L., Farnir, F., Berghmans, S., Snowder, G. D., Nielsen, N.D and Georges, M. (1996). Polar overdominance at the ovine callipyge locus. Science, 273(5272), 236-238. doi:10.1126/science.273.5272.236.

Coggins, P. C. (2012). Attributes of muscle foods: Color, texture, flavor. In L. M. L. Nollet (Ed.), Handbook of meat, poultry and seafood quality (pp. 35-44) Blackwell Publishing Ltd.

doi:10.1002/9781118352434.ch3.Retrievedfromhttps://onlinelibrary.wiley.com/doi/abs/10.1002/9781118352434.ch3.

Coulson, C. J. (1994). Molecular mechanisms of drug action (2. ed.) Taylor and Francis.

Crownover, R. D., Garmyn, A. J., Polkinghorne, R. J., Rathmann, R. J., Bernhard, B. C., and Miller, M. F. (2017). The effects of hot vs. cold boning on eating quality of new zealand grass fed beef. Meat and Muscle Biology, 1(1), 207-217. doi:10.22175/mmb2017.06.0030.

Cundy, T. Reid R.I. and Grey, A. (2014). Metabolic bone disease. In Marshall, W. J., Lapsley, M., Day, A. and Ayling R. (Ed.), Clinical biochemistry E-book: Metabolic and clinical aspects (pp. 604-636) Elsevier Health Sciences.

David E. Birk, John M. Fitch, Joanne P. Babiarz, and Thomas F. Linsenmayer. (1988). Collagen type I and type V are present in the same fibril in the avian corneal stroma. The Journal of Cell Biology, 106(3), 999-1008. doi:10.1083/jcb.106.3.999.

De Vries, A. G., van der Wal, P. G, Long, T., Eikelenboom, G., and Merks, J. W. M. (1994). Genetic parameters of pork quality and production traits in Yorkshire populations. Livestock Production Science, 40(3), 277-289. doi:10.1016/0301-6226(94)90095-7.

Di Pasquale, M. G. (1997). Proteins and amino acids. Amino acids and proteins for the athlete (pp. 1-9) CRC Press.

Dölz, R., Engel, J., and Kühn, K. (1988). Folding of collagen IV. European Journal of Biochemistry, 178(2), 357-366. doi:10.1111/j.1432-1033. 1988.tb14458. x.

Dransfield, E. (1977). Intramuscular composition and texture of beef muscles. Journal of the Science of Food and Agriculture, 28(9), 833-842. doi:10.1002/jsfa.2740280910.

Dransfield, E., Nute, G. R., Roberts, T. A., Boccard, R., Touraille, C., Buchter, L., Cosentino, E., Hood, D.E., Joseph, R.L., Schon, I., and Paardekooper, E. J. C. (1984). Beef quality assessed at European research centers. Meat Science, 10(1), 1-20. doi:10.1016/0309-1740(84)90028-7.

Drescher, L.S., Janneke de Jonge, Goddard, E and Thomas Herzfeld. (2012). Consumer's stated trust in the food industry and meat purchases. Agriculture and Human Values, 29(4), 507. doi:10.1007/s10460-012-9375-9.

Dublet, B S Oh, S P Sugrue, M K Gordon, D R Gerecke, B R Olsen, and M van der Rest. (1989). The structure of avian type XII collagen. alpha 1 (XII) chains contain 190-kDa non-triple helical amino-terminal domains and form homotrimeric molecules. Journal of Biological Chemistry, 264(22), 131150-131156. Retrieved from http://www.jbc.org/content/264/22/13150.abstract.

Dunner, S., Sevane, N., García, D., Cortés, O., Valentini, A., Williams, J. L., Mangin, B., Cañón, J. and Levéziel, H. (2013). Association of genes involved in carcass and meat quality traits in 15 european bovine breeds. Livestock Science, 154(1-3), 34-44. doi:10.1016/j.livsci.2013.02.020.

Eikelenboom, G. (1983). Some Dutch developments on the identification of quality. Proc. E.E.C. Symposium on the Long-Term Definition of Meat Quality. Pp. 139-144.

Eikelenboom, G., and Minkema, D. (1974). Prediction of pale, soft, exudative muscle with a non-lethal test for halothane-induced porcine malignant hyperthermia syndrome. Neth. J. Vet. Sci., (99), 421–426.

Eikelenboom, G., Hoving-Bolink, A. H., and Wal, V. D (1996). The eating quality of pork: 1. the influence of ultimate pH. Fleischwirtschaft, 76, 392-393. Retrieved from https://www.narcis.nl/publication/RecordID/oai:library.wur.nl:wurpubs%2F303447.

Enfalt, A. C., Lundstrom, K., Karlsson, A., and Hansson, I. (1997). Estimated frequency of the RN- allele in Swedish Hampshire pigs and comparison of glycolytic potential, carcass composition, and technological meat quality among Swedish Hampshire, landrace, and Yorkshire pigs. Journal of Animal Science, 75(11), 2924-2935. doi:10.2527/1997.75112924x.

Enfält, A., Lundström, K., Hansson, I., Johansen, S., and Nyström, P. (1997). Comparison of non-carriers and heterozygous carriers of the RN − allele for carcass composition, muscle distribution and technological meat quality in Hampshire-sired pigs. Livestock Production Science, 47(3), 221-229. doi:10.1016/S0301-6226(96)01409-1.

Engel, J., and Prockop, D. J. (1991). The zipper-like folding of collagen triple helices and the effects of mutations that disrupt the zipper. Annual Review of Biophysics and Biophysical Chemistry, 20(1), 137-152. doi:10.1146/annurev.bb.20.060191.001033.

England, E. M., Matarneh, S. K., Scheffler, T. L., and Gerrard, D. E. (2017). Peri-mortal muscle metabolism and its effects on meat quality. In P. P. Purslow (Ed.), New aspects of meat quality (pp. 63-89) Elsevier Ltd. doi:10.1016/B978-0-08-100593-4.00004-7.

Estrade, M., Vignon, X., and Monin, G. (1993). Effect of the RN − gene on ultrastructure and protein fractions in pig muscle. Meat Science, 35(3), 313-319. doi:10.1016/0309-1740(93)90037-I.

Exposito, J., Valcourt, U., Cluzel, C., and Lethias, C. (2010). The fibrillar collagen family. International Journal of Molecular Sciences, 11(2), 407-426. doi:10.3390/ijms11020407.

Feldhusen, F., and Kühne, M. (1992). Effects of ultra-rapid chilling and ageing on length of sarcomeres, and tenderness of pork. Meat Science, 32(2), 161-171. doi:10.1016/0309-1740(92)90103-B.

Fernandez, X., Monin, G., Talmant, A., Mourot, J., and Lebret, B. (1999). Influence of intramuscular fat content on the quality of pig meat — 1. Composition of the lipid fraction and sensory characteristics of m. longissimus lumborum. Meat Science, 53(1), 59-65. doi:10.1016/S0309-1740(99)00037-6.

Fernandez, X., Neyraud, E., Astruc, T., and Sante, V. (2002). Effects of halothane genotype and pre-slaughter treatment on pig meat quality. part 1. post mortem metabolism, meat quality indicators and sensory traits of m. longissimus lumborum. Meat Science, 62(4), 429-437. doi:10.1016/S0309-1740(02)00034-7.

Feru, J., Delobbe, E., Ramont, L., Brassart, B., Terryn, C., Dupont-Deshorgue, A., Garbar C., Monboisse J.C, Maquart, F.X., and Brassart-Pasco, S. (2016). Aging decreases collagen IV expression in vivo in the dermo-epidermal junction and in vitro in dermal fibroblasts: Possible involvement of TGF-β1. European Journal of Dermatology, 26(4), 350-360. doi:10.1684/ejd.2016.2782.

Fisher, P., Mellett, F. D., and Hoffman, L. C. (2000). Halothane genotype and pork quality. 1. carcass and meat quality characteristics of three halothane genotypes. Meat Science, 54(2), 97-105. doi:10.1016/S0309-1740(99)00077-7.

Fitzgerald, J., and Bateman, J. F. (2001). A new FACIT of the collagen family: COL21A1. FEBS Letters, 505(2), 275-280. doi:10.1016/S0014-5793(01)02754-5.

Food and Agriculture Organization of the United Nations (FAO) (2017). Livestock primary: meat, total - production – tonnes. http://www.fao.org/faostat/en/?#data/.

Frantz, C., Stewart, K. M., and Weaver, V. M. (2010). The extracellular matrix at a glance. Journal of Cell Science, 123(Pt 24), 4195-4200. doi:10.1242/jcs.023820.

Fraztl, P. (2008). Collagen: Structure and mechanics, an introduction. Collagen (pp. 1-13) Springer US. doi:10.1007/978-0-387-73906-9_1.

Fujii, J, K Otsu, F Zorzato, S de Leon, VK Khanna, JE Weiler, O'Brien PJ., and MacLennan, D.H. (1991). Identification of a mutation in porcine ryanodine receptor associated with malignant hyperthermia. Science, 253(5018), 448-451. doi:10.1126/science.1862346.

Fujii, K., Tanzer, M. L., Nusgens, B. V., and Lapiere, C. M. (1976). Aldehyde content and cross-linking of type III collagen. Biochemical and Biophysical Research Communications, 69(1), 128-134. doi:10.1016/S0006-291X (76)80282-3.

Gelse, K., Pöschl, E., and Aigner, T. (2003). Collagens—structure, function, and biosynthesis. Advanced Drug Delivery Reviews, 55(12), 1531-1546. doi: 10.1016/j.addr.2003.08.002.

Gerbens, F., van Erp, A. J., Harders, F. L., Verburg, F. J., Meuwissen, T. H., Veerkamp, J. H., and te Pas, M. F. (1999). Effect of genetic variants of the heart fatty acid-binding protein gene on intramuscular fat and performance traits in pigs. Journal of Animal Science, 77(4), 846-852. doi:10.2527/1999.774846x.

Gerbens, F., Jansen, A., van Erp, A. J. M., Harders, F., Meuwissen, T. H. E., Rettenberger, G., Veerkamp, J.H and te Pas, M. F. W. (1998). The adipocyte fatty acid-binding protein locus: Characterization and association with intramuscular fat content in pigs. Mammalian Genome, 9(12), 1022-1026. doi:10.1007/s003359900918.

Gjaltema, R. A. F., and Bank, R. A. (2017). Molecular insights into prolyl and lysyl hydroxylation of fibrillar collagens in health and disease. Critical Reviews in Biochemistry and Molecular Biology, 52(1), 74-95. doi:10.1080/10409238.2016.1269716.

Goldspink, G., Fernandes, K., Williams, P. E., and Wells, D. J. (1994). Age-related changes in collagen gene expression in the muscles of mdx dystrophic and normal mice. Neuromuscular Disorders, 4(3), 183-191. doi:10.1016/0960-8966(94)90019-1.

Gonzalez, J. M., Johnson, D. D., Elzo, M. A., White, M. C., Stelzleni, A. M., and Johnson, S. E. (2014). Effect of brahman genetic influence on collagen enzymatic crosslinking gene expression and meat tenderness. Animal Biotechnology, 25(3), 165-178. doi:10.1080/10495398.2013.846862.

Gordon, M. and Hahn., R.A (2010). Collagens. Cell and Tissue Research, 339(1), 247-257. doi:10.1007/s00441-009-0844-4.

Greaser, M. L. and Guo, W. (2015). Proteins. In F. T. L.M.L. Nollet (Ed.), Handbook of food analysis (3rd ed., pp. 357-369) CRC Press.

Greaves, P. (2007). In Greaves P. (Ed.), 7 - cardiovascular system Academic Press. doi://doi.org/10.1016/B978-044452771-4/50008-0.

Gudmann, N. S., and Karsdal, M. A. (2016). Chapter 10 - type X collagen. Biochemistry of collagens, laminins and elastin (pp. 73-76) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00010-6.

Gudmann, N. S., and Karsdal, M. A. (2016). Chapter 2 - type II collagen. Biochemistry of collagens, laminins and elastin (pp. 13-20) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00002-7.

Guzek, D., Głąbska, D., Głąbski, K., and Wierzbicka, A. (2016). Influence of duroc breed inclusion into polish landrace maternal line on pork meat quality traits. Anais Da Academia Brasileira De Ciencias, 88(2), 1079-1088. doi:10.1590/0001-3765201620140679.

Hagg, R., Bruckner, P., and Hedbom, E (1998). Cartilage fibrils of mammals are biochemically heterogeneous: Differential distribution of decorin and collagen IX. The Journal of Cell Biology, 142(1), 285-294. doi:10.1083/jcb.142.1.285.

Hall, L.D. (1910). Market classes and grades of meat Agricultural Experiment Station Bulletin No 147. Retrieved from http://gateway.proquest.com/openurl?url_ver=Z39.88-2004&res_dat=xri:c19index-us&rft_dat=xri:c19index:NSTC:0315704.

Hamm, R. (1961). Biochemistry of meat hydration. Advances in food research (pp. 355-463) Elsevier Science and Technology. doi:10.1016/S0065-2628(08)60141-X Retrieved from https://www.sciencedirect.com/science/article/pii/S006526280860141X.

Hayes, E. J. (2010). Sensory descriptors for cooked meat products. Sensory analysis of foods of animal origin (1st ed., pp. 147-173) CRC Press. Retrieved from http://www.crcnetbase.com/isbn/9781439847961.

Henriksen, K., and Karsdal, M. A. (2016). Chapter 1 - type I collagen. Biochemistry of collagens, laminins and elastin (pp. 1-11) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00001-5.

Heymann, H., Hedrick, H. B., Karrasch, M. A., Eggeman, M. K., and Ellersieck, M. R. (1990). Sensory and chemical characteristics of fresh pork roasts cooked to different endpoint temperatures. Journal of Food Science, 55(3), 613-617. doi:10.1111/j.1365-2621.1990.tb05189.x.

Hill, F. (1966). The solubility of intramuscular collagen in meat animals of various ages. Journal of Food Science, 31(2), 161-166. doi:10.1111/j.1365-2621. 1966.tb00472.x.

Hofmann, K. (1973). Was ist fleischqualitat? Fleischwirtschaft, (53), 485-489.

Hofmann, K. (1974). Notwendigkeit und vorschlageinereinheitlichen definition des begriffes "fleischqualitat". Fleischwirtschaft, 10, 1607-1609.

Hornstein, I., and Crowe, P. F. (1960). Meat flavor chemistry, flavor studies on beef and pork. Journal of Agricultural and Food Chemistry, 8(6), 494-498. doi:10.1021/jf60112a022.

Hovenier, R., Kanis, E., van Asseldonk, T., and Westerink, N. G. (1992). Genetic parameters of pig meat quality traits in a halothane negative population. Livestock Production Science, 32(4), 309-321. doi:10.1016/0301-6226(92)90002-L.

Huff-Lonergan, E., Zhang, W., and Lonergan, S. M. (2010). Biochemistry of postmortem muscle — lessons on mechanisms of meat tenderization. Meat Science, 86(1), 184-195. doi: 10.1016/j.meatsci.2010.05.004.

Hulmes, D. J. S., Miller, A., Parry, D. A. D., Piez, K. A., and Woodhead-Galloway, J. (1973). Analysis of the primary structure of collagen for the origins of molecular packing. Journal of Molecular Biology, 79(1), 137-148. doi:10.1016/0022-2836(73)90275-1.

Hulmes. D.J.S. (2008). Collagen diversity, synthesis and assembly. In: P. Fratzl (Ed.), Collagen (pp. 15-47) Springer US. doi:10.1007/978-0-387-73906-9_2.

Hynes, R. O. (2002). Integrins: Bidirectional, allosteric signaling machines Elsevier Inc. doi:10.1016/S0092-8674(02)00971-6.

Hynes, R. O. (2009). The extracellular matrix: Not just pretty fibrils. Science, 326(5957), 1216-1219. doi:10.1126/science.1176009.

Ishida, Y., and Nagata, K. (2011). In Whisstock J. C., Bird P. I. (Eds.), Chapter nine - Hsp47 as a collagen-specific molecular chaperone Academic Press. doi://doi.org/10.1016/B978-0-12-386471-0.00009-2.

Jensen, P., Craig, H. B., and Robison, O. W. (1967). Phenotypic and genetic associations among carcass traits of swine. Journal of Animal Science, 26(6), 1252-1260. doi:10.2527/jas1967.2661252x.

Jeremiah, L. E., Dugan, M. E. R., Aalhus, J. L., and Gibson, L. L. (2003). Assessment of the relationship between chemical components and palatability of major beef muscles and muscle groups. Meat Science, 65(3), 1013-1019. doi:10.1016/S0309-1740(02)00309-1.

Jonsäll, A., Johansson, L., and Lundström, K. (2001). Sensory quality and cooking loss of ham muscle (M. biceps femoris) from pigs reared indoors and outdoors. Meat Science, 57(3), 245-250. doi:10.1016/S0309-1740(00)00097-8.

Joo, S., Joo, S., and Hwang, Y. (2017). The relationships between muscle fiber characteristics, intramuscular fat content, and fatty acid compositions in M. longissimus lumborum of hanwoo steers. Korean Journal for Food Science of Animal Resources, 37(5), 780-786. doi:10.5851/kosfa.2017.37.5.780

Järveläinen, H, Sainio, A, Koulu, M, Wight, T.N, and Penttinen, R. (2009). Extracellular matrix molecules: Potential targets in pharmacotherapy. Pharmacological Reviews, 61(2), 198-223. doi:10.1124/pr.109.001289.

Kassianidou, E., Probst, D., Jäger, J., Lee, S., Roguet, A., Schwarz, U. S., and Kumar, S. (2019). Extracellular matrix geometry and initial adhesive position determine stress fiber network organization during cell spreading. Cell Reports, 27(6), 189-1909.e4. doi:10.1016/j.celrep.2019.04.035.

Kauffman, R.G., and Warner, R.D. (1993). Evaluating pork carcasses for composition and quality. In Hollis.W (Ed.), Growth of the pig (pp. 141-166) CAB Internation.

Kaushal, G.P., Elbein, D.A., and Carver., E.W. (2014). The extracellular matrix. In Baynes, J. W and Dominiczak, M.H (Ed.), Medical biochemistry (4. ed. ed., pp. 380-393) Saunders Elsevier.

Kehlet, S. N., and Karsdal, M. A. (2016). Chapter 21 - type XXI collagen. Biochemistry of collagens, laminins and elastin (pp. 131-133) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00021-0.

Kempster, A. J., Dilworth, A. W., Evans, D. G., and Fisher, K. D. (1986). The effects of fat thickness and sex on pig meat quality with special reference to the problems associated with over leanness 1. butcher and consumer panel results. Animal Science, 43(3), 517-533. doi:10.1017/S0003356100002737.

Khorramizadeh, M. R., Tredget, E. E., Telasky, C., Shen, Q., and Ghahary, A. (1999). Aging differentially modulates the expression of collagen and collagenase in dermal fibroblasts. Molecular and Cellular Biochemistry, 194(1), 99-108. doi:1006909021352.

Khoshnoodi, J., Pedchenko, V., and Hudson, B. G. (2008). Mammalian collagen IV. Microscopy Research and Technique, 71(5), 357-370. doi:10.1002/jemt.20564.

Kim, C. W., Ho, G. P., and Ritchey, S. J. (1967). Collagen content and subjective scores for tenderness of connective tissue in animals of different ages. Journal of Food Science, 32(5), 586-588. doi:10.1111/j.1365-2621. 1967.tb00838. x.

Kim, T. H., Choi, B. H., and Beever, J. E. (2004a). Polymorphism in the porcine agouti signalling protein (ASIP) gene. Animal Genetics, 35(5), 418-420. doi:10.1111/j.1365-2052.2004.01179.x.

Kim, K., Kim, J., Dekkers, J., and Rothschild, M. (2004b). Polar overdominant inheritance of a DLK1 polymorphism is associated with growth and fatness in pigs. Mammalian Genome, 15(7), 552-559. doi:10.1007/s00335-004-2341-0.

Kjeld, N. G., and Karsdal, M. A. (2016). Chapter 25 - type XXV collagen. Biochemistry of collagens, laminins and elastin (pp. 147-150) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00025-8.

Knapp, P., Willam, A., and Sölkner, J. (1997). Genetic parameters for lean meat content and meat quality traits in different pig breeds. Livestock Production Science, 52(1), 69-73. doi:10.1016/S0301-6226(97)00120-6.

Knüppel, L., Heinzelmann, K., Lindner, M., Hatz, R., Behr, J., Eickelberg, O., and Staab-Weijnitz, C. A. (2018). FK506-binding protein 10 (FKBP10) regulates lung fibroblast migration via collagen VI synthesis. Respiratory Research, 19(1), 1-14. doi:10.1186/s12931-018-0768-1.

Koch, M., Foley, J. E., Hahn, R., Zhou, P., Burgeson, R. E., Gerecke, D. R., and Gordon, M. K. (2001). Alpha 1(xx) collagen, a new member of the collagen subfamily, fibril-associated collagens with interrupted triple helices. The Journal of Biological Chemistry, 276(25), 23120-23126. doi:10.1074/jbc.M009912200.

Koide, T and Nagata, K. (2005). Collagen biosynthesis. In Jürgen Brinckmann · Holger Notbohm, P. K.Müller (Ed.), Collagen: Primer in structure, processing and assembly (pp. 247: 85–114) Springer. doi:10.1007/b103820.

Kovanen, V. (2002). Intramuscular extracellular matrix: Complex environment of muscle cells. Exercise and Sport Sciences Reviews, 30(1), 20-25. doi:10.1097/00003677-200201000-00005.

Kular, J. K., Basu, S., and Sharma, R. I. (2014). The extracellular matrix: Structure, composition, age-related differences, tools for analysis and applications for tissue engineering. London, England: SAGE Publications. doi:10.1177/2041731414557112

Lampe, A. K., and Bushby, K. M. D. (2005). Collagen VI related muscle disorders. Journal of Medical Genetics, 42(9), 673-685. doi:10.1136/jmg.2002.002311.

Langrock, T, and Hoffmann, R. (2012). Analysis of hydroxyproline in collagen hydrolysates. In Michail A. Alterman and Peter Hunziker (Ed.), Amino acid analysis: Methods and protocols, methods in molecular biology (pp. 271-280) Springer Science. doi:DOI 10.1007/978-1-61779-445-2_21.

Larzul, C., Lefaucheur, L., Ecolan, P., Gogue, J., Talmant, A., Sellier, P., Le Roy., P., and Monin, G. (1997). Phenotypic and genetic parameters for longissimus muscle fiber characteristics in relation to growth, carcass, and meat quality traits in large white pigs. Journal of Animal Science, 75(12), 3126-3137. doi:10.2527/1997.75123126x.

Le Roy, P., Naveau, J., Elsen, J. M., and Sellier, P. (1990). Evidence for a new major gene influencing meat quality in pigs. Genetics Research, 55(1), 33-40. doi:10.1017/S0016672300025179.

Lebret, B. (2008). Effects of feeding and rearing systems on growth, carcass composition and meat quality in pigs. Animal, 2(10), 1548-1558. doi:10.1017/S1751731108002796.

Lebret, B., Le Roy, P., Monin, G., and Lefaucheur. L. (1999). Influence of the three RN genotypes on chemical composition, enzyme activities, and myofiber characteristics of porcine skeletal muscle. Journal of Animal Science, 77(6), 1482. Retrieved from https://search.proquest.com/docview/218108626.

Lee, F. A. (2012). Basic food chemistry Springer Netherlands. Retrieved from https://ebookcentral.proquest.com/lib/ [SITE_ID]/detail.action?docID=3568176.

Lee, S. K., Lee, S. H., Choe, J. H., Choi, Y. M., Jung, K. C., Rhee, M. S., Ryu Y.C and Kim, B. C. (2012). The influence of pork quality traits and muscle fiber characteristics on the eating quality of pork from various breeds. Meat Science, 90(2), 284-291. doi:10.1016/j.meatsci.2011.07.012.

Leeming, D. J., and Karsdal, M. A. (2016). Chapter 5 - type V collagen. Biochemistry of collagens, laminins and elastin (pp. 43-48) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00005-2.

Li, K Tamai, K Tan, E M and Uitto, J. (1993). Cloning of type XVII collagen. complementary and genomic DNA sequences of mouse 180-kilodalton bullous pemphigoid antigen (BPAG2) predict an interrupted collagenous domain, a transmembrane segment, and unusual features in the 5'-end of the gene and the 3'-untranslated region of the mRNA. Journal of Biological Chemistry, 268(12), 8825. Retrieved from http://www.jbc.org/content/268/12/8825.abstract.

Li, P., and Wu, G. (2018). Roles of dietary glycine, proline, and hydroxyproline in collagen synthesis and animal growth. Amino Acids, 50(1), 29-38. doi:10.1007/s00726-017-2490-6.

Light, N., and Champion, A. E. (1984). Characterization of muscle epimysium, perimysium and endomysium collagens. The Biochemical Journal, 219(3), 1017-1026. doi:10.1042/bj2191017.

Light, N., Champion, A. E., Voyle, C., and Bailey, A. J. (1985). The role of epimysial, perimysial and endomysial collagen in determining texture in six bovine muscles. Meat Science, 13(3), 137-149. doi:10.1016/0309-1740(85)90054-3.

Listrat, A., Lebret, B., Louveau, I., Astruc, T., Bonnet, M., Lefaucheur, L., Brigitte, P, and Bugeon, J. (2016). How muscle structure and composition influence meat and flesh quality. The Scientific World Journal, 2016 doi:10.1155/2016/3182746

Lo, L. L., McLaren, D. G., McKeith, F. K., Fernando, R. L., and Novakofski, J. (1992). Genetic analyses of growth, real-time ultrasound, carcass, and pork quality traits in duroc and landrace pigs: II. Heritabilities and correlations. Journal of Animal Science, 70(8), 2387-2396. doi:10.2527/1992.7082387x.

Mackenzie, K. J. J. (1919). Cattle and the future of beef-production in England University press. Retrieved from http://www.econis.eu/PPNSET?PPN=322064252.

MacLeod, G. and Seyyedain-Ardebili, M. (1981). Natural and simulated meat flavors (with particular reference to beef) doi:10.1080/10408398109527309.

Mahlapuu, M, Göran,H, Andersson, L., Johansson, C., Krook, A., Barnes, B., Zierath, J., Andersson., L and Marklund, S. (2004). Expression profiling of the gamma-subunit isoforms of AMP-activated protein kinase suggests a major role for gamma 3 in white skeletal muscle. American Journal of Physiology-Endocrinology and Metabolism, 286(2), E194. doi:10.1152/ajpendo.00147.2003.

Malmfors, B., and Nilsson, R. (1978). Meat quality traits in Swedish landrace and Yorkshire pigs with special emphasis on genetics. Acta Agriculturae Scandinavica, 28(sup21), 81-90. doi:10.1080/09064702.1978.11884472.

Mammalian Gene Collection (MGC) Program Team. (2002). Generation and initial analysis of more than 15,000 full-length human and mouse cDNA sequences. Proceedings of the

National Academy of Sciences of the United States of America, 99(26), 16899-16903. doi:10.1073/pnas.242603899.

Mane, B.G., Mendiratta, S.K., and Dhanze, H. (2014). Tenderization of meat and meat products: A detailed review. In Haghi, A.K., Carvajal-Millan, Elizabeth (Ed.), Food composition and analysis. Pp.95-113. Apple Academic Press. Retrieved from http://www.crcnetbase.com/isbn/9781482231663.

Matsuo, N., Tanaka, S., Yoshioka, H., Koch, M., Gordon, M. K., and Ramirez, F. (2008). Collagen XXIV (Col24a1) gene expression is a specific marker of osteoblast differentiation and bone formation. Connective Tissue Research, 49(2), 68-75. doi:10.1080/03008200801913502.

McClain, P. E., Wiley, E. R. and McCague, K. E. (1971). Species variation in the crosslinking characteristics of collagen from the intramuscular connective tissue of striated muscles (bos taurus, ovis aries, sus scrofa). International Journal of Biochemistry,2,167-172.

McNerny, Erin, M. B., Bo, G., Morris Michael, D., and Kohn David, H. (2015). Bone fracture toughness and strength correlate with collagen cross-link maturity in a dose-controlled lathyrism mouse model. Journal of Bone and Mineral Research, 30(3), 455-464. doi:10.1002/jbmr.2356.

Meek, K.M., Chapman, J.A, and Hardcastle, R.A. (1979). The staining pattern of collagen fibrils. improved correlation with sequence data. Journal of Biological Chemistry, 254(21): 10710-10714. Retrieved from http://www.jbc.org/content/254/21/10710.abstract.

Miar, Y., Plastow, G. S., Moore, S. S., Manafiazar, G., Charagu, P., Kemp, R. A., Van Haandel, B., Huisman, A.E, Zhang, C.Y., McKay, R.M., Bruce, H.L., and Wang, Z. (2014). Genetic and phenotypic parameters for carcass and meat quality traits in commercial crossbred pigs. Journal of Animal Science, 92(7), 2869-2884. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/24778330.

Milan, D., Jeon, J., Looft, C., Amarger, V., Robic, A., Thelander., M., Rogel-Gaillard, C., Paul, S., Iannuccelli, N., Rask, L., Ronne, H., Lundström, K., Reinsch, N., Gellin, J., Kalm, E., Roy, P.L., Chardon, P., and Andersson, L. (2000). A mutation in PRKAG3 associated with excess glycogen content in pig skeletal muscle. Science, 288(5469), 1248-1251. doi:10.1126/science.288.5469.1248.

Miles, C. A., Avery, N. C., Rodin, V. V. and Bailey, A. J. (2005). The increase in denaturation temperature following cross-linking of collagen is caused by dehydration of the fibres. Journal of Molecular Biology, 346(2), 551-556.

Miller, K. D., Ellis, M., McKeith, F. K., Bidner, B. S., and Meisinger, D. J. (2000). Frequency of the rendement napole RN- allele in a population of american hampshire pigs. Journal of Animal Science, 78(7), 1811. doi:10.2527/2000.7871811x.

Milz, S., Ockert, B., and Putz, R. (2009). Tenocytes and the extracellular matrix: A reciprocal relationship. Der Orthopade, 38(11), 10711079. doi:10.1007/s00132-009-1490-y.

Mir, N. A., Rafiq, A., Kumar, F., Singh, V., and Shukla, V. (2017). Determinants of broiler chicken meat quality and factors affecting them: A review. Journal of Food Science and Technology, 54(10), 2997-3009. doi:10.1007/s13197-017-2789-z.

Moeller, S. J., Baas, T. J., Leeds, T. D., Emnett, R. S., and Irvin, K. M. (2003). Rendement napole gene effects and a comparison of glycolytic potentialand DNA genotyping for classification of rendement napole status in hampshire-sired pigs12. Journal of Animal Science, 81(2), 402-410. doi:10.2527/2003.812402x.

Monin, G., and Santé-Lhoutellier, V. (2014). Conversion of muscle to meat color and texture deviations. In C. Devine and M. Dikeman (Ed.), Encyclopedia of meat sciences (pp. 339-345) Elsevier Ltd. doi:10.1016/B978-0-12-384731-7.00097-0.

Monin, G., and Sellier, P. (1985). Pork of low technological quality with a normal rate of muscle pH fall in the immediate post-mortem period: The case of the Hampshire breed. Meat Science, 13(1), 49-63. doi:10.1016/S0309-1740(85)80004-8.

Morris, N P and Bachinger, H.P. (1987). Type XI collagen is a heterotrimer with the composition (1 alpha, 2 alpha, 3 alpha) retaining non-triple-helical domains. Journal of Biological Chemistry, 262(23), 11345-11350. Retrieved from http://www.jbc.org/content/262/23/11345.abstract.

Morton I.D, Akroyd P., and May C.G. (1960). Flavoring substances and their preparation. Retrievedfromhttps://worldwide.espacenet.com/publicationDetails/biblio?FT=D&date=19600426&DB=EPODOC&locale=&CC=US&NR=2934437A.

Mottram, D. S. (1994). Some aspects of the chemistry of meat flavour. In F. Shahidi (Ed.), Flavor of meat and meat products. (pp. 210-231) Springer, Boston, MA. doi://doi.org/10.1007/978-1-4615-2177-8_12.

Mottram, D. S. (1998). Flavor formation in meat and meat products: A review. Food Chemistry, 62(4), 415-424. doi:10.1016/S0308-8146(98)00076-4.

Murphy, S. K., Nolan, C. M., Huang, Z., Kucera, K. S., Freking, B. A., Smith, T. P., Leymaster, KA., Weidman,J.R and Jirtle, R. L. (2006). Callipyge mutation affects gene expression in cis: a potential role for chromatin structure. Genome research, 16(3), 340–346. doi:10.1101/gr.4389306

Myllyharju, J. (2005). Intracellular post-translational modifications of collagens. Collagen: Primer in structure, processing and assembly (pp. 115-147) Springer Berlin Heidelberg. doi:10.1007/b103821.

Myllyharju, J., and Kivirikko, K. I. (2001). Collagens and collagen-related diseases. Annals of Medicine, 33(1), 7-21. doi:10.3109/07853890109002055.

Myllyharju, J., and Kivirikko, K. I. (2004). Collagens, modifying enzymes and their mutations in humans, flies and worms. Trends in Genetics, 20(1), 33-43. doi: 10.1016/j.tig.2003.11.004.

Nagata, K. and Yamada, K.M. (1986). Phosphorylation and transformation sensitivity of a major collagen-binding protein of fibroblasts. Journal of Biological Chemistry, 261(16), 7531-7536. Retrieved from http://www.jbc.org/content/261/16/7531.abstract.

Neuman, R. E. and Logan, M.A. (1950). The determination of hydroxyproline. Journal of Biological Chemistry, (184), 299-306.

Nielsen, M. J., and Karsdal, M. A. (2016). Chapter 3 - type III collagen. Biochemistry of collagens, laminins and elastin (pp. 21-30) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00003-9.

Nishimura, T. (2010). The role of intramuscular connective tissue in meat texture. Animal Science Journal, 81(1), 21-27. doi:10.1111/j.1740-0929.2009.00696.x.

Nishimura, T., Hattori, A., and Takahashi, K. (1999). Structural changes in intramuscular connective tissue during the fattening of Japanese black cattle: Effect of marbling on beef tenderization. Journal of Animal Science, 77(1), 93. doi:10.2527/1999.77193x.

Nonneman, D. J., Brown-Brandl, T., Jones, S. A., Wiedmann, R. T., & Rohrer, G. A. (2012). A defect in dystrophin causes a novel porcine stress syndrome. BMC Genomics, 13(1), 233. doi:10.1186/1471-2164-13-233.

Oczkowicz, M. (2009). Polar overdominance – a putative molecular mechanism and the new examples in mammals. Journal of Animal and Feed Sciences, 18(1), 17-27. doi:10.22358/jafs/66362/2009.

Okumura, M., Kadokura, H., and Inaba, K. (2015). Structures and functions of protein disulfide isomerase family members involved in proteostasis in the endoplasmic reticulum. Free Radical Biology and Medicine, 83, 314-322. doi: 10.1016/j.freeradbiomed.2015.02.010.

Olsen, B. R. (1997). Collagen IX. International Journal of Biochemistry and Cell Biology, 29(4), 555-558. doi:10.1016/S1357-2725(96)00100-8.

Papadopoulos, S., Jürgens, K. D., and Gros, G. (2000). Protein diffusion in living skeletal muscle fibers: Dependence on protein size, fiber type, and contraction. Biophysical Journal, 79(4), 2084-2094. doi:10.1016/S0006-3495(00)76456-3.

Parvizi, J. and Kim, G.K. (2010). Chapter 53 - collagen. In: Javad Parvizi, Gregory K. Kim (Ed.), High yield orthopedics (pp. 107-109) W.B. Saunders. doi:10.1016/B978-1-4160-0236-9.00064-X.

Petitclerc, E., Boutaud, A., Prestayko, A., Xu, J., Sado, Y., Ninomiya, Y., Sarras M.P. Jr, Hudson, B.G., and Brooks, P. C. (2000). New functions for non-collagenous domains of human collagen type IV. novel integrin ligands inhibiting angiogenesis and tumor growth in vivo. The Journal of Biological Chemistry, 275(11), 8051-8061. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/10713126.

Petruska, J.A. and Hodge, A.J. (1964). A subunit model for the tropocollagen macromolecule. Proceedings of the National Academy of Sciences of the United States of America, 51(5), 871-876. doi:10.1073/pnas.51.5.871.

Phillips, C. J. C., (2001). Breeding and reproduction. Principles of cattle production (pp. 108-141) CABI Publishers.

Pinto, N., Beraquet, M., N. J., and Cardoso, S. (2013). Effects of chilling methods and hot boning on quality parameters of M. longissimus lumborum from Bos indicus Nellore steer. Meat Science, 93(2), 201-206. doi: 10.1016/j.meatsci.2012.08.024.

Plumb, D.A, Ferrara, L, Torbica, T, Knowles, L, Mironov Jr, A, Kadler,K.E, Briggs M.D., and Boot-Handford, R.P (2011). Collagen XXVII organises the pericellular matrix in the growth plate. PLoS One, 6(12), e29422. doi: 10.1371/journal.pone.0029422.

Prockop, D. J., Sieron, A. L., and Li, S. (1998). Procollagen N-proteinase and procollagen C-proteinase. two unusual metalloproteinases that are essential for procollagen processing probably have important roles in development and cell signaling Elsevier B.V. doi:10.1016/S0945-053X (98)90013-0.

Provost, J., Kelly, B., Bodwin, J., and Wallert, M. (2016). The science of cooking: Understanding the biology and chemistry behind food and cooking John Wiley and Sons, Incorporated. Retrieved from https://ebookcentral.proquest.com/lib/[SITE_ID]/detail.action?docID=4530809.

Purslow, P. P. (2005). Intramuscular connective tissue and its role in meat quality. Meat Science, 70(3), 435-447. doi:10.1016/j.meatsci.2004.06.028.

Purslow, P. P., Oiseth, S., Hughes, J., and Warner, R. D. (2016). The structural basis of cooking loss in beef: Variations with temperature and ageing. Food Research International, 89(Pt 1), 739-748. doi:10.1016/j.foodres.2016.09.010.

Purslow, P. P. (2018). Contribution of collagen and connective tissue to cooked meat toughness; some paradigms reviewed. Meat Science, 144, 127-134. doi: 10.1016/j.meatsci.2018.03.026.

Reineccius, G. (2016). Flavor chemistry and technology, second edition CRC Press. Retrieved from http://www.crcnetbase.com/isbn/9780203485347.

Ritchie, H. and Roser M. (2019). "Meat and Seafood Production and Consumption". Published online at OurWorldInData.org. Retrieved from: 'https://ourworldindata.org/meat-and-seafood-production-consumption'.

Ryan, M. T., Hamill, R. M., O'Halloran, A. M., Davey, G. C., McBryan, J., Mullen, A. M., McGee, C., Gispert, M., Southwood, O.I., and Sweeney, T. (2012). SNP variation in the promoter of the PRKAG3 gene and association with meat quality traits in pig. BMC Genetics, 13(1), 66. doi:10.1186/1471-2156-13-66.

Ruoslahti, E. (1988). Structure and biology of proteoglycans. Annual Review of Cell Biology, 4, 229-255

Sainio, A., and Järveläinen, H. (2014). Extracellular matrix macromolecules: Potential tools and targets in cancer gene therapy. Molecular and Cellular Therapies, 2(1), 14. doi:10.1186/2052-8426-2-14.

Salas, R. C. D., and Mingala, C. N. (2017). Genetic factors affecting pork quality: Halothane and Rendement napole genes. Animal Biotechnology, 28(2), 148-155. doi:10.1080/10495398.2016.1243550.

Sand, J. M. B., Genovese, F., and Karsdal, M. A. (2016). Chapter 4 - type IV collagen. Biochemistry of collagens, laminins and elastin (pp. 31-41) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00004-0.

Sato, K., Mera, H., Wakitani, S., and Takagi, M. (2017). Effect of epigallocatechin-3-gallate on the increase in type II collagen accumulation in cartilage-like MSC sheets. Bioscience, Biotechnology, and Biochemistry, 81(6), 1241-1245. doi:10.1080/09168451.2017.1282809.

Schmelzer, C. E. H., Getie, M., and Neubert, R. H. H. (2005). Mass spectrometric characterization of human skin elastin peptides produced by proteolytic digestion with pepsin and thermitase. Journal of Chromatography. A, 1083(1-2), 120. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/16078697.

Scott, J. E., Hughes, E. W., and Shuttleworth, A. (1981). A collagen-associated ehrlich chromogen: A pyrrolic cross-link? Bioscience Reports, 1(8), 611-618. doi:10.1007/BF01116276

Scott, J. E., Qian, R., Henkel, W. and Glanville, R. W. (1983). An Ehrlich chromogen in collagen cross-links. Biochemical Journal, 209(1), 263-264.

Serra, X., Gil, F., Pérez-Enciso, M., Oliver, M. A., Vázquez, J. M., Gispert, M., Díaz, I, Moreno, F, Latorre, R and Noguera, J. L. (1998). A comparison of carcass, meat quality and histochemical characteristics of iberian (guadyerbas line) and landrace pigs. Livestock Production Science, 56(3), 215-223. doi:10.1016/S0301-6226(98)00151-1.

Sheard, P. R., Nute, G. R., Richardson, R. I., Perry, A., and Taylor, A. A. (1999). Injection of water and polyphosphate into pork to improve juiciness and tenderness after cooking. Meat Science, 51(4), 371-376. doi:10.1016/S0309-1740(98)00136-3.

Shen, L. Y., Luo, J., Lei, H. G., Jiang, Y. Z., Bai, L., Li, M. Z., Tang, G.Q, Li, X W, Zhang, S.H. and Zhu, L. (2015). Effects of muscle fiber type on glycolytic potential and meat quality traits in different tibetan pig muscles and their association with glycolysis-related gene expression. Genetics and Molecular Research: GMR, 14(4), 14366-14378. doi: 10.4238/2015.November.13.22.

Shimokomaki, M., Elsden, D. F., and Bailey, A. J. (1972). Meat tenderness: Age related changes in bovine intramuscular collagen. Journal of Food Science, 37(6), 892-896. doi:10.1111/j.1365-2621. 1972.tb03696. x.

Shingfield, K. J., Bonnet, M., and Scollan, N. D. (2013). Recent developments in altering the fatty acid composition of ruminant-derived foods. Animal: An International Journal of Animal Bioscience, 7 Suppl 1(s1), 132-162. doi:10.1017/S1751731112001681.

Shuttleworth, C. A. (1997). Type VIII collagen. International Journal of Biochemistry and Cell Biology, 29(10), 1145-1148. doi:10.1016/S1357-2725(97)00033-2.

Shuttleworth, C. A., and Forrest, L. (1975). Changes in guinea-pig dermal collagen during development. European Journal of Biochemistry, 55(2), 391-395. doi:10.1111/j.1432-1033. 1975.tb02174. x.

Siebuhr, A. S., and Karsdal, M. A. (2016). Chapter 13 - type XIII collagen. Biochemistry of collagens, laminins and elastin (pp. 87-91) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00013-1.

Sikes, A., Tornberg, E., and Tume, R. (2010). A proposed mechanism of tenderizing post-rigor beef using high pressure–heat treatment. Meat Science, 84(3), 390-399. doi: 10.1016/j.meatsci.2009.09.007.

Smith G. C. and Z. L. Carpenter. (1974). National research council (US) board on agriculture and renewable resources. fat content and composition of animal products: Proceedings of a symposium Washington, D.C. December 12-13, 1974. washington (DC): National academies press (US); 1976. eating quality of meat animal products and their fat content. available from: Https://Www.ncbi.nlm.nih.gov/books/NBK216525/., 147-182.

Spanier, A. M., Flores, M., Toldrá, F., Aristoy, M. C., Bett, K. L., Bystricky, P., and Bland, J. M. (2004). Meat flavor: Contribution of proteins and peptides to the flavor of beef. Advances in Experimental Medicine and Biology, 542, 33. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15174571.

Spanier, A. M., Vercellotti, J. R., and James, C. (1992). Correlation of sensory, instrumental and chemical attributes of beef as influenced by meat structure and oxygen exclusion. Journal of Food Science, 57(1), 10-15. doi:10.1111/j.1365-2621. 1992.tb05413. x.

Staab-Weijnitz, C. A., Fernandez, I. E., Knüppel, L., Maul, J., Heinzelmann, K., Juan-Guardela, B. M., Hennen, E., Preissler, G., Winter, H., Neurohr, C., Hatz, R., Lindner, M., Behr, J., Kaminski, N., and Eickelberg, O. (2015). FK506-binding protein 10, a potential novel drug target for idiopathic pulmonary fibrosis. American Journal of Respiratory and Critical Care Medicine, 192(4), 455-467. doi:10.1164/rccm.201412-2233OC.

Stoilov, I., Starcher, B. C., Mecham, R. P., and Broekelmann, T. J. (2018). Measurement of elastin, collagen, and total protein levels in tissues. Methods in Cell Biology, 143, 133-146. doi: 10.1016/bs.mcb.2017.08.008

Suman, S. P. (2012). Application of proteomics to understand meat quality. In Y. H. Hui (Ed.), Handbook of meat and meat processing (2nd ed. ed., pp. 286-303) CRC Press. Retrieved from http://www.crcnetbase.com/isbn/9781439836842.

Sun, S., and Karsdal, M. A. (2016). Chapter 6 - type VI collagen. Biochemistry of collagens, laminins and elastin (pp. 49-55) doi:10.1016/B978-0-12-809847-9.00006-4.

Sundaramoorthy, M., Meiyappan, M., Todd, P., and Hudson, B. G. (2002). Crystal structure of NC1 domains. structural basis for type IV collagen assembly in basement membranes. The Journal of Biological Chemistry, 277(34), 31142-31153. doi:10.1074/jbc.M201740200.

Sutmulle, M., Bruijn, J. A., and De Heer, E. (1997). Collagen types vlll and X, two non-fibrillar, short-chain collagens. structure homologies, functions and involvement in pathology. Histol Histopathol. 557-566. Retrieved from http://hdl.handle.net/10201/18946.

Suzuki, K., Irie, M., Kadowaki, H., Shibata, T., Kumagai, M., and Nishida, A. (2005). Genetic parameter estimates of meat quality traits in Duroc pigs selected for average daily gain, longissimus muscle area, backfat thickness, and intramuscular fat content. Journal of Animal Science, 83(9), 2058-2065. doi:10.2527/2005.8392058x.

Swatland, H. J. (1994). Connective tissues of the carcass. Structure and development of meat animals and poultry (pp. 65-143) CRC Press.

Söderhäll, C., Marenholz, I., Kerscher, T., Rüschendorf, F., Esparza-Gordillo, J., Worm, M., Gruber, C., Mayr, G., Albrecht, M., Rohde, K., Schulz, H., Wahn, U., Hubner, N. and Lee, Y. A. (2007). Variants in a novel epidermal collagen gene (COL29A1) are associated with atopic dermatitis. PLoS Biology, 5(9), 1952-1961.

Takahara, K., Hoffman, G. G., and Greenspan, D. S. (1995). Complete structural organization of the human alpha 1 (V) collagen gene (COL5A1): Divergence from the conserved organization of other characterized fibrillar collagen genes. Genomics, 29(3), 588. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/8575750.

Tannor, B., Clark, N. G. and Hankins, O. G. (1943). Mechanical determination of the juiciness of meat. illus. Journal of Agricultural Research, 66, 403. Retrieved from https://search.proquest.com/docview/1308248426.

Taye, M., Kim, J., Yoon, S. H., Lee, W., Hanotte, O., Dessie, T., Kemp, S., Mwai O.A., Caetano-Anolles, K., Cho, S., Oh S.J., Lee H.K..and Kim, H. (2017). Whole genome scan reveals the genetic signature of african ankole cattle breed and potential for higher quality beef. BMC Genetics, 18(1), 11. doi:10.1186/s12863-016-0467-1.

Thomas, D. P. Scott D. Zimmerman, Thomas R. Hansen, David T. Martin, and Richard J. McCormick. (2000). Collagen gene expression in rat left ventricle: Interactive effect of age and exercise training. Journal of Applied Physiology, 89(4), 1462-1468. doi:10.1152/jappl.2000.89.4.1462.

Tornberg, E. (2005). Effects of heat on meat proteins – implications on structure and quality of meat products. Meat Science, 70(3), 493-508. doi:10.1016/j.meatsci.2004.11.021

Thompson, J. M. (2004). The effects of marbling on flavor and juiciness scores of cooked beef, after adjusting to a constant tenderness. Animal Production Science, 44(7), 645-652. doi:10.1071/EA02171.

Torrescano, G., Sánchez-Escalante, A., Giménez, B., Roncalés, P., and Beltrán, J. A. (2003). Shear values of raw samples of 14 bovine muscles and their relation to muscle collagen characteristics. Meat Science, 64(1), 85-91. doi:10.1016/S0309-1740(02)00165-1.

Van Wijk, H. J., Arts, D. J. G., Matthews, J. O., Webster, M., Ducro, B. J., and Knol, E. F., (2005). Genetic parameters for carcass composition and pork quality estimated in a commercial production chain1. Journal of Animal Science, 83(2), 324-333. doi:10.2527/2005.832324x.

Ventanas, J., Ventanas, S., Ruiz, J., and García, C. (2007). Preference and juiciness of iberian dry-cured loin as affected by intramuscular fat content, crossbreeding and rearing system. Meat Science, 77(3), 324-330. doi: 10.1016/j.meatsci.2007.04.001

Voutila, I L., Mullen, A.M., Ruusunen, M., Troy, D., and Puolanne E. (2007). Thermal stability of connective tissue from porcine muscles. Meat Science, 76(3), 474-480.

Voyle, C. A. (1979). Meat. In J. G. Vaughan (Ed.), Food microscopy (pp. 193-231) Acad. Press.

Wang, C., Jackson, G., Jones, T. H., Matsumoto, A. M., Nehra, A., Perelman, M. A., Ronald S Swerdloff, S.R., Traish, A., Zitzmann M and Cunningham, G. (2011). Low testosterone associated with obesity and the metabolic syndrome contributes to sexual dysfunction and cardiovascular disease risk in men with type 2 diabetes. Diabetes Care, 34(7), 1669-1675. doi:10.2337/dc10-2339.

Wang, K., Li, W., Bai, Y., Yang, W., Ling, Y., and Fang, M. (2017). Ssc-miR-7134-3p regulates fat accumulation in castrated male pigs by targeting MARK4 gene. International Journal of Biological Sciences, 13(2), 189-197. doi:10.7150/ijbs.17386.

Warner, R. D. (2017). Chapter 14 - the eating quality of Meat—IV water-holding capacity and juiciness. In F. Toldra (Ed.), Lawrie's meat science (pp. 419-459) Elsevier Ltd. doi:10.1016/B978-0-08-100694-8.00014-5.

Wayne, D. (2019). Rendement napole gene and pork quality. http://www.omafra.gov.on.ca/english/livestock/swine/facts/04-083.htm. Date Retrieved: October 15, 2019.

Werfel, T., Kiess., W., and Spergel. J.M. (2011). Atopic dermatitis in childhood and adolescence (1., neue Ausg. (ed.) Karger. Pp. 41.

Wheeler, T. L., Shackelford, S. D., and Koohmaraie, M. (2000). Variation in proteolysis, sarcomere length, collagen content, and tenderness among major pork muscles. Journal of Animal Science, 78(4), 958-965. doi:10.2527/2000.784958x.

Williams, C.S., Williams, J.W., and Chung, R.A. (1986). Comparative microscopy and morphometry of skeletal muscle fibers in poultry.5(2), 207-217. Retrieved from http://digitalcommons.usu.edu/foodmicrostructure/vol5/iss2/4.

Winder. W. W. (2001). Energy-sensing and signaling by AMP-activated protein kinase in skeletal muscle. Journal of Applied Physiology, 91(3), 1017-1028. doi:10.1152/jappl.2001.91.3.1017.

Winger R.J. and Hagyard C. J. (1994). Juiciness — its importance and some contributing factors. (pp. 94-116) Springer US. doi:10.1007/978-1-4615-2167-9 Retrieved from http://dx.doi.org/10.1007/978-1-4615-2167-9.

Wood, J. D., Brown, S. N., Nute, G. R., Whittington, F. M., Perry, A. M., Johnson, S. P., and Enser, M. (1996). Effects of breed, feed level and conditioning time on the tenderness of pork. Meat Science, 44(1), 105-112. doi:10.1016/S0309-1740(96)00044-7.

Wood, J. D., Nute, G. R., Richardson, R. I., Whittington, F. M., Southwood, O., Plastow, G., Mansbridge R., Da Costa, N., and Chang, K. C. (2004). Effects of breed, diet and muscle on fat deposition and eating quality in pigs. Meat Science, 67(4), 651-667. doi: 10.1016/j.meatsci.2004.01.007.

Xiong, Y. L. (1997). Structure function relationships of muscle proteins. In S. Damodaran (Ed.), Food proteins and their applications (pp. 341-392) Dekker.

Yang, J., Jeong, D., Na, C., and Hwang, I. (2016). Eating quality traits of Han woo longissimus dorsi muscle as a function of end-point cooking temperature. Korean Journal for Food Science of Animal Resources, 36(3), 291-299. doi:10.5851/kosfa.2016.36.3.291.

Zaher, H. S., and Green, R. (2009). Fidelity at the molecular level: Lessons from protein synthesis. Cell, 136(4), 746-762. doi: 10.1016/j.cell.2009.01.036.

Zhang, W., Kuhlers, D. L., and Rempel, W. E. (1992). Halothane gene and swine performance. Journal of Animal Science, 70(5), 1307-1313. doi:10.2527/1992.7051307x.

Zheng, Y., Wang, S., and Yan, P. (2018). The meat quality, muscle fiber characteristics and fatty acid profile in Jinjiang and F1 Simmental×Jinjiang yellow cattle. Asian-Australasian Journal of Animal Sciences, 31(2), 301-308. doi:10.5713/ajas.17.0319.

Chapter 2

Estimates of genetic parameters for loin physical, meat quality and intramuscular collagen traits in Canadian commercial crossbred swine populations

2.1 Introduction

Since the Canadian swine industry has over the years been efficiently, reliably, and effectively producing pork to meet market demands, it is increasingly becoming imperative for the industry to progressively shift its focus towards improving meat quality. Indeed, consumer preferences and standards for quality pork have changed in recent years and for the industry to successfully meet such demands, a clear appreciation of the factors contributing to meat quality and the capacity to forecast, control and influence certain aspects of meat quality is necessary (Hocquette et al., 2012). In fact, the pork industry's ability to meet the demands and preferences of their consumers, by finding the connection between consumer benchmarks/standards for meat and eating quality, will be critical to the future survival and competitiveness of the swine industry in the overall food sector.

Profitable lean pork production has, over the years, been a major selection objective in swine breeding programs with traits like loin eye area, carcass length and reduced fat thickness being favorably weighted in indices (Enfield and Whatley, 1961; Cameron, 1990). However, research studies are showing that selection for traits of economic merit could negatively affect pork quality (Miar et al., 2014; Lonergan et al., 2001). Retail butchers and consumers alike have complained about meat quality issues associated with very lean meat (Kempster et al., 1986). They protest that such products are less juicy, flavorful, have aberrant sliceability and are unappealing (Kempster et al., 1986). This is most probably the reason why traits related to fat content are also increasingly gaining attention due to their promising potential to improve eating quality.

One major aim of animal breeding in commercial livestock species is the improvement of predefined heritable traits by altering their genetic potential/abilities with the aim of shifting the population average phenotype towards a desired direction (Bourdon, 2013). Thus, determining the important traits to select in breeding programs as well as how selection for certain traits may cause responses in correlated traits is important to the success of swine breeding programs as selection on a trait may bring about changes in the phenotypes of correlated traits by causing changes in allele frequencies at loci in linkage disequilibrium or pleiotropic loci (Conner and Hartl, 2004).

In recent decades, breeders are increasingly interested in the relationships between relatively easy to measure sub-primal traits and meat quality traits as well as specific biochemical traits. Intramuscular connective tissue properties and collagen characteristics to some degree influence meat structure and texture. There has indeed, been a surge in meat science research studies focusing on the inherent characteristics of intramuscular connective tissue mainly due to its potential influence on muscle texture variability and the disintegration of meat structure (Voutilla et al., 2007). In fact, pertaining to muscle disintegration, destructured muscles have lower insoluble and total collagen content compared to normal muscles (Hugenschmidt et al., 2009). Indeed, as Swatland (1990) aptly noted, the rapid growth rate of commercial meat producing animals in our time may have led to skeletal muscle fibers outgrowing their connective tissue sheaths, thus resulting in a weakening of intramuscular connective tissues and predisposing the muscle to disintegration. A possible reversal of this trend will require information on the heritabilities of inherent connective tissue characteristics. However, collagen content and heat solubility are two biochemical traits with very limited research on their heritabilities and relationships with various sub-primal and meat quality traits. Collagen indeed is the most abundant protein in mammals and a key constituent of most extracellular matrices where it offers major mechanical and structural support to tissues (Sionkowska, 2005; Wagner et al., 2009). Research in meat science has implicated the ratio of soluble to insoluble collagen as having a profound influence on meat toughness in raw meat (Hill, 1966) although a debate still exists on its role in cooked meat toughness. It is therefore imperative to examine the potential presence of genetic variability and relationships.

In 2010, a series of research studies were initiated at the University of Alberta to estimate genetic and phenotypic parameters in two Canadian crossbred pig populations. Those experiments examined a total of 43 carcass and pork quality traits. However, those studies did not investigate the sub-primal physical, intramuscular fat and collagen characteristics of those swine populations. This current study seeks to fill the gap in those studies by testing the hypothesis that genetic relationships exist between collagen characteristics, sub-primal and meat quality traits. Therefore, the objectives of this study are to:

1. Estimate the heritabilities for the loin physical, meat quality traits and collagen characteristics; and
2. Estimate phenotypic and genetic correlations between and among the loin physical, meat quality traits and collagen characteristics.

2.2 Materials and methods

2.2.1 Animals and study design

Experimental animals were managed in accordance with the recommendations stipulated in the Canadian Council for Animal Care guide (CCAC, 1993). The use of these animals was reviewed by an animal research ethics committee and considered Category A and so no formal approval was required. Pigs were from two Canadian breeding populations. Total number of pigs for this study amounted to 500 commercial animals of a combination of full sib and half sibs obtained from crosses between 139 Duroc boars and 429 first cross hybrid Landrace × Yorkshire sows. Pedigree information of 8 ancestral generations encompassing 8,372 animals composed of 487 sires and 1105 dams was available.

2.2.2. Animal management

Management of experimental pigs in this study was as described by Miar et al. (2014) as these animals were a subset of that experimental population. Male piglets were neutered at 3 to 5 days post birth. Piglets were weaned at approximately 7.5 kg at about 21 days of age. Weanlings were subsequently housed in nursery pens for 5 weeks, then raised in pre-grower barns for a pre-growing period of 4 weeks. Following this, pigs were transitioned to commercial finishing conditions with *ad libitum* access to feed and water. The final body weight of the animals was approximately 115 kg. The pigs were transported to East 40 Packers, a provincially inspected abattoir, Brandon, MB, Canada, on a weekly basis in groups of 20-35 pigs. They were rested in lairage overnight with *ab libitum* access to water and slaughtered the following morning. Provincial regulations were followed in the slaughter of the animals. They were electrically stunned prior to exsanguination and their carcasses fabricated within 24 hours post-slaughter.

They were on average 160 days old at slaughter with an average live weight of 124 kg at slaughter.

2.2.3 Loin physical measurements

A 3 and 4 rib loin section excised from the right side of the pork carcasses during fabrication were harvested, vacuum packaged and refrigerated at 4°C within 24 hours. They were then frozen (-20°C) for 96 hours and transported in coolers to the carcass and meat science laboratory at Agri-Food Discovery place, Department of Agricultural, Food and Nutritional Science, University of Alberta, and stored at -20°C until analysis. Prior to analysis, the samples were thawed at refrigerated temperature (4°C) for 61 hours.

The sub-primals used in this study, that is the loin samples, were weighed and recorded as loin weight (LWT). Loin eye muscles excised from the loin sub-primals were weighed and reported as loin eye weight (LEW). Back fat trimmed from the loins were weighed and reported as thick fat weight (TFW). Meat and fat trimmings remaining after removing chops to be used for other meat quality measurements were weighed and recorded as rib trim weight (RTW) while remaining bones were reported as bone weight (BWT). The ribeye weight, thick fat weight, rib trim weight were expressed as percentages of the whole loin weight after subtracting the diaphragm weight from the whole loin weight. Diaphragm weight was comprised of nerves and diaphragm tissues of no significance to the goals of the current study.

2.2.4 Meat quality measurements

2.2.4.1 Muscle pH

The pH measurements on frozen-thawed samples were taken at 3 different locations on the loin eye (Figure 2.1). This was done by making an incision with a knife about halfway (5cm) through the meat, waiting for some fluid to accumulate in the incision and then inserting the pH probe (Accumet® AP71 portable waterproof pH meter, Fisher Scientific, ON, Canada). The average of three measurements for each loin eye was used for statistical analysis.

2.2.4.2 Objective color measurements

A hand-held Konica Minolta CR 400 (Konica Minolta Sensing Inc., Japan) chroma meter set at illuminant D65 was used for L^{*}, a^{*}, b^{*} , hue and chroma determinations. These measurements were taken at three different sites on the thawed loin eye muscle after blooming for a period of 1 hour at 4°C to allow for pigment oxygenation. The measuring head of the chroma meter was placed vertically on the surface of the loin chop for the readings (Figure 2.2). The colour of each loin chop was characterized using the $L*$, $a*$, $b*$ colour space, where L^{*}= lightness/ brightness with 0 = black and 100 = white; a^{*}= redness (+a) to greenness (-a) axis, and b^{*}= yellowness (+b) to blueness (-b) axis as recommended by the Commission Internationale de L'Eclairage (CIE). The average of 3 readings was used for statistical analysis of the color space coordinates.

2.2.4.3 Cooking loss

An approximately 200g loin roast from each animal trimmed of fat and epimysium was used for this assessment. Average weight after trimming was 192 ± 12g. The roasts were weighed and inserted into thin walled Whirl-pak^{TM} bags and placed in a water bath set at 73°C ensuring that the opening of the bags was above the water levels. A TinyTag^{TM} thermistor probe (model: TV-4020, Gemini Data loggers, West Sussex, UK) was used to record temperature changes in the chops. The average cooking time was 57 ± 13 mins. When an internal temperature of 71°C was reached, chops were removed from the water bath and cooled in an ice slurry. The samples were subsequently stored at 4°C for 24 hours, gently blotted and re-weighed. Percent cooking loss was determined with the following formula:

$$\frac{Muscle\ weight\ precook - Muscle\ weight\ post\ cook}{Muscle\ weight\ precook} \times 100$$

2.2.4.4 Instrumental measure of tenderness

Cooked pork chops were refrigerated overnight at 4℃ before Warner-Bratzler shear force determinations. Six 1cm^2 rectangular cores were obtained longitudinal to the fiber direction of each chop. A material testing machine (Lloyd Instruments Ltd, Surrey, UK) fitted with a Warner-Bratzler-like shear head was used to shear through the cores across the muscle fibre direction at a crosshead speed of 200mm/min. NEXYGEN Plus texture analysis software was used to record resistance (peak force) values in Newtons. The average readings of six cores were used for statistical analysis.

2.2.4.5 Ether extract/intramuscular fat

This procedure was performed using the Soxhlet method 960.39 (AOAC, 2000). For each loin, duplicate determinations were made. A Soxtec™ 2050 Automatic Extraction apparatus (FOSS Analytical AB, Höganäs, Sweden) consisting mainly of an extraction unit, control unit and a drive unit was used for intramuscular fat determinations in the loin samples.

2.2.4.5.1 Sample preparation

Aluminum extraction cups to be used for the extraction were oven dried at 103°C for 2hours, cooled in a desiccator for 45min and weighed. Approximately 2.0g ($\pm 0.003g$) of lyophilized, ground *Longissimus dorsi* muscle were weighed into tared assembled cellulose extraction thimbles (33mm × 80mm). De-fatted cotton was subsequently plugged into the thimbles to prevent sample loss during the extraction process. With the aid of a thimble handler, the samples were transferred to a thimble stand. Sample thimbles were then inserted into the extraction unit followed by the insertion of the pre-weighed aluminum extraction cups. Petroleum ether (40-60°C) was used as the solvent for the extraction process. Approximately 80mL of petroleum ether were dispensed into each of the aluminum extraction cups by a dispenser connected to the extraction unit.

2.2.4.5.2 Ether extraction procedure

Samples were immersed in the boiling petroleum ether (solvent) for 30min, followed by 45min rinsing/refluxing which involved rinsing the thimble contents in cold solvent to ensure removal of any remaining soluble material. The thimbles were then dried for 15min.

After completion of the extraction, the aluminum extraction cups containing the extracted fat were air dried in an oven for 20min at 105°C and subsequently cooled to room temperature for 15min in a desiccator. After cooling, the cups were weighed again and intramuscular fat contents were calculated with the following formula: intramuscular fat (%)=$\frac{fat\ recovered}{weight\ of\ the\ sample\ used\ for\ fat\ extraction\ (g)} \times 100$

where fat recovered= weight of aluminum extraction cup after extraction-weight of aluminum extraction cup before extraction. Percent intramuscular fat was expressed on a moisture free basis.

2.2.4.6 Crude protein, fat and moisture content

Traces of meat remaining on the rib bones and vertebrae after excision of the loin eye muscle were ground into a homogenized state and analyzed for crude protein, crude fat and crude moisture content using a FOSS Food Scan™ Near-Infrared Spectrophotometer (FOSS, DK-3400, Hillerød, Denmark) calibrated with FOSS Artificial Neural Network calibration. The Artificial Neural Network uses a correlative approach to predict sample composition. Thus, it assesses the relationship between sample constituent values and established spectral characteristics to decipher the test spectra and relay results for the constituents (crude protein, fat and moisture).

Each ground meat sample was uniformly spread on a glass-bottom sample cup and was subsequently inserted in the sample chamber of the FOSS Food Scan™. The product profile of the sample was then selected, and the scanning procedure initiated with the press of the start button. The analysis relies on near infra-red transmittance technology for the determination of protein, fat and moisture content simultaneously in the samples. A detector measures the amount of unabsorbed light after transmission of the light through the sample. The displayed results were in grams per 100g of sample for crude protein, fat and moisture. Duplicate readings were obtained for each sample, and the mean of the duplicates used in subsequent statistical analyses.

2.2.4 Collagen characterization

2.2.4.1 Initial sample preparation

An approximately 2.5cm thick loin chop was excised from the loin of each animal. The steaks were weighed on a Navigator™ portable balance (Model: N08110, OHAUS, Ontario, Canada) and appropriately labelled. The epimysium around the steaks was trimmed and the chops were cut into 1cm^3 cubes. The cubes were weighed again, placed in aluminum drip pans and covered with perforated aluminum foil to enhance water vapor escape during freeze drying. The samples were then frozen at -20°C for 24 hours and lyophilized for 5 days. After freeze drying, the samples were reweighed and a Waring blender (Model 7011C, Waring Commercial, Torrington, CT, USA) together with dry ice was used to crush the lyophilized samples into a coarse powder which was subsequently kept at -20°C until analysis.

The moisture content in each sample was determined with the following formula:

$$\text{Moisture content} = \frac{weight\ prefreeze\ drying - weight\ post\ freeze\ drying}{weight\ prefreeze\ dring} \times 100$$

2.2.4.2 Heat solubility of collagen

The soluble and insoluble fractions of collagen were obtained using the method described by Hill (1966) (Figure 2.3). This method estimates the amount or proportion of collagen that is soluble or dissolves at 77°C (Zayas, 1997). Freeze dried sample powder ($1.000 \pm 0.003g$) was weighed into labelled 50mL test tubes on a Denver Analytical Balance (Model: SI-234, Denver Instrument Company, CL, USA). After weighing, 20mL of $^1/_4$ strength Ringer's solution (4.5g sodium chloride, 0.21g potassium chloride, 0.318g calcium chloride dehydrate, 2000mL deionized water, pH 7.4) were added to the sample tubes. The tubes were then placed in a digital controlled water bath (Fisher Scientific Isotemp™ 228, NJ, USA) set at 77°C for 60mins and vortexed every 10mins.

After incubation, the tubes were cooled in ice slurry for 15mins and their contents were transferred into pre-weighed centrifuge tubes. The centrifuge tubes were balanced on a Harvard trip mechanical balance (Model 1450-SD, OHAUS® Corporation, NJ, USA). The tubes were then centrifuged (AVANTI® J-E centrifuge, Beckmann Coulter Inc., CA, USA) for 10mins at

3500×g at 4°C. The resulting supernatant was decanted into pre-labelled vials. The centrifuge tubes containing the pellets were drained at a 45°C angle for 1hour (Figure 2.4) and the wet residue was subsequently scraped into separate vials for future analysis.

2.2.4.3 Acid hydrolysis and neutralization

Two 1 mL aliquots of soluble supernatant per sample were pipetted into 20mL test tubes. For insoluble fractions, $0.3000g \pm 0.003g$ was weighed into the test tubes (Figure 2.5). For the soluble fraction test tubes, 1mL 12M HCL and 4mL 6M HCL were added to each tube and the head space of each tube was purged of oxygen with nitrogen gas for about 10 seconds and immediately capped. The tubes were then placed in a test tube heating block (Accublock™ Digital dry bath, LABNET International Inc., NJ, USA) (Figure 2.6) and hydrolyzed for 20hours at 110°C (Suzuki et al., 1995; Colgrave et al., 2012). For the residue fraction, 6mL 6M HCL were added to each tube and hydrolyzed as described above. Such conditions ensure that the peptide bonds are hydrolyzed quantitatively (Aitken and Learmonth, 1996; Hsiang and Cole, 1974).

After hydrolysis, the tubes were cooled in ice slurry for 10mins. The cooled hydrolysates were then filtered through pleated Whatman™ No. 4 qualitative filter papers (GE Healthcare Ltd, Buckinghamshire, UK) wetted with deionized water into round-bottom evaporating flasks.

The acid solution of each sample was evaporated using a rotary evaporator (Heidolph Collegiate LABORTA 4000WB ECO ROTOVAP, Schwabach, Germany) with a rotation speed of about 30rpm equipped with a self-cleaning dry vacuum system (Model: 2026, WELCH-ILMVAC, IL, USA), heating bath temperature of 42°C, a vacuum pressure of 680-700mmHg and a circulating water bath (Model: OB-13L, Fisher Scientific, PA,USA) for maintaining condenser temperature between 7°C to 10°C; as well as a dry ice trap (Model: UST 800, KNF Neuberger Inc., NJ, USA) to improve pump efficiency and prevent condensed liquids from getting to the pump.

After the solutions had been evaporated to dryness, they were reconstituted with 2mL deionized water. Reconstituted hydrolysis solution pH was tested using cut litmus paper and reconstituted solutions were neutralized as required with either 2M NaOH or 0.5 NaOH. After neutralization, samples where evaporated again as described above. After the final evaporation, dried hydrolysates from the soluble supernatant fraction were finally reconstituted with 5mL deionized water while those of the insoluble fraction were reconstituted with 8mL deionized (DI) water. Solutions were then transferred into vials and stored at -20°C for hydroxyproline determinations.

2.2.4.4 Hydroxyproline determination

The procedure for hydroxyproline quantification in experimental samples was undertaken as described by Neuman and Logan (1960) (figure 2.7). The Neuman and Logan method relies on the oxidative dehydrogenation of hydroxyproline by hydrogen peroxide in an alkaline environment (NaOH) with copper ions present to produce a chromophore which upon acid (sulphuric acid) and heat treatment, produces an orange-lilac color with p-dimethylaminobenzaldehyde (Baker et al., 1953).

2.2.4.4.1 Hydroxyproline standards preparation

One milliliter of hydroxyproline standard stock solution ([0.100g trans-4-hydroxy-L-proline SIGMA-ALDRICH, MO, USA], 25µL 12M HCL, 250mL deionized water) was added to 9mL deionized water in a screw capped glass vial to yield 10mL of 40µg/mL hydroxyproline assay standard. This solution was gently mixed by vortex and 5mL of the solution were pipetted into a different vial containing 5mL deionized water to yield 10mL of 20µg/mL hydroxyproline. This serial dilution was continued until a 10mL solution of 2.5µg/mL hydroxyproline assay standard was obtained. This process was repeated whenever hydroxyproline determinations on experimental samples were made.

2.2.4.4.2 Hydroxyproline determination in experimental samples

Two aliquots of 1mL per sample were pipetted into sealable glass test tubes. Afterwards, 1mL 0.01M copper (II) sulfate solution (0.250g copper (II) sulfate pentahydrate, 100mL DI water), 1mL 2.5N sodium hydroxide solution (100g NaOH pellets, 1000mL DI water) and 1mL 6% hydrogen peroxide solution (10mL 30% hydrogen peroxide, 100mL DI water) were added in succession. A yellowish-brown color forms after addition of these solutions. The tubes were then allowed to stand at room temperature for 5 minutes with occasional shaking. Tubes were then transferred to a water bath (Isotemp™ 228 Digital Control water bath, Fisher Scientific, NH, USA) set at 80°C and vigorously shaken with tube contents fully immersed in the water. This was done to ensure destruction of excess peroxide (Neuman and Logan, 1960). Tubes were then cooled in an ice slurry. After cooling, 4mL 3.0 N sulfuric acid solution and 2mL 5% p-dimethylaminobenzaldehyde (5g p-dimethylaminobenzaldehyde powder dissolved in 100mL 2-propanol) were added to each tube. The tubes were then capped, gently vortexed and incubated in a water bath set at 70°C for 16mins.

After incubation, the tubes were cooled with tap water for 5mins and 1mL aliquots of tube contents were transferred into 1.5mL plastic cuvettes for measurements of the extinctions (optical densities) of the colors generated with a UV-Vis spectrophotometer (GENESYS™ 20 visible spectrophotometer, Thermo Scientific, ON, Canada) at a 550nm wavelength against a blank solution (no hydroxyproline) and a set of hydroxyproline standard solutions with concentrations 2.5, 5, 10, 20 and 40µg hydroxyproline per mL. The absorbance readings of these standards were used to plot standard curves which were subsequently used to determine the hydroxyproline content of the experimental samples. That is, a linear regression model of y=mx+ b fitted for the standards, where y= relative absorbance, x= analyte concentration, m= slope of the model and b=intercept was used to determine the hydroxyproline concentrations of the experimental samples (Colgrave et al., 2012). The average absorbance reading for duplicate solutions per sample was used for subsequent calculations. Hydroxyproline content in both the soluble and insoluble fractions of the experimental samples were multiplied by 7.14 (Dransfield, 1977) This assumes that collagen comprises about 14% 4-hydroxyproline (Patiyal and Katoch, 2006; Jackson et al., 1996; Dransfield et al 1983; Naveena et al., 2011; Clark et al., 2005; Ando et al., 2006).

2.2.4.5 Calculating collagen content in the raw meat

2.2.4.5.1 Soluble collagen

Firstly, the total hydroxyproline (μg) in 1mL of reconstituted samples was determined by inserting the averages of their spectrophotometric readings into standard curve regression equations. The resultant value was multiplied by the total/ final reconstituted solution which was 5mL to obtain total hydroxyproline in the 5mL reconstituted volume.

Since 20mL Ringer's solution was used to incubate the freeze-dried muscle tissues, the total hydroxyproline in 5mL was multiplied by a factor of 20 to obtain total hydroxyproline (μg) in 20mL Ringer's solution. This hydroxyproline amount (μg) *ceteris paribus*, is assumed to be same in the freeze-dried meat (1g±0.003).

Total soluble collagen (μg) in the freeze-dried meat used for collagen characterization was determined by multiplying the total hydroxyproline in the tissue by the conversion factor 7.14. The values obtained were subsequently converted to milligrams (mg).

Total soluble collagen in total freeze-dried meat was determined by multiplying total soluble collagen per gram freeze dried meat by total freeze-dried meat (g). Total soluble collagen (mg) in total raw meat was assumed to be the same as the amount in the total freeze-dried meat. Total soluble collagen per gram raw meat was determined by dividing total soluble collagen in total raw meat by the total raw meat.

2.2.4.5.2 Insoluble collagen

In the case of the residue (insoluble fraction), after determining the total hydroxyproline in the total reconstituted volume (8mL), total hydroxyproline per gram wet residue was determined by dividing the total hydroxyproline in the used wet residue by the actual weight (g) of the wet residue used for hydrolysis which was 0.3g ± 0.003. Total hydroxyproline in the total wet residue that remained after the heat solubility of collagen phase was determined by multiplying the total hydroxyproline in the wet residue used for hydrolysis by the weight (g) of the wet residue that remained after heat solubility. All further determinations were as described for soluble collagen. Total collagen per gram raw meat was determined by summing the total soluble and insoluble collagens per gram raw meat.

2.2.5 Statistical analysis

Lilliefors (Kolmogorov-Smirnov) test of normality (Lilliefors 1967; Gross and Ligges, 2015) was implemented in an R statistical computing environment to test the hypothesis that the samples were drawn from normally distributed populations. Significance of fixed effects to be included in the various models were tested using the glm2 (Marschner, 2011) package which fits generalized linear models and was further confirmed by fitted univariate models in AsReml version 4.1 (Butler, 2009; Gilmour et al., 2015). Fixed and random effects of all fitted models are presented in Tables 2.1 and 2.2. Means and standard deviations were obtained using the base package (R Core Team, 2018), whilst the coefficients of variation was determined with the FinCal package (Fan, 2016).

In order to estimate phenotypic and genetic correlations among the traits under consideration, phenotypic and genetic (co) variances were estimated with bivariate animal models using the AsReml 4.1 software (Gilmour et al., 2015). Random additive polygenic effects were included in animal models for all traits under consideration. Kill date (slaughter batch), sex and company of origin were fitted as fixed effects (Table 2.1 and 2.2). Cooking time was used a linear covariate for cooking loss (%). The model formula is as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

Where $y_1$and y_2 are vectors of phenotypic value for 2 paired traits under consideration, b_1 and b_2 are vectors of fixed effects for the 2 paired traits and covariate, a_1 and a_2 are vectors of random additive genetic effects of traits 1 and 2. e_1 and e_2 are vectors of random residual effects, X_i and Z_i are known design matrices for fixed effects and random additive genetic effects respectively.

The variance-covariance matrix is as follows: $$var \begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A_{\sigma^2_{a1}} & A_{\sigma_{a12}} & 0 & 0 \\ A_{\sigma_{a21}} & A_{\sigma^2_{a2}} & 0 & 0 \\ 0 & 0 & I_{\sigma^2_{e1}} & I_{\sigma e1e2} \\ 0 & 0 & I_{\sigma_{e_{2e1}}} & I_{\sigma^2_{e2}} \end{bmatrix}$$

Where A is the numerator relationship matrix (Meuwissen and Luo, 1992) built from a pedigree composed of 8,372 animals. I is the identity matrix whose order is equivalent to the number of animals. Genetic (r_G) and phenotypic correlations (r_P) were estimated as: $r_G = \frac{Cov_{1,2}}{\sqrt{\sigma^2_{G1}\sigma^2_{G2}}}$ where:

Cov$_{1,2}$ = additive genetic covariance of trait 1 and 2

σ^2_1= additive genetic variance for trait 1

σ^2_2= additive genetic variance for trait 2

$r_P = \frac{Cov_{p1,p2}}{\sqrt{\sigma^2_{p1}\sigma^2_{p2}}}$ where Covp$_{1,\ P2}$ = additive phenotypic covariance for trait 1 and 2

σ^2_{p1}= phenotypic variance for trait 1

σ^2_{p2}= phenotypic variance for trait 2

$\sigma^2_p = \sigma^2_a + \sigma^2_e$

Cov_{p1p2}=Cov_{a1a2}+Cov_{e1e2}

A univariate animal model: y= Xb+$Z_a + e$; was fitted in AsReml (Gilmour et al. 2015) to estimate genetic and phenotypic variance and residual components, where:

y= vector of phenotypic value

b= vector of fixed effects

a= vector of additive genetic effects

e= vector of residual effects

X= incidence matrix for the fixed effects

Z= incidence matrix linking observation to random effect of animal

Heritabilitites were then estimated using these variance components as follows:

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2+\sigma_E^2} = \frac{\sigma_A^2}{\sigma_P^2},$$

where σ_A^2= direct additive genetic variance

σ_E^2=residual variance

σ_p^2= phenotypic variance

2.3 Results

2.3.1 Loin physical, meat quality and collagen characteristics

Phenotypic means, standard deviations, minimum and maximum values and coefficient of variation for loin physical traits are shown in Table 2.3, while those for meat quality and collagen characteristics are given in Table 2.4. A total of 11 loin physical and 13 meat quality traits were examined in this study. The loin physical traits had 500 observations except for Meat Trim Weight (MTW) and Fat Trim Weight (FTW) which had 455 and 456 respectively due to unavailability of phenotypic records for some individuals. Five hundred records are reported for meat quality traits except for intramuscular fat which had 464 records. Collagen solubility percent and total collagen had 499 observations while collagen insolubility percent had 492. Significance of fixed effects and random effect used for fitting mixed models for analysis are presented in Table 2.1 and 2.2.

Loin Eye Weight (LEW) was on average 39% of the loin weight (1.4±0.2 kg) (after adjusting for diaphragm weight) with a population mean of 0.5±0.1 kg while thick fat weight (TFW) was 24% with a population mean of 0.3±0.1 kg. Bone weight (BWT) had a mean of 0.2±0.0 kg and accounted for 13% of the loin weight (LWT). The mean pH of the muscles after thawing was 5.6±0.1 while mean losses (CL) upon cooking to an internal temperature of 71°C was 25% and ranged from 19.0% to 36.8% while average Warner-Braztler shear force (WBSF) was 47.2N±10.1. Mean Moisture content (MC) measured after oven drying was 72% while crude moisture (FOM) measured with a FOSS Food Scan was 57%. Mean FOSS crude protein (FOP) was 16.8%±1.2 while mean FOSS crude fat (FOF) and intramuscular fat content (IMF) were 24.1%±4.2 and 8.1%±3.0 respectively. The average combined-component percentage of loins in this study was 98.29. With respect to collagen characteristics, a mean of 18.0%±6.6 was obtained for percent collagen solubility (SOLC) in raw meat while 82.2%±6.4 was reported for collagen insolubility percent (ISOLC). Total collagen (TCOL) (mean= 3.1±1.0 mg/g raw meat) ranged from 1.5 to 6.3 mg/g raw meat. The L^* a^* b^* color space measured with a Minolta chroma meter produced mean values of 45.5±3.0 for lightness (LOINL), 7.7±1.3 for a^* (LOINA) and 3.5±1.1 for b* (LOINB) with hue (LOINH) and chroma (LOINC) means being 24.6±8.7 and 8.4±1.2, respectively. Of the color traits, hue had the highest coefficient of variation (35%) while L^* had the lowest 8%. As the ratio of the standard deviation to the mean, the coefficient of variation depicts the level of variability in relation to a population mean, the estimates obtained reveal that dispersion of MC was about 5 times less than for FOM while variability in insoluble collagen percent was approximately 3 times lesser than WBSF.

2.3.2 Heritabilities

Additive genetic variances, residual variances, and heritabilities with their standard errors are presented in Tables 2.5 and 2.6 for sub-primal and meat quality traits respectively. Estimates for collagen characteristics are also found in Table 2.6.

Moderate heritabilities were obtained for sub-primal traits, ranging from 0.22±0.10 for BWT to 0.44±0.11 for LEW although heritability estimates for bone percent (BP) (0.09±0.08), LWT (0.19±0.08) and TFW (0.16±0.10) were low. Loin eye percent (LEP) and thick fat percent (TFP) were moderately heritable with estimates of 0.28±0.12 and 0.42±0.13 respectively. Meat trim weight (0.30±0.12) and RTW (0.31±0.11) were also moderately heritable while FTW (0.13±0.10) was lowly heritable.

Heritability estimates for meat quality traits were low to moderately heritable. Estimates ranged from 0.12±0.09 for pH to 0.42±0.12 for LOINA. Minolta color traits were moderately heritable ranging from 0.21±0.10 for LOINB to the estimate stated earlier for LOINA. Heritability estimate for LOINL was 0.25±0.11.

With respect to juiciness traits, moisture content (0.36±0.11) was more heritable than crude moisture (0.21±0.10). Warner-Braztler shear force value (WBSF) was moderately heritable (0.31±0.12). The marbling traits, IMF and FOSS crude fat (FOF) were not heritable to the same degree, IMF (0.42±0.13) had a higher heritability estimate than FOF (0.24±0.10). Hue and Chroma are calculated based on LOINA and LOINB values and their heritabilities were

0.21±0.10 and 0.36±0.12 which indeed gives an indication of the influence of these underlying constituent traits. Cooking loss (CL), which gives an indication of the level of shrinkage, lipid and moisture loss had a heritability estimate of 0.24±0.10.

Of the traits describing collagen characteristics of the raw pork samples, collagen solubility and insolubility percent were lowly heritable with heritabilities of 0.12±0.10 and 0.15±0.10, respectively, while total collagen had a moderate heritability estimate of 0.33±0.12.

2.3.3 Correlations among traits

2.3.3.1 Correlations among loin physical traits

The phenotypic and genetic correlations for loin physical traits are shown in Table 2.7. Generally, significant genetic correlations ($p<0.05$) among loin physical traits were moderate to high, ranging between 0.48±0.23 to 0.93±0.23. There was a widespread negative correlation between traits related to muscle content/percent and fat content/percent.

For LWT, a trait equivalent to loin sub-primal cut weight was highly correlated with LEW (0.87±0.14), MTW (0.93±0.23), FTW (0.64± 0.28), RTW (0.76±0.16) and BWT (0.77±0.26). There was a strong negative correlation between LEW and TFP (-0.60±0.16). LEW was moderately to highly correlated with BWT (0.45±0.23), MTW (0.61±0.17), RTW (0.60±0.16) and LEP (0.73±0.14); it was however not correlated with BP (-0.02±0.38). For TFW, it was highly negatively correlated (-0.76±0.14) with LEP and positively correlated with TFP (0.91±0.06). MTW had a high genetic correlation with RTW (0.92±0.08), BWT (0.64±0.22) and RTP (0.76±0.16) and a moderate negative genetic relationship with TFP (-0.50±0.22). The genetic correlations of FTW with RTW and LEP were 0.62±0.25 and -0.80±0.28 respectively. RTW was highly correlated with BWT (0.71±0.19) and RTP (0.84±0.11) but moderately correlated with TFP (-0.50±0.23). Genetic correlations of BWT with LEP (-0.13±0.35) and TFP (-0.25±0.29) were not significant; BWT was however significantly correlated with BP (0.77±0.23). A high negative correlation was obtained between LEP and TFP (-0.76±0.10) and TFP was further negatively correlated with RTP (-0.66±0.17).

This study obtained moderately to high phenotypic correlations among the sub-primal traits. However, low phenotypic correlations were obtained between LWT with LEP (-0.20±0.05), TFP (0.19±0.05) and BP (-0.22±0.04); LEW and FTW (0.11±0.05), TFW and RTP (-0.27±0.04), MTW and LEP (0.11±0.05), RTW with LEP (-0.16±0.05) and BP (-0.15±0.05), BW and TFP (-0.13±0.05), LEP and BP (0.12±0.05).

2.3.3.2 Correlations among meat quality and collagen traits

Presented in Table 2.8 are the summaries of phenotypic and genetic correlations among meat quality and collagen traits considered in this study. In general, Minolta color traits were significantly correlated amongst themselves. Further, moisture traits were largely negatively correlated with fat traits.

High negative correlations were obtained for pH with LOINL (-0.95±0.35), LOINB (-0.87±0.31), and LOINH (-0.93±0.28). Muscle pH further had a strong positive correlation with MC (0.98±0.27). A negative genetic correlation was obtained between muscle pH and CL (-0.65±0.31). Cooking loss on other hand, had a strong positive genetic correlation with LOINB (0.69±0.31) and moderate correlations with WBSF (0.45±0.19) and LOINL (0.44±0.19).

With regard to CIE *L*a*b** results, LOINL had a moderate to high genetic correlation with other color traits. It had a moderate correlation with LOINA (0.53±0.20), LOINB (0.46±0.22) and a high correlation with LOINH (0.85±0.09). Minolta *L** was further strongly correlated with

ISOLC (-0.71±0.35) and SOLC (0.68±0.30). For LOINA, it was highly correlated with LOINC (0.97±0.01), FOM (0.62±0.30), and moderately correlated with LOINB (0.49±0.23). Genetic correlations of LOINB with LOINH, LOINC and IMF were 0.69±0.15, 0.64±0.17 and 0.61±0.22, respectively-all strong and positive. LOINB further had a strong negative correlation with MC (-0.76±0.17). With respect to LOINH, a high negative correlation was with MC (-0.62±0.21) although its relationship with other traits were generally moderate and not significant.

Moisture content (MC) is a measure of the amount of water contained in the pork samples. Higher chemical MC was associated genetically with lower IMF content (-0.64±0.14) and higher FOM percent (0.63±0.22). A moderate genetic correlation was found for WBSF with SOLC (-0.38±0.10) and ISOLC (0.42±0.16). For FOF, it was highly genetically correlated with FOM (-0.98±0.01), FOP (-0.93±0.05) and IMF (0.79±0.14). With respect to FOP, it was positively correlated with FOM (0.86±0.09) and negatively correlated with IMF (-0.67±0.18). A strong negative genetic correlation was also found between FOM and IMF (-0.83±0.13). Soluble collagen percent (SOLC) was highly negatively correlated with TCOL (-0.63±0.23) while ISOLC (0.66±0.28) had a positive correlation with TCOL.

Significant phenotypic correlations among Minolta color traits were generally moderate to high ranging from 0.58±0.03 to 0.94±0.02 although correlations of LOINL with LOINA (-0.24±0.05), LOINA with LOINH (-0.12±0.05) and LOINC with LOINH (0.15±0.05) were low. Moisture content was moderately correlated with all the Minolta color traits phenotypically except with LOINA (-0.18±0.05) which was low. Meat composition traits measured with the commercial FoodScan Meat analyzer were highly correlated among themselves phenotypically, ranging from 0.90±0.01 between FOP and FOM, to -0.99±0.00 between FOF and FOM. Phenotypic correlation found between FOM and IMF was high (-0.61±0.03). TCOL had a moderate phenotypic correlation with SOLC (-0.46±0.04) and ISOLC (0.48±0.04).

2.3.3.3 Correlations of loin physical traits with meat quality and collagen traits

In Tables 2.9 and 2.10, the phenotypic and genetic correlations of loin physical traits with meat quality and collagen traits are provided. Generally, there were more significant phenotypic correlation ($p<0.05$) than genetic correlations.

Loin weight (LWT) had a moderate genetic correlation with WBSF and FOP with estimates of 0.36±0.12 and 0.50±0.15 respectively. Loin eye weight (LEW) had moderate correlations with LOINA (-0.36±0.12), FOF (-0.30±0.10), FOP (0.52±0.20) and TCOL (-0.32±0.13). Thick fat weight (TFW) was moderately correlated with meat quality fat traits as its correlation with FOF and IMF were 0.55±0.25 and 0.53±0.26 respectively. Thick fat weight was further negatively correlated with CL (-0.41±0.16) and FOM (-0.52±0.18). With respect to MTW, it was highly correlated with CL (0.64±0.27) and moderately with FOM (0.53±0.26). A high positive genetic correlation was obtained between FTW and other fat traits like FOF (0.73±0.24) and IMF (0.66±0.31) but was negatively correlated with moisture traits like MC (-0.65±0.28) and FOM (-0.70±0.27). Moreover, FTW was also negative correlated with FOP (-0.71±0.27). Correlations of RTW and BW were all not significant. LEP was estimated to have a negative moderately correlation with FOF (-0.41±0.15), LOINA (-0.58±0.19) but was positively correlated with LOINL (0.52±0.26), FOP (0.47±0.16) and FOM (0.38±0.17). A moderate genetic correlation was obtained for FOP (-0.52±0.23) and FOM (-0.53±0.21) with TFP. Further, FOF and IMF as expected, were significantly correlated with TFP with estimates of 0.55±0.20 and 0.43±0.21 respectively. RTP was highly correlated with CL (0.68±0.23) and moderately correlated with IMF (-0.54±0.23). Bone percent was moderately correlated with ISOLC (0.53±0.10) and TCOL (0.51±0.27) and lowly correlated with SOLC (-0.26±0.11).

In terms of their phenotypic correlations, TFW was moderately correlated with FOF (0.52±0.03), FOP (-0.50±0.03), FOM (-0.51±0.03) and IMF (0.35±0.04). loin eye percent on the other hand had moderate phenotypic correlations with FOF (-0.49±0.04), FOP (0.47±0.04), FOM (0.47±0.04) and IMF (-0.38±0.05), however, its correlation with Minolta color traits were low, ranging between -0.11±0.05 with LOINH to 0.24±0.05 with LOINA and LOINB.

2.4 Discussion

2.4.1 Genetics of collagen characteristics

The mean total collagen (mg/g raw meat) obtained in this study fell within the range of the those in the literature reviewed, that is 2.6 to 5.0mg/g raw muscle (Correa et al., 2006; Therkildsen et al., 2002; Wheeler et al., 2000; Boutten et al., 2000). Correa et al. (2006) in their study of Canadian crossbred pigs with similar genetic makeup (Duroc × (Landrace × Large White)) as this study obtained mean total collagen slightly higher (4.0 mg/g wet tissue) than this study's mean. This difference could most probably be due to the fact they used a factor of 8 to convert hydroxyproline to collagen while this study used 7.14 as well as factors like study design and potential differences in breeding values. They further reported heat soluble collagen (%) ranging from 11.1% to 13.4%, a range less variable than the range obtained in this study. Heat soluble collagen percent gives an indication of the amount of heat labile cross-links in a sample and therefore a useful indicator of tenderness. Wheeler et al. (2000) obtained variable total collagen across different Large White composite barrow muscles ranging from 4.1mg/g raw muscle in the longissimus muscle to 7.1 mg/g raw muscle in the bicep femoris. These variations are most probably a function of anatomical location as highly exercised muscles tend to have more total collagen (Thakur et al., 2002). With respect to species-species comparison, total collagen in this study was generally lower than those reported in bovines (Cross et al., 1973; Hill, 1966; Raes et al., 2003), turkeys (Fernandez et al., 2001) and chickens (Liu et al., 1996; Sakakibara et al., 2000; Roy et al., 2007); although some studies in chickens reported relatively lower values (Nakamura et al., 2003; Nakamura et al., 2004). The ratio of soluble to insoluble collagen gives an indication of how tender or tough a muscle cut will likely be. Lebret et al. (1998) obtained similar (17.4%) collagen solubility percent from the loins of crossbred (Large White ✕ (Large White ✕ Landrace)) pigs slaughtered at 5.5 months. Correa et al. (2006) obtained lower (12.3%) collagen soluble percent, however, the approximate ages of the animal were not provided and as age influences solubility percent (Fang et al., 1999), interpretation of this result is difficult. Fang et al. (1999) in their study of the relationship between connective tissue development and Landrace growth and development reported heat soluble collagen percent of 24 at 6 months of age. Heat soluble collagen percent of this study was higher than those generally reported in beef studies (Nakano and Thompson, 1980; Dikeman et al., 1986) and lower than those reported for chickens and turkeys (Fernandez et al., 2001, Liu et al., 1996). Nishimura et al. (1999) in their study of the Japanese Black cattle, known for its high marbling content, obtained solubility percent 28% in 9-month olds and 16% solubility percent for 24-month olds.

To the author’s knowledge, this is the first study to report on the heritabilities of collagen solubility and insolubility percentages in pork. The low heritabilities of SOLC and ISOLC suggest that, of the observed variations in the population, only a small fraction is due to variation in genetics (Visscher et al., 2008) and this could limit genetic improvement of these traits. The moderate heritability estimates of TCOL (0.33) obtained in this study indicates a potential for making genetic progress in this trait. This estimate was, however, higher than the estimate reported by Suzuki et al. (2005) (0.23).

The high positive genetic correlation of LOINL with SOLC coupled with its high negative genetic correlation with ISOLC suggest that selecting for LOINL with genomic tools over time will increase solubility percent and decrease insoluble collagen thereby potentially improving tenderness. However, LOINL has an antagonistic relationship with pH and therefore selecting for LOINL will lead to a decrease in pH over time, which may potentially lead to the denaturation of myofibrillar proteins and subsequently lead to a pale, soft and, if the correlation between pH and CL is taken into account, exudative meat. Indeed, Marchi et al. (2011) reported a 25 % increase in soluble collagen in PSE meat compared to normal meat. The results of this study brings to bear the genetic relationships among ISOLC, pH, LOINL and SOLC. Thus, the high correlation of LOINL with SOLC and ISOLC presents a potential to predict SOLC and ISOLC with LOINL in pigs although appropriate selection indexes may need to be established. Secondly, collagen fibers are fluorescent (Biela et al. 2013) when excited with ultra-violet light. Indeed, methods have been developed to measure biological age in humans and rats through collagen fluorescence (Odetti et al., 1992). With respect to livestock, Swatland and Findlay (1997) developed an on-line UV fibre optic fluorescence probe to predict beef toughness based on detection of collagen-linked fluorescence. They found that narrow fluorescence peaks frequencies with smaller peak widths were higher in tougher parts and peak width was significantly correlated with tenderness (r=0.57). It is therefore interesting that genetic relationships were found between luminosity and collagen characteristics. It is plausible to suggest that genes influencing muscle luminosity also to a degree influence collagen characteristic, although further studies may be needed to establish this relationship.

Also, to the author’s knowledge, this is the first study to report a genetic relationship of WBSF with SOLC and ISOLC. The moderate genetic correlation of WBSF with SOLC and ISOLC indicate a possible influence of similar gene networks on these traits. Indeed, the relationship suggests that selecting for WBSF may in time increase collagen solubility percent and decrease collagen insolubility percent ultimately resulting in a tender product. As expected, TCOL was highly correlated with SOLC and ISOLC as TCOL was calculated based on soluble and insoluble collagen mg/g raw meat.

2.4.2 Loin physical and meat quality traits

Loin sub-primals are obtained through further fabrication of primals into manageable cuts. They are easier to handle and more cost effective to transport (Underly, 2012). Pork is mostly sold as packaged sub-primals on a fresh or processed basis at the retail level (Hodgson et al., 1991) and therefore taking measurements at this level of fabrication is very important as breeding objectives in pigs are driven by feedback from these cuts (Van Wilk et al., 2005).

Selection for rapid growth rate has led to an increase in carcass lean percent (Newcom et al., 2002). Even as early as the 1960s, Buck et al. (1962) noted that during pig carcass assessments, lean meat percent was considered of utmost importance. It was therefore not surprising that LEP was almost twice that of TFP in this study. This agrees with the results obtained by Van Wijk et al. (2005) in their study of commercial crossbred pigs as they reported 59.3mm mean loin eye depth vs 25.1 mm mean back fat depth. Newcom et al. (2002) also reported similar observation in their study of lean efficiency pigs, in which the ratio of loin muscle area to carcass back fat was approximately 3:1. Furthermore, when compared to this study, Correa et al. (2006) reported higher loin eye and fat percent but lower bone percent in crossbred Canadian pigs (Duroc × (Landrace × Yorkshire)) slaughtered at approximately the same slaughter weight as this study. This difference could be a function of the fact that they took their measurement on the whole loin primal while this study worked with a sub-primal. Devol et al. (1988) obtained only a 19mm difference between loin eye area and back fat while Van Wijk et al. (2005) recorded 34mm. This difference provides perspective on the level of improvement that has occurred over the years although breed differences may need to be considered when making such comparisons. Devol et al. (1988) however did not report on breed composition of their population.

Intramuscular pH is a measure of muscle acidity and is crucial in the prediction of major meat quality defects. Average pH obtained was similar to those reported by Therkildsen et al. (2002), Van Wijk et al. (2005), Hodgson et al. (1991) and De Vol et al. (1987) even though pH measurements for this study were taken on frozen-thawed samples while those from the aforementioned studies were on unfrozen samples. Monin and Sellier (1985) also reported similar results in the longissimus dorsi of Large Whites, however, their values for halothane negative and positive Pietrains and Hampshires were lower: 5.45, 5.41 and 5.40 respectively. In a review by Bendall and Swatland (1988), the mean ultimate pH (pHu) of 9,600 Alberta crossbred pigs in 1978 was 5.75 with 45% of the animals having pHu fall within ranges of 5.7 and 6.5. This is slightly higher than the value obtained in this study. However, this difference could be due to factors such as breed composition, sampling and measurement approaches.

Juiciness is of critical significance to eating quality and is influenced mainly by the quality of the raw meat and cooking procedure (end-point temperature, heating method) (Aaslyng et al., 2003).

This study used an end-point temperature of 71°C. Indeed, increasing end-point temperature is known to decrease juiciness (Heyman et al., 1990). Cooking loss is a trait intimately linked to juiciness and with tremendous influence on juiciness as it accounted for approximately 75% of the variation in juiciness scores according to a study by Bouton et al. (1975). Hodgson et al. (1991) obtained a slightly higher cooking loss percent (28%) which is mostly likely due to the final meat sample internal temperature used in their study being 75°C. Therkildsen et al. (2002) and Kristensen et al. (2002) reported higher cooking loss percent ranging between 29.9 to 33.4%. It is however worth noting that in their study, chops were cooked for 60min at 80°C. Further, their treatment effects (ageing period and feeding strategy) may have influenced these averages. Indeed, the influence of endpoint temperature in cooking loss (%) cannot be overstated. In a study by Heymann et al. (1990), changing endpoint temperature from 65.6 °C to 82.2°C resulted in a 35% increase in cooking loss. This necessitates a standard endpoint temperature in research studies to ensure ease of comparison such as those recommended by AMSA (1995).

A trait closely linked to cooking loss is Warner-Bratzler shear force (WBSF) (Barbanti and Pasquini, 2005; Møller, 1981). Warner-Bratzler shear force values are widely accepted as important indicators of pork tenderness (Cai et al., 2011). Shackelford et al. (2004) reported a significantly high correlation (r= -0.66, p<0.001) between trained sensory panel tenderness scores and WBSF of meat for porcine longissimus muscle. Warner-Bratzler shear force values reported by Hodgson et al. (1991) of 34N, De Vol et al. (1988) of 37N, Shackelford et al. (1999) of 38N, Heymann et al. (1990) of 25N, and Therkildsen et al. (2002) of 34N were lower than the mean obtained in this study. However, Kristensen et al. (2002) reported values ranging between 57-70N while Oksbjerg et al. (2000) obtained a value of 50N. Oksbjerg et al. (2000) indeed compared meat quality traits between fast growing and slow growing Danish Landrace pigs and found the former to have slightly higher shear force values and cooking loss (%), giving a hint of the effect of selection for fast growth on meat quality traits. Huffman et al. (1996) suggested a tenderness threshold of 40.2N for beef steaks, as tenderness ratings corresponding to values less than or equal to 40.2N were rated as having acceptable tenderness by consumers in both restaurant and home settings. If this threshold is to be used as a standard in pork then, on average, loin chops in the present study were tough. In general, comparing WBSF values reported by studies in the 1990s (Heymann et al., 1991; Hogson et al., 1990) with those of the 2000s (Oksbjerg et al., (2000); Kristensen et al., 2002), one can only get the impression that pork is getting tougher. Shear force values reported for wild boars by Cifuni et al. (2014) ranged between 44-53N and thus falls within the range of values reported for domestic pigs.

Shackelford et al. (2004) employed similar WBSF methodologies as this study but reported lower WBSF values compared to this study. Their research study looked, in part, at the effect of cooking method on WBSF and found belt grill cooking to have significantly ($p<0.05$) lower mean WBSF value (3.9 kg) than open hearth broiling (4.1 kg). The WBSF coefficient of variation (CV) of this study (24) falls within the range obtained by Shackelford et al. (1999) (20.8-34.4). Jones et al. (1980) indeed reported animal to animal variability to be the major source of variation in 14 out of 19 pork quality traits they studied including WBSF. These variations are most probably the results of differences in a number of known and unexplained factors of either genetic and/or environmental origin that interact and dictate the effects of metabolic processes at the time of slaughter and after slaughter (Brocks et al., 2000). The relatively high SD and CV for some traits in this study are likely due to the wide variation in phenotypes in the populations studied. Similar high variation was reported by Hodgson et al. (1991) and DeVol et al. (1988) on meat quality traits of pork longissimus dorsi. The CV reported for ether extractable material in this study was lower than the CVs of the fat percentages reported by Hodgson et al. (1991). Indeed, DeVol et al. (1988) in their evaluation of random pork carcasses in a commercial packing plant in the US concluded that there is substantial variability in carcass composition and meat quality traits of pork moving into the market. Variability in this circumstance is not advantageous as consumers usually prefer consistency in the food products they consume.

Mean chemical moisture percent and its low level of variability was similar to the results of DeVol et al. (1988), Hodgson et al. (1991), Ramsey et al. (1989) and Novakofski et al. (1989). Crude moisture content obtained with the FOSS FoodScan was lower (57%) than those obtained after freeze drying (72%). Woolley et al. (2016) made similar observations in their comparison of chemical analysis and FOSS FoodScan for proximate composition of bovine inside round lean and fat trimmings. However, they found a high correlation between chemical moisture and FOSS moisture (r= 0.993). The combined-component percentages reported by other researchers who have studied the proximate composition of porcine longissimus muscle (Hodgson et al. 1990; Bacon et al., 1989) were 98.54 and 98.94 respectively, which agrees with this study. The large difference between the mean ether extractable material and mean FOF is most likely due to the fact that loin trimmings were used FOF measurements while for IMF, whole loin chops cut into 1cm^3 pieces and oven dried were used. Compared to this current study, Bacon et al. (1989) reported lower protein % (15.7) and moisture % (50.9) but higher fat % (32.5) using a FOSS Superscan complete meat analyzer. Crude protein % obtained by the Kjeldahl method in the studies of Ramsey et al. (1989) and Novakosfski et al. (1989) 22.4 and 27.2, respectively, was higher than the mean obtained in this study with the FOSS meat analyzer. Intramuscular fat is found between muscle fibers and its greatest accumulation occurs during the later phases of physiological maturity. This trait is important due to its influence on fresh meat marketing and for meeting export standards especially in loin cuts (Lonergan et al., 2019). Ramsey et al. (1989) reported a high ether extract % (8.5) for their high marbling groups while their moderate groups had a mean of 5.5 which suggests that the mean ether extract of this study (8.1) falls within the range of moderate to abundant. The moderate-abundant marbling level of this study could be due to the Duroc sire line included in the mating system, as high levels of marbling have been reported for Durocs (Lonergan et al., 2019). With the exception of this study, all other research studies reviewed reported low ether extract % (DeVol et al., 1988; Novakosfki et al., 1989; Heymann et al., 1990).

2.4.3 Freeze-thawing affects meat colour

Meat products on retail shelves are generally selected or rejected by consumers based on their appearance and color (Brewer et al., 2006). Therefore, the ability of meat suppliers to create and maintain desirable color characteristics is essential (AMSA, 2012). Color assessment, either through instrumental or visual appraisals, is critical for tracing and correcting product development problems as well as detecting quality defects in meat research (Yancey and Kropf, 2008). The state of the primary red meat pigment, myoglobin, determines muscle color (AMSA, 2012; Brewer et al., 2006). However, factors such as nutrition, genetic background, species, post slaughter storage, muscle conversion to meat, lighting and display all play a role in determining perceived meat color (AMSA, 2012). Kristensen et al. (2002) and Friese et al. (2005) reported higher values for the Minolta color parameters regardless of their treatment groups. This is most probably due to the fact that they took their measurements of fresh pork chops as well as differences in blooming (myoglobin oxygenation) times. Kristensen et al. (2002) bloomed for 1hr at 3°C while Freise et al. (2005) bloomed overnight at about 2°C, however, in this current study, chops were bloomed for about 1hr at 4°C. Brewer et al. (2001) in fact reported a significant effect of bloom time on the Minolta color parameters. Typical PSE pork Minolta L* is 61.0 (Friese et al., 2005), thus the LOINL range of this study (37.2-55.2) suggest that none of the loin samples exhibited PSE characteristics. Hue angle is a measurement of the level of deviation off the true red axis (*a**) in CIE *L*a*b** color space (Brewer et al., 2006). It is computed from *a** and *b** values while chroma indicates how dull or vivid a color is (AMSA, 2012). Wilkinson et al. (2006) studied the influence of modified atmosphere packaging on pork longissimus muscle and reported slightly similar chroma (8.5) and hue (22.7) as this study under their 100% CO_2 treatment group before blooming. This similarity could be due to a number of factors, including the frozen thawed state of this study's samples. Wilkinson et al. (2006) further reported increased hue and chroma values after blooming although their bloom time was not reported. Since increasing hue angle indicates that samples become less red (Brewer et al., 2006), the samples of this study were on average less red than those of the aforementioned study. This is most likely due to the fact that in fresh muscles cuts, metmyoglobin reducing activity (MRA) is high and thus formed metmyoglobin is immediately reduced to deoxymyoglobin and subsequently oxygenated during blooming. However, during aging or freeze-thaw treatment, metmyoglobin activity reduces leading to an accumulation of metmyoglobin on the meat surface. (Lanari and Cassen, 1991; Bekhit and Faustman, 2005). Also, co-factors like NADH may leach out with the exudates during thawing or be used for reactions not associated with MRA (Abdallah et al., 1999).

2.4.4 Moderate to high heritability estimates of loin physical and meat quality traits presents potential for improving these traits

One key inquiry in biology is determining whether the variations observed in a trait of interest is due to biological and/or environmental factors (Hill et al., 2008). The concept of heritability is key to answering this inquiry. Heritability is a population parameter that provides an estimate of the proportion of the total phenotypic variance for a trait of interest in a population, measured at a specified age period or time that is due to additive genetic variation (Hill et al., 2008). To the authors knowledge, no literature on heritability estimates of the loin physical traits measured this study were available apart from those presented in an earlier publication from the larger study (Miar et al., 2014). The generally moderate to high heritability estimates of loin physical traits suggests a potential for improving these traits through the traditional breeding approaches. However, genomic selection, with its high accuracy on lowly heritable traits (Gorjanc et al., 2015) will be appropriate for loin physical traits like LWT, FTW, TFW and BP. Indeed, the low heritability of LWT and BP could be due to sampling errors during sub-primal excision as differences in rib numbers of pigs has been reported to range between 13.5 to 17.0 (Fredeen and Newman, 1962). Thus, this variation could cause errors in sampling sites and result in faulty representations. Generally, however, traits related to carcass composition are moderate to highly heritable (Van Wilk et al., 2005; Enfield and Whatley, 1961; Ciobanu et al., 2011).

The low heritability estimate of muscle pH fell within the range (0.00-0.39) reported in the literature reviewed (Bidanel et al., 1994; Jensen et al., 1967; Knapp et al., 1997; Hovenier et al., 1992; Suzuki et al., 2005). In fact, it was in agreement with the estimates reported by Van Wijk et al. (2005) (0.11) and Hermesch et al. (2000) (0.14). Breed difference can have a tremendous influence on muscle pH estimates as Johansson, (1987) reported higher heritability estimates of pH in Landrace (0.27) and Large White (0.30). Low genetic variation, as obtained for muscle pH, limits our efforts to rank sires for their genetic endowment when using it as an indicator trait (Van Wijk et al., 2005). The low heritability of pH indeed seemed not to be species specific, as Mortimer et al. (2014) obtained an estimate of 0.08 in Sheep, Hamzah et al. (2016) reported 0.09 in fish, Aass (1996) obtained 0.19 for dual purpose cattle and Bihan-Duval et al. (2003) had 0.16 for turkey toms.

Cooking loss (CL) is a measure of water holding capacity that quantifies the fluid released from meat samples upon heat application with or without application of external forces (Hamm, 1986). Cooking loss heritability estimated in the present study (0.24) was higher than estimates reported by Lo et al. (1992) (0.06), Suzuki et al. (2005) (0.09), Scheper (1978) (0.10) and De Vries et al. (0.11) but lower than estimates of Lee et al. (2015) (0.45). These differences could most probably be due to differences in statistical modelling techniques implemented in the above studies as well as differences in population structure. Bidanel et al. (1994) however reported similar cooking loss percent heritability estimates (0.24) as this study despite their study population being Pietrain pigs. Differences in heritability estimates of cooking loss due to breed have also been reported by Malmfors and Nilson (1978) as they did not obtain additive genetic variation in Landrace (h^2=0.00) in Landrace but reported a high heritability estimate in Large White (h^2 =0.51). Heritability of a trait to a large extent depends on the originating population since variations in non-additive and additive genetic aspects as well as environmental variances are population specific. Further, genetic variances are dependent on alleles influencing a trait of interest in a population, variants effect sizes, mode of gene action and allele frequencies; and as the above variables can vary across populations, heritability of a trait in one population from a theoretical stand point does not necessarily predict heritability of that trait in a different population (Visscher et al., 2008). However, in actuality, heritability of similar traits for the most part tend to be notably similar in different populations of the same species and in some cases across species (Visscher et al., 2008).

Heritability estimates of LOINL were in agreement with estimates reported by Larzul et al. (1997) (0.23) and Cherel et al. (2012) (0.20) while Van Wijk et al. (2005) obtained slightly lower estimates (0.18). Van Wijk et al. (2005) further reported lower LOINA (0.21) and LOINB (0.15) estimates. These differences could be a result of statistical modelling differences but this is unlikely as Van Wijk et al. (2005) measured tristimulus values under C illuminant while this study used D65 illuminant and Sun et al. (2017) reported a high correlation (r>0.96) between the aforementioned illuminants. Lee et al. (2015) and Cherel et al. (2012) also reported similar LOINA and LOINB estimates as this study. Furthermore, heritability estimates of LOINL (0.28) and LOINA (0.43) reported for Durocs by Gjerlaug-Enger et al (2010) agreed with this study's estimates although their LOINB (0.33) was higher. Cameron (1990) obtained slightly higher estimates for LOINC (0.42) although that study's LOINH (0.19) was lower than this study. The generally moderate heritabilities of the Minolta color traits in this study suggests that selection for meat color traits will lead to genetic changes in the average population means for meat color resulting in improved attractiveness of pork. It must be noted that meat color is a critical visual feature influencing the meat quality, as it influences consumer acceptability and purchasing decisions (Karumathil et al., 2016; Lonergan et al., 2019).

For moisture content measurement, the estimated heritability was within range of the estimates reported by Gjerlaug-Enger et al. (2010) (0.31-0.50) while Carbling et al. (2015), Cameron (1990) and Lo et al. (1992) obtained lower estimates of 0.27, 0.26 and 0.14 respectively. Jensen et al. (1967) on the other hand, reported a high (0.81) heritability estimate for moisture content.

These differences in estimates could most probably be due to differences in population structure, variations in sample size, statistical modelling, as well as differences in trait measurement procedures. For instance, Jensen et al. (1967) used hot air oven 80℃ for 48hrs in the moisture content assay while the current study freeze-dried samples for 5days.

Warner-Bratzler shear force is a measurement that serves as a valuable indicator of meat tenderness (Bratzler, 1932, Warner, 1952, Hovenier et al., 1993) and thus, a trait of tremendous importance in the food industry. The moderate heritability estimate of shear force conforms to estimates reported by Malmfors and Nilsson (1978) (0.34); Jensen et al. (1967) (0.25); Lee et al. (2015) (0.39); Cherel et al. (2012) (0.26) and Hovenier et al. (1993) (0.30). However, Suzuki et al. (2005) and Jung et al. (2015) obtained higher estimates of 0.45 and 0.56 respectively. Cabling et al. (2015) and Lo et al. (1992) on the other hand reported low estimates of 0.04 and 0.17 respectively. These differences could be due to population differences and differences in measurement approaches. For instance, Cabling et al. (2015) used a crosshead speed of 400 mm/min while this study used 200mm/min. Wheeler et al. (1997) in point of fact reported that Warner-Braztler shear values decreased with increasing shearing cross head speed.

2.4.5 Additive genetic variance for intramuscular fat makes a substantial contribution to its total phenotypic variance

The moderate heritability estimate of IMF (0.42) was in conformance with estimates reported by Scheper (1978) (0.35), Suzuki et al. (2005) (0.39), De Vries et al. (1994) (0.41) and Larzul et al. (1997) (0.44). Knapp et al. (1997) obtained varying estimates for different pig breeds, with the Large White, Landrace and Pietrain having estimates of 0.38, 0.67 and 0.42 respectively. Enfield and Whatley (1961), Jensen et al. (1967) and Allen et al. (1966) reported much higher estimates of 0.63, 0.86 and 0.70 respectively. Looking at the reduction in IMF heritability estimates over time, one may be led to the opinion that selection against fat traits over time may have led to changes in allele frequencies of some genes related to IMF although studies need to be done to verify this assertion. However, the general trend of moderate to high estimate of IMF indicates that a substantial proportion of this trait is determined by additive genetic effects (Lo et al., 1992). Thus, the moderate-high estimate obtained in the present study suggests that additive genetic variance for IMF makes a substantial contribution to its total phenotypic variance and thus, there is tremendous potential to improve this trait through selective breeding. In terms of IMF heritability in other livestock species, Mortimer et al. (2014) and Mateescu et al. (2015) reported similar heritability estimates in Australian crossbred sheep (0.48) and Angus cattle (0.38) respectively, as those reported for swine breeds.

The high negative correlation of FOSSF with FOSSM and FOSSP agrees with results obtained by Gjerlaug-Enger et al. (2010) for Durocs. This finding supports the established fact that an antagonistic relationship exists for fat with muscle and moisture content. Indeed, Peñagaricano et al. (2015) through a scan of the porcine genome showed that muscularity and fat deposition are influenced by the additive pleiotropic effects of a genomic region on SCC6. They also reported on 7 significant eQLT's in this region many of which play vital roles in cell differentiation and proliferation. The antagonistic relationship of moisture and muscular fat has also been reported in fish (-0.89) by García-Celrán et al. (2015) and Cattle (-0.99) by Sakuma et al. (2017). Heritabilities of meat composition traits as measured with FOSS FoodScan NIR spectrophotometer were much lower than those reported by Gjerlaug-Enger et al. (2010) as they obtained estimates of 0.54, 0.50 and 0.62 for FOP, FOM and FOF respectively. It is worth stating that these estimates were obtained from Duroc breeds as well as the fact that they used ground whole loin chop for measurements while the current study used trimmings. Even though Scheper (1978) used chemical analysis to estimate protein percent, the heritability estimate reported in that study (0.22) was similar to that found in this study.

2.4.6 Continuous selection for lean percent will negatively impact correlated fat traits

Carcass and meat quality characteristics in terms of its lean to fat ratio, tenderness, color and water holding capacity are determined for the most part, by structural and biochemical features of muscle and meat (Lonergan et al., 2019). However, on the fundamental level, these characteristics, for the most part, are determined by background genes. At the core of this current study was testing the hypothesis that genetic relationships exist between and among loin physical, meat quality and collagen traits. Genetic correlations provide a measure of the magnitude of association between breeding or genotypic values of individuals. Thus, it is valuable for describing how traits are connected at the genetic level and for predicting the impact of selection on a trait of interest and the changes that occurs in correlated traits (Hill, 2001). It is caused by linkage disequilibrium between genes impacting a trait and pleiotropic gene effects, although the former in most cases is transient while the latter leads to stable correlations (Goodnight, 2010). Phenotypic correlation on the other hand is a population measure that provides an estimate of the extent to which two metric traits co-vary among a population of related individuals (Conner and Hartl, 2004; Hill, 2001). Genetic and environmental correlations are two components that make up phenotypic correlation which could make phenotypic correlations of limited interpretative value as differences in environmental factors could impact its estimates. Phenotypic correlations are determined mainly by additive genetic correlation when heritability estimates are high while with lowly heritable traits, environmental correlations are paramount (Conner and Hartl, 2004). The moderate to high significant phenotypic correlations generally obtained among the loin physical traits suggest a potential for prediction among loin physical traits in the population of the present study.

Even though meat quality is increasingly becoming important, meat yield is still crucial for carcass valuation as well as primal and sub-primal pricing (Van Wijk et al., 2005). Pork loin is one of the most valued cuts of a porcine carcass (Van Wijk et al., 2005) and indeed, one of the most tender parts of the carcass. The generally moderate to high genetic correlations between the sub-primal traits obtained in this study agree with the results of Newcom et al. (2002). The favorably high genetic correlation of LWT with LEW, MTW and RTW indicate a positive effect of selection for increased loin weight on muscling traits. However, LWT was also positively highly correlated with BWT, which is not a favorable correlation since selecting for increased loin weight will potentially also increase bone weight, a trait of little economic value. It must however be noted that bone weight and integrity is of vital importance from an animal welfare standpoint as it prevents broken bones from occurring during transport and handling.

The high negative correlation between LEW and TFP and between TFW and LEP supports the results of other research studies. Newcom et al. (2002) also reported a negative correlation between carcass back fat and loin muscle although it was moderate (-0.43) while Johnson et al. (1999) reported a low correlation (-0.27). Furthermore, Van Wijk et al. (2005) reported a negative genetic correlation for back fat with whole loin weight (-0.41) and boneless loin weight (-0.60). Hovenier et al. (1992) also reported a high negative correlation (-0.71) between lean meat content and back fat thickness. All these studies used different pig breeds with varying population structures; however, they all obtained a negative genetic relationship between muscling traits and fat traits which are in agreement with the findings of this study and thus suggest that exercising continuous selection on lean percent could have an undesirable impact on correlated fat traits and indirectly affect eating quality. To the author's knowledge, this is the first study to report on the genetic correlations of meat trimmings. FTW, which was essentially fat trimmings from the loin was highly negatively correlated with LEP while MTW, which was essentially meat trimmings from the loin was moderately negatively correlated with TFP. These findings in a sense indicate that regardless of whether samples used were whole cuts or trimmings, plausible results can still be obtained. The results of Van Wijk et al. (2005) partially affirm this point as they obtained high genetic correlations between primals and sub-primals.

2.4.7 Linkage disequilibrium and/or pleiotropic gene effects potentially exist among traits related to the PSE defect

To integrate meat quality traits into swine breeding programs, relatively cheaper and objective measurements should be readily available to researchers and breeders, especially when routine data collection is necessary. The strong negative genetic correlation between pH and cooking loss obtained in this study indicates the potential of pH as an indicator trait for cooking loss (%). This result agrees with those reported by Bidanel et al. (1994) (-0.72) and De Vries et al. (1994) (-0.82), further suggesting that effective selection for higher pH may increase water holding capacity. Gjerlaug-Enger et al. (2010) and Cameron (1990) reported moderate negative genetic correlations between pH and LOINL with estimates of -0.44 and -0.38 respectively. The directions of the relationships are in congruity with this study although this current study reported higher estimates. De Vries et al. (1994) and Van Wijk et al. (2005) also reported high genetic correlations of -0.60 between pH and LOINL. A high genetic correlation of pH and L^* has also been reported in poultry (Bihan-Duval et al. 2003). Muscle pH of this study was further, highly correlated with moisture content. The relationship of pH with LOINL and MC highlights the economically important meat defects PSE and DFD, as the correlations indicate that selection for high pH will lead to high moisture content muscles and a darker color while low pH meat will tend to be exudative and pale and this supports the conclusions of Van Wijk et al. (2005). A high correlation of pH with ISOLC (0.76) and SOLC (-0.72) was obtained although associated with a high standard error. This relationship merits further investigation with a larger sample size as this may lead to a reduction in the magnitude of the standard error. Muscle pH is an easy to measure trait and thus, a good indicator trait candidate for the relatively expensive and difficult to measure traits highly correlated with it in this study.

De Vries et al. (1994) obtained similar moderate genetic correlations for CL with $L*$ (0.47) and WBSF (0.57) as this study. Suzuki et al. (2005) on the other hand, obtained a low negative correlation (-0.22) which could be due to differences in population composition and statistical modelling. The high positive genetic relationships between LOINB and CL offer the possibility of using LOINB, a relatively easy to measure trait, to predict cooking loss in breeding programs, as the correlated response of selecting against LOINB will lead to a reductions in cooking losses and therefore an increase in water holding capacity.

The strong genetic correlations of LOINB with LOINH and LOINC as well as LOINA with LOINC is expected since calculation of LOINH and LOINC is based on $a*$ and $b*$ coordinates. Van Wijk et al. (2005) and Gjerlaug-Enger et al. (2010) reported a high genetic correlation for LOINB with LOINL (0.89) and LOINA (0.79), higher than the moderate correlations obtained in this study. The correlation between MC and FOM (0.63) as well as IMF and FOF (0.79) is expected as they are just different measuring approaches for the same trait, moisture content in the case of MC and FOSSM and fat content in the case of IMF and FOSSM. It is quite interesting that these high correlations were obtained even though different parts of the loin were used for the measurements. However, the variation in correlation of these traits with other traits under consideration suggests that they must not be considered as identical traits. The high genetic correlation between MC and IMF obtained in this study were of the similar order of magnitude as those reported by Jensen et al. (1967) (-0.95), Malmfors and Nilsson (1978) (-0.72), Allen et al. (1966) (-0.78) and Cameron (1990) (-0.68) suggesting that similar background genes affect these traits.

The correlation estimates obtained for TFW with CL, MC and IMF suggest that genetic selection for improved back fat is expected to result in pork with decreased cooking loss and moisture content and increased intramuscular fat content. Indeed, Jensen et al. (1967) reported a strong positive genetic relationship between IMF and pork organoleptic properties, indicating that improved IMF will improve eating quality. In a study with Duroc and Landrace pigs, the genetic correlation estimates obtained between fat and eating quality traits led Cameron (1990) to suggest that effective selection for increased lean percent would adversely affect pork juiciness, tenderness and flavor. The moderate genetic correlation of TFW and TFP with IMF suggest the deposition of back fat and intramuscular fat is brought about by similar physiological factors which disagrees with the results of Jensen et al. (1967), as in their study ether extractable lipid was not genetically correlated with back fat thickness. The negative genetic correlation of TFW with CL and FOM coupled with the correlation estimates of LEP with LOINL, LOINA and FOF supports the conclusion arrived by Jensen et al. (1967) that selecting for decreased back fat and increased lean percent would negatively affect meat quality. The moderate correlation of BP with ISOLC and TCOL suggest the influence of similar gene networks on these traits. Indeed, type 1 collagen, the most abundant collagen type, can be found in both bone matrix and intramuscular connective tissues, where it provides biomechanical support.

The genetic correlation estimates of LEP with LOINL, LOINA and FOSSF indicated that selection based on muscling data will result in increased LOINL, and decreased LOINA and fat content. The genetic correlation of LWT with WBSF and FOP suggests that selection for increased loin weight is expected to result in improved muscling but tougher pork over time. Lo et al. (1992) came to similar conclusions from their correlation estimates between loin muscle area and shear force.

2.5 Conclusions

Genetic correlations between WBSF and collagen characteristics indicated that similar gene networks potentially influence these traits and thus, despite the relative youthfulness of pigs at slaughter, genetic selection for collagen solubility may decrease pork toughness. Furthermore, the genetic correlations of Minolta *L** with collagen characteristics present a potential to use Minolta *L** as an indicator trait for percentage soluble and insoluble collagen. Results from this study also hint at a possible linkage disequilibrium and/or pleiotropic gene effect in color, pH and moisture content. Results further indicated that additive genetic variance for intramuscular fat and Minolta *a** makes a substantial contribution to its total phenotypic variance indicating that selection for these traits will lead to relatively rapid genetic changes in the average population means. In summary, the genetic parameters estimated in this study will make it feasible to predict response to genetic selection of loin physical and collagen characteristics and further add to the already established research database on meat quality traits. The genetic correlations agree with published reports that continuous selection for increased lean will adversely affect fat traits.

2.6 Figures

Figure 2. 1: intramuscular pH measurement on a loin chop.

Figure 2. 2: Color measurements using a Konica Minolta chroma meter.

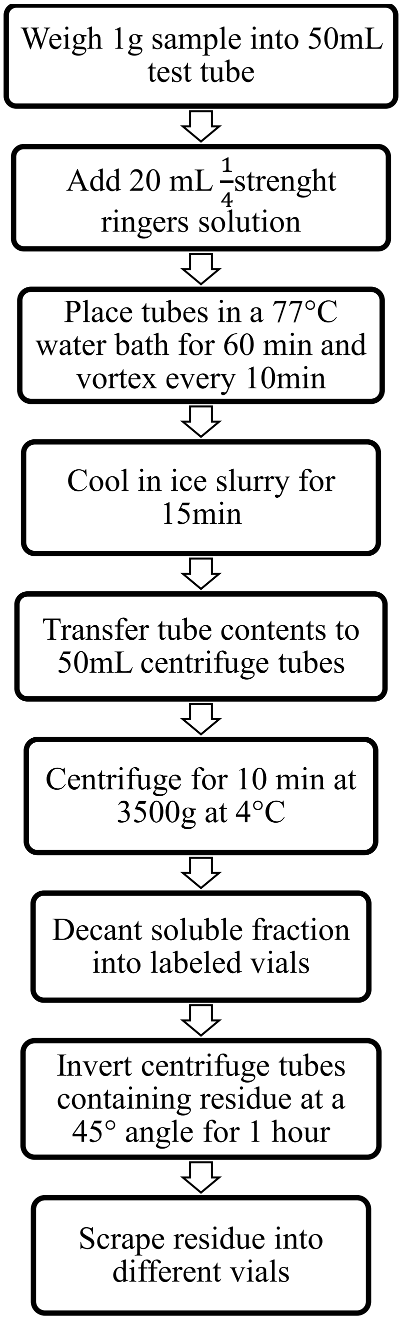

Figure 2. 3: Flow chart for collagen heat solubility using the method described by Hill (1966).

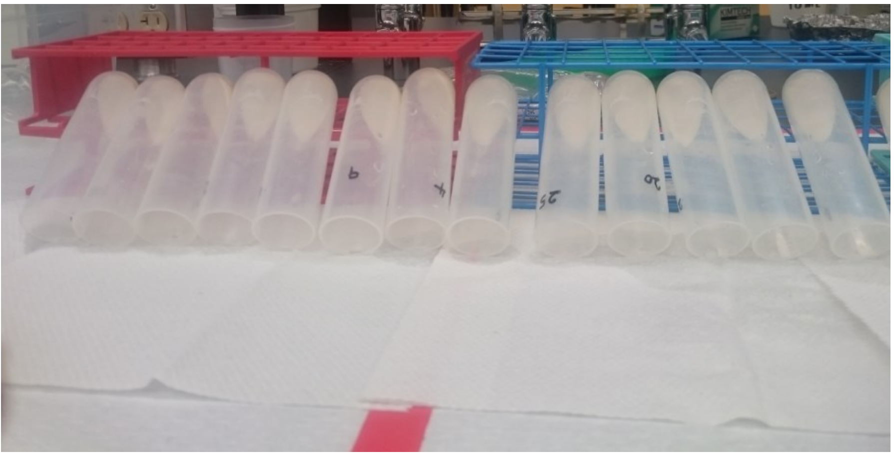

Figure 2. 4: Inversion of wet residue to ensure drainage

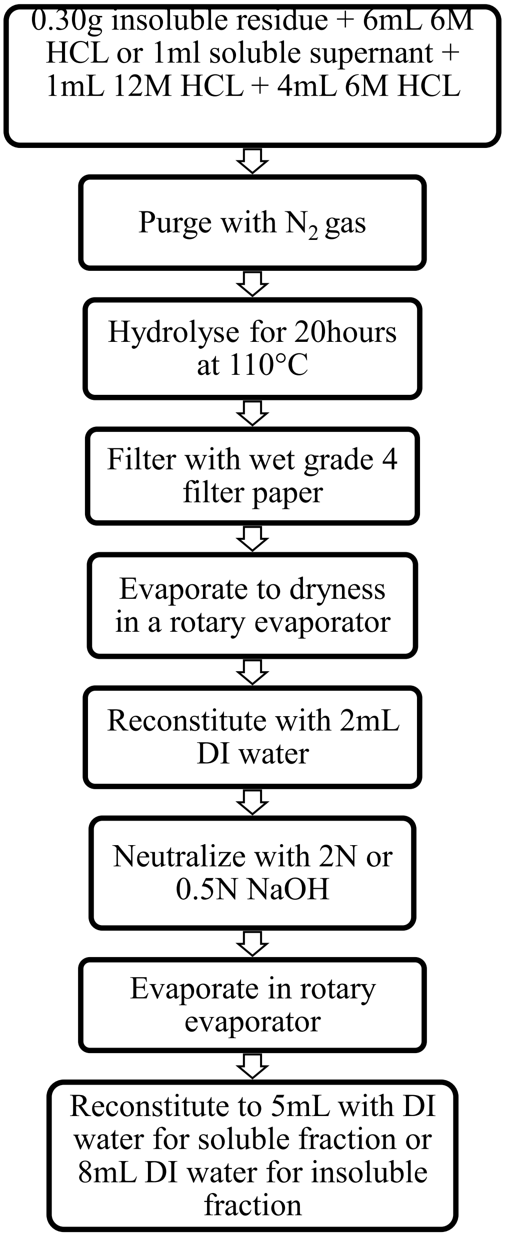

Figure 2. 5: Flow chart for acid hydrolysis and neutralization assay used in this study.

Figure 2. 6: Acid hydrolysis on a heating block

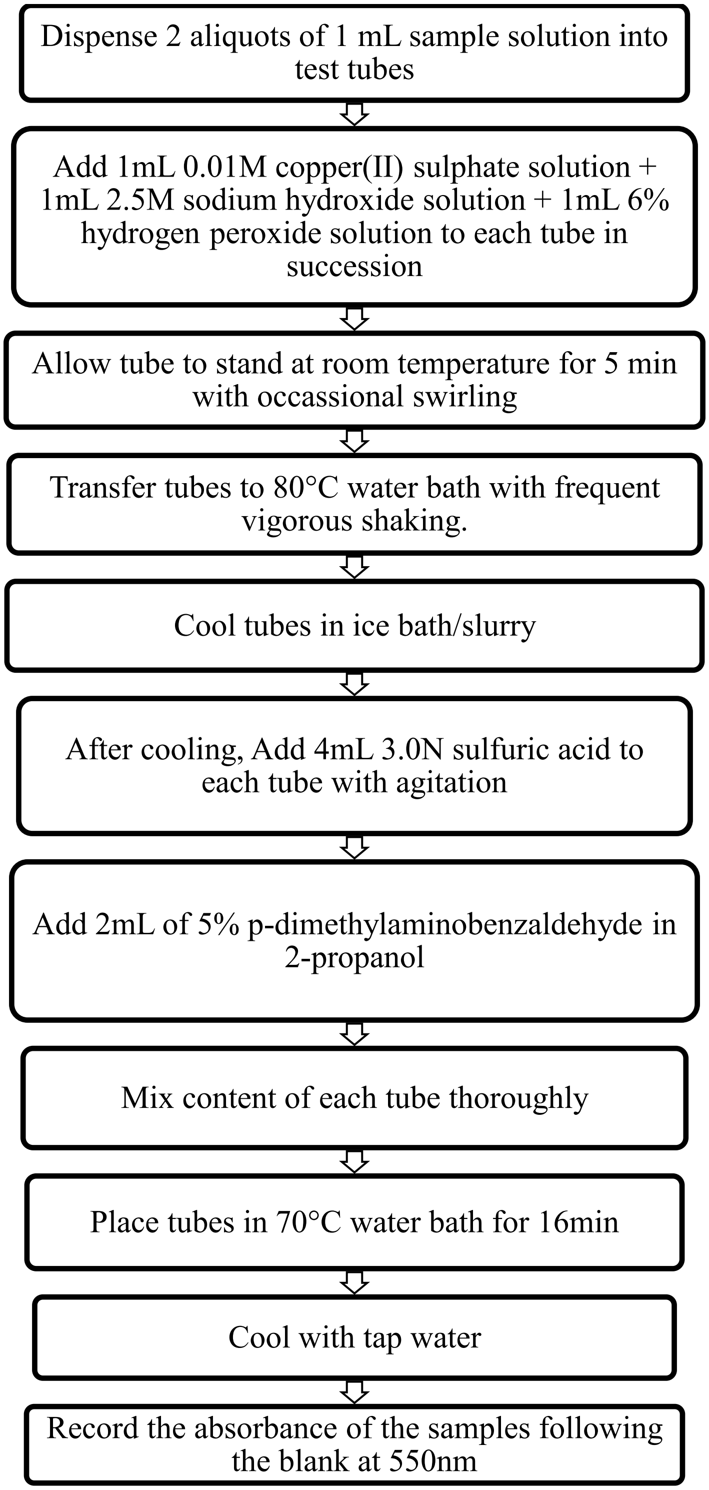

Figure 2. 7: Flow chart for assay for hydroxyproline determination.

2.7 Tables

Table 2. 1: Significance of fixed and random effects included in the models for the analysis of loin physical traits.

Trait	Fixed effects				Random effect
	Slaughter batch	Company	Sex	TCT[2]	Animal
Loin Weight (kg)	***[1]	***	ns	-	✓
Loin Eye Weight (kg)	***	***	ns	-	✓
Thick Fat (kg)	***	***	ns	-	✓
Meat Trim Weight (kg)	***	***	ns	-	✓
Fat Trim Weight (kg)	***	**	ns	-	✓
Rib Trim Weight (kg)	***	**	ns	-	✓
Bone/Neural Weight (kg)	***	***	ns	-	✓
Loin Eye percent (%)	***	***	ns	-	✓
Thick fat percent (%)	*	***	ns	-	✓
Rib trim percent (%)	***	***	ns	-	✓
Bone percent (%)	***	ns	ns	-	✓

[1] ns, *, **, ***, represent not significant, $p<0.10$, $p<0.05$ and $p<0.001$, respectively; [2] Total cooking time.

Table 2. 2: Significance of fixed and random effects included in the models for the analysis of meat quality traits.

Trait	Fixed effects				Random effect
	Slaughter batch	Company	Sex	TCT[2]	Animal
PH	***[1]	***	ns	-	✓
Cooking loss (%)	***	***	ns	**	✓
*L**	***	ns	ns	-	✓
*a**	***	*	ns	-	✓
*b**	***	***	ns	-	✓
Hue	***	**	ns	-	✓
Chroma	***	ns	ns	-	✓
Weight loss (%)	***	ns	ns	-	✓
Warner-Bratzler Shear force (N)	***	ns	ns	-	✓
Fat	***	*	ns	-	✓
Protein	***	ns	ns	-	✓
Moisture	***	**	ns	-	✓
Ether Extract	*	ns	ns	-	✓
Collagen solubility (%) in raw meat	***	*	ns	-	✓
Collagen insolubility (%) in raw meat	***	*	ns	-	✓
Total collagen mg/ g raw meat	***	ns	ns	-	✓

[1] ns, *, **, ***, represent not significant, $p<0.10$, $p<0.05$ and $p<0.001$ respectively; [2]total cooking time

Table 2. 3: Descriptive statistics of loin physical traits measured on frozen-thawed loin: abbreviations, number of animals (n) per measure trait, mean, standard deviation (SD), Minimum value (Min), Maximum value (Max), Coefficient of variation (CV).

Trait	Abbrev-iation	Pigs (n)	Mean	SD	Min	Max	CV (×100)
Loin Weight (kg)	LWT	500	1.42	0.17	1.11	1.81	11.82
Loin Eye Weight (kg)	LEW	500	0.54	0.07	0.40	0.68	12.53
Thick Fat Weight (kg)	TFW	500	0.32	0.08	0.15	0.49	24.45
Meat Trim Weight (kg)	MTW	455	0.23	0.05	0.10	0.49	23.74
Fat Trim Weight (kg)	FTW	456	0.12	0.04	0.04	0.35	36.15
Rib Trim Weight (kg)	RTW	500	0.32	0.05	0.21	0.47	14.95
Bone/Neural Weight (kg)	BWT	500	0.17	0.03	0.1	0.29	18.00
Loin Eye percent (%)	LEP	500	38.85	3.25	31.62	45.96	8.37
Thick fat percent (%)	TFP	500	23.59	4.18	15.95	32.98	17.71
Rib trim percent (%)	RTP	500	23.79	2.66	19.03	33.33	11.17
Bone percent (%)	BP	500	12.52	1.45	9.52	15.91	11.58

Table 2. 4: Descriptive statistics of meat quality and collagen traits measured on frozen-thawed loin: (standard deviation (SD), minimum value (Min), maximum value (Max), coefficient of variation (CV)).

Trait	Abbrev-iation	Pigs (n)	Mean	SD	Min	Max	CV (×100)
pH	-	500	5.56	0.14	5.20	5.92	-
Cooking loss (%)	CL	500	25.17	2.99	18.99	36.76	11.89
*L**	LOINL	500	45.46	3.02	37.23	55.18	7.55
*a**	LOINA	500	7.65	1.31	5.09	11.17	17.12
*b**	LOINB	500	3.50	1.14	1.07	7.48	32.50
Hue	LOINH	500	24.64	8.66	6.15	44.22	35.13
Chroma	LOINC	500	8.39	1.16	5.83	11.18	13.82
Chemical Moisture (%)	MC	500	72.21	0.73	70.81	73.96	1.01
Warner-Bratzler Shear force (N)	WBSF	500	47.16	10.05	21.62	84.68	24.00
FOSS fat	FOF	500	24.08	4.20	14.57	32.64	17.44
FOSS protein	FOP	500	16.79	1.19	14.33	19.98	7.08
FOSS moisture	FOM	500	57.42	3.23	50.63	64.87	5.62
Intramuscular fat	IMF	464	8.11	2.95	2.42	22.08	36.43
Collagen solubility (%) in raw meat	SOLC	499	18.03	6.59	1.98	34.28	36.52
Collagen insolubility (%) in raw meat	ISOLC	492	82.18	6.38	68.51	98.02	7.76
Total collagen (mg/ g raw meat)	TCOL	499	3.09	0.99	1.53	6.29	32.00

Table 2. 5: Heritabilities (h^2) among loin physical traits on frozen thawed three-rib pork loin sections with standard errors

Trait	h^2 ±se$^{(1)}$	$\sigma_e^{2(2)}$±se	$\sigma_a^{2(3)}$±se
Loin Weight (kg)	0.19±0.08	0.019±0.002	0.005±0.002
Loin Eye Weight (kg)	0.44±0.11	0.002±0.000	0.002±0.000
Thick Fat (kg)	0.16±0.10	0.004±0.000	0.001±0.000
Meat Trim Weight (kg)	0.30±0.11	0.001±0.000	0.000±0.000
Fat Trim Weight (kg)	0.13±0.09	0.001±0.000	0.000±0.000
Rib Trim Weight (kg)	0.31±0.11	0.001±0.000	0.001±0.000
Bone Weight (kg)	0.22±0.10	0.002±0.000	0.001±0.000
Loin Eye percent (%)	0.28±0.12	6.745 ±0.966	2.658±1.231
Thick fat percent (%)	0.42±0.13	9.445±1.752	6.83±2.495
Rib trim percent (%)	0.39±0.12	2.350±0.376	1.430±0.514
Bone percent (%)	0.09±0.08	1.645±0.161	0.165±0.153

(1)-Standard error; (2)-Residual variance; (3)-Additive genetic variance.

Table 2. 6: Heritabilities (h^2) of meat quality and collagen traits measured on frozen-thawed pork longissimus muscle with standard errors

Trait	$h^2 \pm se^{(1)}$	$\sigma_e^{2(2)}$±se	$\sigma_a^{2(3)}$±se
PH	0.12±0.08	0.116±0.01	0.002±0.001
Cooking loss (%)	0.24±0.10	4.226±0.503	1.242±0.589
$L*$	0.25±0.11	3.525±0.452	1.176±0.552
$a*$	0.42±0.11	0.559±0.092	0.394±0.130
$b*$	0.21±0.10	0.646±0.076	0.176±0.088
Hue	0.25±0.10	20.847±2.574	6.981±3.102
Chroma	0.36±0.11	0.689±0.106	0.384±0.144
Moisture content (%)	0.36±0.11	0.293±0.044	0.167±0.060
Warner-Bratzler shear force (N)	0.31±0.11	56.414±8.188	24.917±10.603
Crude Fat	0.24±0.10	11.904±1.462	3.721±1.747
Crude Protein	0.17±0.09	0.994±0.108	0.196±0.117
Crude Moisture	0.21±0.09	7.171±0.836	1.865±0.961
Collagen solubility (%) in raw meat	0.12±0.09	32.241±3.497	4.413±3.677
Collagen insolubility (%) in raw meat	0.15±0.09	29.409±3.289	5.084±3.555
Total collagen mg/ g raw meat	0.33±0.12	0.617±0.095	0.306±0.127
Intramuscular fat	0.42±0.13	4.851±0.913	3.541±1.297

(1)-Standard error; (2)-Residual variance; (3)-Additive genetic variance

Table 2. 7: Genetic (below diagonal) and phenotypic (above diagonal) correlation estimates and their standard errors among loin physical traits

Trait[1]	LWT	LEW	TFW	MTW	FTW	RTW	BWT	LEP	TFP	RTP	BP
LWT		**0.65** **±.02**	**0.56** **±.03**	**0.48** **±.04**	**0.50** **±.03**	**0.71** **±.02**	**0.49** **±.03**	**-0.20** **±.05**	**0.19** **±.05**	-0.04 ±.05	**-0.22** **±.04**
LEW	**0.87** **±.13**[2]		-0.04 ±.05	**0.51** **±.04**	**0.11** **±.05**	**0.51** **±.04**	**0.41** **±.04**	**0.47** **±.04**	**-0.37** **±.05**	0.01 ±.05	-0.05 ±.05
TFW	0.32 ±.36	-0.37 ±.29		-0.08 ±.05	**0.45** **±.04**	**0.30** **±.05**	0.12 ±.04	**-0.71** **±.02**	**0.88** **±.01**	**-0.27** **±.04**	**-0.34** **±.04**
MTW	**0.93** **±.22**	**0.61** **±.17**	-0.31 ±.36		-0.10 ±.05	**0.73** **±.02**	**0.44** **±.04**	**0.11** **± .05**	**-0.30** **±.05**	**0.52** **±.04**	0.09 ±.05
FTW	**0.64** **±.28**	0.06 ±.36	0.35 ±.42	0.30 ±.43		**0.61** **±.03**	0.09 ±.05	**-0.35** **±.04**	**0.28** **±.05**	**0.28** **±.05**	**-0.33** **±.04**
RTW	**0.76** **±.16**	**0.60** **±.16**	-0.14 ±.35	**0.92** **±.08**	**0.62** **±.25**		**0.44** **±.04**	**-0.16** **±.05**	-0.05 ±.05	**0.61** **±.03**	**-0.15** **±.05**
BWT	**0.77** **±.26**	**0.48** **±.23**	0.32 ±.39	**0.64** **±.22**	0.50 ±.44	**0.71** **±.19**		-0.07 ±.05	**-0.13** **±.05**	0.09 ±.05	**0.64** **±.02**
LEP	0.28 ±.39	**0.73** **±.14**	**-0.76** **±.14**	0.18 ±.30	**-0.80** **±.28**	0.10 ±.29	-0.13 ±.35		**-0.78** **±.02**	-0.01 ±.05	**0.12** **±.05**
TFP	-0.09 ±.38	**-0.60** **±.16**	**0.91** **±.06**	**-0.50** **±.22**	0.32 ±.35	**-0.50** **±.23**	-0.25 ±.29	**-0.76** **±.10**		**-0.37** **±.04**	**-0.35** **±.04**
RTP	-0.08 ±.40	0.21 ±.23	-0.48 ±.27	**0.76** **±.15**	0.44 ±.35	**0.84** **±.11**	0.43 ±.28	0.01 ±.29	**-0.66** **±.17**		0.04 ±.05
BP	0.35 ±.66	-0.02 ±.38	0.19 ±.67	0.12 ±.44	0.44 ±.82	0.32 ±.47	**0.77** **±.23**	-0.15 ±.47	-0.21 ±.39	0.36 ±.39	

[1] LWT=Loin Eye Weight; LEW= Loin Eye Weight; TFW= Thick Fat weight; MTW= Meat Trim Weight; FTW= Fat Trim Weight; RTW= Rib Trim Weight; BWT= Bone Weight; LEP= Loin Eye percent; TFP= Thick fat percent; RTP= Rib trim percent; BP= Bone percent. [2] Significant correlations (P < 0.05) are highlighted in bold.

Table 2. 8: Genetic (below diagonal) and phenotypic (above diagonal) correlation estimates among meat quality traits

Trait[1]	pH	CL	LOI NL	LOI NA	LOI NB	LOI NH	LOI NC	MC	WBSF[1]	FOF	FOP	FOM	IMF	SOLC	ISOLC	TCOL
PH		**-0.13 ±.05**	**-0.40 ±.04**	0.04 ±.05	**-0.32 ±.04**	**-0.37 ±.04**	-0.06 ±.05	**0.34 ±.04**	0.01 ±.05	0.05 ±.05	**-0.10 ±.05**	-0.02 ±.05	0.05 ±.05	-0.08 ±.04	0.09 ±.05	-0.10 ±.05
CL	**-0.65[2] ±.31**		0.07 ±.05	0.00 ±.05	0.05 ±.05	0.03 ±.05	0.01 ±.05	0.07 ±.05	**0.26 ±.04**	**-0.14 ±.05**	**0.14 ±.05**	**0.12 ±.05**	**-0.14 ±.05**	0.07 ±.05	-0.07 ±.05	0.05 ±.05
LOI NL	**-0.95 ±.35**	**0.44 ±.19**		**-0.24 ±.05**	**0.58 ±.03**	**0.74 ±.02**	-0.03 ±.05	**-0.39 ±.04**	**-0.16 ±.05**	**0.16 ±.05**	**-0.14 ±.05**	**-0.18 ±.05**	**0.27 ±.05**	**0.14 ±.05**	**-0.14 ±.05**	0.01 ±.05
LOI NA	0.20 ±.36	0.32 ±.27	**-0.53 ±.20**		**0.41 ±.04**	**-0.12 ±.05**	**0.94 ±.00**	**-0.18 ±.05**	-0.10 ±.05	0.08 ±.05	-0.08 ±.05	-0.07 ±.05	**0.21 ±.05**	-0.00 ±.05	0.02 ± .05	-0.03 ±.05
LOI NB	**-0.87 ±.31**	**0.69 ±.31**	**0.46 ±.22**	**0.49 ±.23**		**0.77 ±.02**	**0.65 ±.03**	**-0.54 ±.03**	**-0.13 ±.05**	**0.16 ±.05**	**-0.15 ±.05**	**-0.20 ±.04**	**0.40 ±.04**	0.06 ±.05	-0.06 ±.05	0.01 ±.05
LOI NH	**-0.93 ±.28**	0.48 ±.32	**0.85 ±.09**	-0.30 ±.25	**0.69 ±.15**		**0.15 ±.05**	**-0.33 ±.05**	**-0.13 ±.05**	**0.12 ±.05**	**-0.12 ±.05**	**-0.15 ±.05**	**0.29 ±.05**	0.06 ±.05	-0.08 ±.05	0.02 ±.05
LOI NC	0.06 ±.37	0.30 ±.28	-0.43 ±.25	**0.97 ±.02**	**0.64 ±.17**	-0.15 ±.29		**-0.33 ±.05**	**-0.14 ±.05**	**0.11 ±.05**	**-0.13 ±.05**	**-0.11 ±.05**	**0.30 ±.05**	0.01 ±.05	-0.01 ±.05	-0.04 ±.05
MC	**0.98 ±.27**	0.32 ±.34	-0.39 ±.28	-0.10 ±.24	**-0.76 ±.17**	**-0.62 ±.21**	-0.25 ±.23		0.06 ±.05	**-0.27 ±.05**	**0.20 ±.05**	**0.35 ±.04**	**-0.61 ±.03**	-0.02 ±.05	0.04 ±.05	0.03 ±.05
WBSF	0.01 ±.42	**0.45 ±. 19**	-0.22 ±.29	0.08 ±.28	0.04 ±.34	-0.23 ±.31	0.01 ±.30	-0.21 ±.28		**-0.22 ±.04**	**0.20 ±.04**	**0.17 ±.05**	**-0.13 ±.05**	-0.05 ±.05	0.06 ±.05	0.04 ±.05
FOF	-0.20 ±.42	-0.43 ±.31	0.35 ±.27	-0.55 ±.28	0.06 ±.34	0.32 ±.30	-0.54 ±.28	-0.39 ±.26	-0.20 ±.32		**-0.93 ±.00**	**-0.99 ±.00**	**0.45 ±.04**	-0.01 ±.05	0.01 ±.05	-0.00 ±.05
FOP	0.04 ±.47	0.33 ±.36	-0.08 ±.34	0.40 ±.34	0.16 ±.40	-0.25 ±.35	0.40 ±.35	0.05 ±.32	0.33 ±.36	**-0.93 ±.05**		**0.90 ±.01**	**-0.45 ±.04**	0.01 ±.05	-0.01 ±.05	-0.00 ±.05
FOM	0.40 ±.44	0.32 ±.34	-0.37 ±.32	**0.62 ±.30**	-0.15 ±.35	-0.40 ±.31	0.56 ±.30	**0.63 ±.22**	-0.00 ±.35	**-0.98 ±.01**	**0.86 ±.09**		**-0.47 ±.04**	-0.02 ±.05	0.02 ±.05	0.03 ±.05
IMF	0.15 ±.36	-0.20 ±.28	0.12 ±.26	0.17 ±.23	**0.61 ±.22**	0.40 ±.25	0.25 ±.24	**-0.64 ±.14**	-0.02 ±.30	**0.79 ±.14**	**-0.67 ±.18**	**-0.83 ±.13**		-0.05 ±.05	0.05 ±.05	0.01 ±.05
SOLC	-0.72 ±.64	-0.10 ±.43	**0.68 ±.30**	-0.50 ±.39	0.00 ±.45	0.66 ±.50	-0.40 ±.41	-0.60 ±.43	**-0.38 ±.10**	0.17 ±.42	-0.33 ±.45	-0.17 ±.45	0.37 ±.41		N.E*	**-0.46 ±.04**

ISOLC	0.76 ±.56	0.11 ±.40	**-0.71** **±.35**	0.45 ±.33	-0.12 ±.42	-0.57 ±.41	0.34 ±.36	0.60 ±.38	**0.42** **±.16**	-0.12 ±.40	0.16 ±.44	0.12 ±.42	-0.35 ±.37	N.E		**0.48** **±.04**
TCOL	0.03 ±.41	0.07 ±.32	-0.08 ±.28	0.12 ±.26	0.31 ±.32	0.06 ±.30	0.06 ±.28	0.17 ±.27	0.10 ±.31	0.19 ±.32	-0.08 ±.37	-0.17 ±.34	-0.21 ±.26	**-0.60** **±.23**	**0.66** **±.28**	

1-CL= Cooking loss (%); LOINL=Minolta *L**; LOINA=Minolta *a**; LOINB= Minolta *b**; LOINH= Minolta hue; LOINC= Minolta chroma; MC= Moisture content (%); WBSF= Warner-Bratzler shear force (N); FOF= FOSS crude fat; FOP= FOSS crude protein; FOM= FOSS crude moisture; IMF= Intramuscular fat; SOLC= Soluble collagen percent (%) raw meat; ISOLC= Insoluble collagen percent (%) raw meat; TCOL= Total collagen mg/g raw meat. 2-Significant correlations ($P < 0.05$) are highlighted in bold.

*Not estimable-ASReml assumes the 2 traits are not perfectly correlated, but here, the 2 traits are perfectly correlated, one is a simple transformation of the other, soluble collagen percent =100-insoluble collagen percent; consequently, the two US matrices are singular and cannot be inverted. Thus, variance components for the two traits are the same.

Table 2. 9: Phenotypic correlation between sub primal and meat quality

Trait[1]	LWT	LEW	TFW	MTW	FTW	RTW	BWT	LEP	TFP	RTP	BP
PH	**0.13[2]**	0.08	0.09	0.08	0.05	**0.10**	0.09	0.01	**0.10**	-0.04	-0.06
	±.04	±.05	±.04	±.05	±.05	**±.05**	±.04	±.05	**±.05**	±.03	±.04
CL	-0.02	**0.12**	**-0.12**	**0.24**	-0.03	0.09	0.03	0.09	**-0.17**	**0.12**	0.01
	±.05	**±.05**	**±.05**	**±.05**	±.05	±.05	±.01	±.05	**±.05**	**±.05**	±.00
LOINL	-0.02	**-0.11**	0.04	-0.08	0.00	-0.06	-0.01	-0.08	0.04	-0.03	0.01
	±.05	**±.05**	±.05	±.05	±.05	±.05	±.05	±.05	±.05	±.05	±.05
LOINA	0.04	**-0.15**	**0.15**	-0.05	**0.13**	0.03	0.02	**-0.24**	**0.18**	-0.03	-0.02
	±.05	**±.05**	**± .05**	±.05	**±.05**	±.05	±.05	**±.05**	**±.05**	±.05	±.05
LOINB	0.02	**-0.16**	**0.18**	-0.09	0.08	-0.02	0.01	**-0.24**	**0.17**	-0.05	-0.04
	±.05	**±.05**	**±.05**	±.05	±.05	±.05	±.05	**±.05**	**±.05**	±.05	±.05
LOINH	-0.00	-0.09	0.08	-0.06	0.03	-0.03	0.04	**-0.11**	0.05	-0.03	0.02
	±.05	±.05	±.05	±.05	±.05	±.05	±.05	**±.05**	±.05	±.05	±.05
LOINC	0.06	**-0.14**	**0.19**	-0.05	**0.14**	0.03	0.05	**-0.26**	**0.20**	-0.05	-0.02
	±.05	**±.05**	**±.05**	±.05	**±.05**	±.05	±.05	**±.05**	**±.05**	±.05	±.05
MC	0.07	**0.24**	**-0.13**	**0.20**	-0.10	0.10	0.05	**0.25**	**-0.20**	0.08	0.08
	±.05	**±.05**	**±.05**	**±.05**	±.05	±.05	±.05	**±.05**	**±.05**	±.05	±.05
WBSF	-0.09	0.08	**-0.23**	**0.11**	**-0.18**	-0.10	-0.04	**0.21**	**-0.24**	-0.01	0.05
	±.04	±.05	**±.04**	**±.05**	**±.05**	±.05	±.04	**±.05**	**±.05**	±.05	±.04
FOF	**0.18**	**-0.16**	**0.52**	**-0.41**	**0.56**	0.06	-0.07	**-0.49**	**0.58**	**-0.19**	**-0.24**
	±.04	**±.05**	**±.03**	**±.04**	**±.03**	±.05	±.05	**±.04**	**±.03**	**±.05**	**±.04**
FOP	**-0.16**	**0.17**	**-0.50**	**0.33**	**-0.60**	-0.10	0.02	**0.47**	**-0.53**	**0.13**	**0.18**
	±.04	**±.05**	**±.03**	**±.04**	**±.03**	±.05	±.05	**±.04**	**±.03**	**±.05**	**±.04**
FOM	**-0.13**	**0.16**	**-0.51**	**0.42**	**-0.55**	-0.05	0.07	**0.47**	**-0.57**	**0.18**	**0.26**
	±.04	**±.05**	**±.03**	**±.04**	**±.03**	±.05	±.05	**±.04**	**±.03**	**±.05**	**±.04**
SOLC	-0.04	0.04	-0.09	-0.03	0.00	-0.02	0.02	0.09	-0.08	0.02	0.06
	±.05	±.05	±.05	±.05	±.05	±.05	±.04	±.05	±.05	±.05	±.04
ISOLC	0.03	-0.07	0.10	0.01	-0.01	-0.00	-0.01	**-0.12**	0.10	-0.03	-0.05
	±.05	±.05	±.05	±.05	±.05	±.05	±.05	**±.05**	±.05	±.05	±.05
TCOL	-0.01	-0.09	0.03	-0.03	0.06	0.02	-0.03	-0.09	0.00±	0.06	-0.02
	±.05	±.05	±.05	±.05	±.05	±.05	±.05	±.05	.05	±.05	±.05
IMF	0.07	**-0.26**	**0.35**	**-0.21**	**0.23**	-0.03	-0.06	**-0.38**	**0.44**	**-0.18**	**-0.15**

	±.05	**±.05**	**±.04**	**±.05**	**±.05**	±.05	±.05	**±.05**	**±.04**	**±.05**	**± .05**

[1] LWT=Loin Eye Weight; LEW= Loin Eye Weight; TFW= Thick Fat weight; MTW= Meat Trim Weight; FTW= Fat Trim Weight; RTW= Rib Trim Weight; BWT=Bone Weight; LEP= Loin Eye percent; TFP= Thick fat percent; RTP= Rib trim percent; BP= Bone percent; CL= Cooking loss (%); LOINL=Minolta $L*$; LOINA=Minolta $a*$; LOINB= Minolta $b*$; LOINH= Minolta hue; LOINC= Minolta chroma; MC= Moisture content (%); WBSF= Warner-Bratzler shear force (N); FOF= FOSS crude fat; FOP= FOSS crude protein; FOM= FOSS crude moisture; IMF= Intramuscular fat; SOLC= Soluble collagen percent (%) raw meat; ISOLC= Insoluble collagen percent (%) raw meat; TCOL= Total collagen mg/g raw meat. [2] Significant correlations ($P < 0.05$) are highlighted in bold.

Table 2. 10**:** Genetic correlation between loin physical and meat quality traits

Trait[1]	LWT	LEW	TFW	MTW	FTW	RTW	BWT	LEP	TFP	RTP	BP
PH	-0.30 ±.54	-0.24 ±.35	0.14 ±.49	0.26 ±.38	-0.32 ±.56	0.06 ±.39	0.24 ±.42	-0.58 ±.40	0.30 ±.35	0.08 ±.38	0.56 ±.62
CL	-0.42 ±.42	-0.33 ±.26	**-0.41 ±.16**[2]	**0.64 ±.27**	-0.06 ±.45	0.20 ±.30	0.20 ±.34	-0.33 ±.31	-0.10 ±.29	**0.68 ±.23**	0.34 ±.42
LOINL	0.22 ±.40	0.20 ±.24	-0.07 ±.35	0.10 ±.30	0.38 ±.41	-0.08 ±.28	-0.24 ±.32	**0.53 ±.26**	-0.36 ±.24	-0.04 ±.26	-0.52 ±.44
LOINA	-0.19 ±.35	**-0.37 ±.12**	-0.21 ±.35	0.26 ±.30	-0.01 ±.38	0.08 ±.26	0.35 ±.32	**-0.58 ±.19**	0.17 ±.23	0.13 ±.25	0.20 ±.41
LOINB	0.61 ±.51	0.25 ±.32	-0.18 ±.43	0.40 ±.36	0.76 ±.39	0.56 ±.35	0.39 ±.38	-0.05 ±.32	-0.39 ±.31	0.15 ±.31	0.01 ±.48
LOINH	0.23 ±.44	0.31 ±.27	-0.27 ±.39	0.19 ±.33	0.60 ±.39	0.11 ±.31	0.31 ±.35	0.29 ±.31	**-0.50 ±.25**	0.02 ±.28	0.25 ±.45
LOINC	-0.11 ±.38	-0.25 ±.22	-0.29 ±.36	0.34 ±.31	-0.04 ±.39	0.05 ±.27	0.56 ±.33	-0.35 ±.25	-0.09 ±.27	0.03 ±.26	0.47 ±.45
MC	0.01 ±.40	-0.10 ±.25	0.20 ±.35	0.17 ±.27	**-0.65 ±.28**	-0.09 ±.28	-0.15 ±.31	-0.19 ±.29	0.23 ±.25	0.08 ±.25	0.06 ±.40
WBSF	**0.36 ±. 12**	0.23 ±.26	0.28 ±.38	0.45 ±.29	-0.41 ±.42	0.23 ±.30	0.21 ±.35	-0.30 ±.32	0.05 ±.29	-0.02 ±.29	-0.27 ±.47
FOF	-0.06 ±.45	**-0.30 ±.10**	**0.55 ±.25**	-0.47 ±.26	**0.73 ±.24**	-0.19 ±.31	-0.12 ±.34	**-0.41 ±.15**	**0.55 ±.20**	-0.41 ±.27	-0.10 ±.46
FOP	**0.50 ±.15**	**0.52 ±. 20**	-0.26 ±.37	0.57 ±.29	**-0.71 ±.27**	0.50 ±.34	-0.07 ±.39	**0.47 ±.16**	**-0.52 ±.23**	0.51 ±.29	-0.79 ±.76
FOM	0.15 ±.48	0.26 ±.27	**-0.52 ±.18**	**0.53 ±.26**	**-0.70 ±.27**	0.23 ±.32	0.07 ±.36	**0.38 ±.17**	**-0.53 ±.21**	0.44 ±.29	0.07 ±.49
SOLC	0.02 ±.58	0.00 ±.36	-0.06 ±.51	-0.13 ±.42	0.36 ±.53	-0.10 ±.42	-0.04 ±.46	0.06 ±.43	0.23 ±.39	-0.17 ±.40	**-0.25 ±. 11**
ISOLC	-0.19 ±.53	-0.15 ±.33	0.20 ±.47	0.02 ±.39	-0.42 ±.49	-0.09 ±.38	0.12 ±.43	-0.21 ±.40	-0.04 ±.36	-0.00 ±.36	**0.53 ±. 10**

TCOL	-0.18 ±.40	**-0.32 ±.13**	0.43 ±.37	-0.24 ±.29	0.20 ±.41	-0.03 ±.29	0.03 ±.32	-0.40 ±.30	0.03 ±.28	0.03 ±.27	**0.51 ±. 27**
IMF	0.29 ±.39	-0.04 ±.25	**0.53 ±.26**	-0.29 ±.26	**0.66 ±.31**	-0.05 ±.27	0.22 ±.34	-0.34 ±.25	**0.43 ±.21**	**-0.54 ±. 22**	0.16 ±.48

[1] LWT=Loin Weight; LEW= Loin Eye Weight; TFW= Thick Fat weight; MTW= Meat Trim Weight; FTW= Fat Trim Weight; RTW= Rib Trim Weight; BWT= Bone Weight; LEP= Loin Eye percent; TFP= Thick fat percent; RTP= Rib trim percent; BP= Bone percent; CL= Cooking loss (%); LOINL=Minolta L^*; LOINA=Minolta a^*; LOINB= Minolta b^*; LOINH= Minolta hue; LOINC= Minolta chroma; MC= Moisture content (%); WBSF= Warner-Bratzler shear force (N); FOF= FOSS crude fat; FOP= FOSS crude protein; FOM= FOSS crude moisture; IMF= Intramuscular fat; SOLC= Soluble collagen percent (%) raw meat; ISOLC= Insoluble collagen percent (%) raw meat; TCOL= Total collagen (mg/g raw meat)

[2] Significant correlations ($P < 0.05$) are highlighted in bold.

2.8 References

Aaslyng, M. D., Bejerholm, C., Ertbjerg, P., Bertram, H. C., and Andersen, H. J. (2003). Cooking loss and juiciness of pork in relation to raw meat quality and cooking procedure. Food Quality and Preference, 14(4), 277-288. doi:10.1016/S0950-3293(02)00086-1.

Abdallah, B.M., Marchello, J. A., and Ahmad, H. A. (1999). Effect of freezing and microbial growth on myoglobin derivatives of beef. Journal of Agricultural and Food Chemistry, 47(10), 4093-4099. doi:10.1021/jf9809434.

Aass, L. (1996). Variation in carcass and meat quality traits and their relations to growth in dual purpose cattle. Livestock Production Science, 46(1), 1-12. doi:10.1016/0301-6226(96)00005-X.

Aitken, A and Learmonth, M. (1996). Quantitation of tryptophan in proteins. in: The protein protocols handbook. In M. J. Walker (Ed.), (pp. 29) Humana Press.

Allen, E., Forrest, J. C., Chapman, A. B., First, N., Bray, R. W., and Briskey, E. J. (1966). Phenotypic and genetic associations between porcine muscle properties. Journal of Animal Science, 25(4), 962-966. doi:10.2527/jas1966.254962x.

American Meat Science Association (AMSA) (1995). Research guidelines for cookery, sensory evaluation, and instrumental tenderness measurements of fresh meat. Chicago: Published by American Meat Science Association in cooperation with National Livestock and Meat Board.

AMSA. (2012). AMSA meat color measurement guidelines. Pp: 1-12.

Ando, M., Nakagishi, Y., Yoshida, K., Nakao, M., Nakagawa, T., Makinodan, Y. and Kawasaki, K. (2006). Pyridinoline concentrations in muscular and skin collagen of fish and relationship between collagen solubility and pyridinoline concentration in fish muscular collagen. Fisheries Science, 72(5), 1104-1108. doi:10.1111/j.1444-2906.2006.01262.x.

Archile-Contreras, A. C., Mandell, I. B., and Purslow, P. P. (2010). Disparity of dietary effects on collagen characteristics and toughness between two beef muscles. Meat Science, 86(2), 491-497. doi:10.1016/j.meatsci.2010.05.041.

Arthur R. Gilmour, Robin Thompson, and Brian R. Cullis. (1995). Average information REML: An efficient algorithm for variance parameter estimation in linear mixed models. Biometrics, 51(4), 1440-1450. doi:10.2307/2533274.

Barbanti, D., and Pasquini, M. (2005). Influence of cooking conditions on cooking loss and tenderness of raw and marinated chicken breast meat. LWT - Food Science and Technology, 38(8), 895-901. doi:10.1016/j.lwt.2004.08.017.

Bacon, C. D., Loveday, H. D., Pace, R. D., and Riemann, M. J. (1989). Prediction of pork carcass composition by the pork loin 3-6 rib section. Journal of Animal Science, 67(9), 2328-2332. doi:10.2527/jas1989.6792328x.

Baker, L. C., Lampitt, L. H., and Brown, K. P. (1953). Connective tissue of meat. II.—Determination of hydroxyproline. Journal of the Science of Food and Agriculture, 4(4), 165-172. doi:10.1002/jsfa.2740040402.

Barton-Gade, P. A., Demeyer, D., Honikel, K. O., Joseph, R. L., Puolanne, E., Severini, M., Smulders, F. and Tornberg, E. (1993). Final version (I) of reference methods for water holding capacity in meat and meat products. Procedures Recommended by an OECD Working Group and Presented at the 39th ICoMST in 1993. in: Proceedings 39th Intern. Congress of Meat Science and Technology, Calgary, Canada, File S4, PO2.WP.

Bekhit, A. E. D., and Faustman, C. (2005). Metmyoglobin reducing activity. Meat Science, 71(3), 407-439. doi:10.1016/j.meatsci.2005.04.032.

Bendall, J. R., and Swatland, H. J. (1988). A review of the relationships of pH with physical aspects of pork quality. Meat Science, 24(2), 85-126. doi:10.1016/0309-1740(88)90052-6.

Bidanel, J., Ducos, A., Labroue, F., Guéblez, R., and Gasnier, C. (1994). Genetic parameters of backfat thickness, age at 100 kg and meat quality traits in Pietrain pigs. Annales de zootechnie, 43(2), 141-149. Retrieved from https://hal.archives-ouvertes.fr/hal-00888966.

Biela, E., Galas, J., Lee, B., Johnson, G. L., Darzynkiewicz, Z., and Dobrucki, J. W. (2013). Col-F, a fluorescent probe for ex vivo confocal imaging of collagen and elastin in animal tissues. Cytometry Part A, 83A(6), 533-539. doi:10.1002/cyto.a.22264.

Bourdon, R. M. (2013). Understanding animal breeding. Pearson Education. Pp1-111.

Bouton, P. E., Ford, A. L., Harris, P. V., and Ratcliff, D. (1975). Objective-subjective assessment of meat tenderness. Journal of Texture Studies, 6(3), 315-328. doi:10.1111/j.1745-4603.1975.tb01128.x.

Boutten, B., Brazier, M., Morche, N., Morel, A. and Vendeuvre, J.L (2000). Effects of animal and muscle characteristics on collagen and consequences for ham production. Meat Science, 55(2), 233-238. doi: https://doi.org/10.1016/S0309-1740(99)00148-5.

Bratzler, L. J. (1932). Measuring the tenderness of meat by means of a mechanical shear. M.S. Thesis.Pp1-33.

Brewer, M. S., Novakofski, J., and Freise, K. (2006). Instrumental evaluation of pH effects on ability of pork chops to bloom. Meat Science, 72(4), 596-602. doi:10.1016/j.meatsci.2005.09.009.

Brewer, M. S., Zhu, L. G., Bidner, B., Meisinger, D. J., and McKeith, F. K. (2001). Measuring pork color: Effects of bloom time, muscle, pH and relationship to instrumental parameters. Meat Science, 57(2), 169-176. doi:10.1016/S0309-1740(00)00089-9.

Buck, S. F., Harrington, G., and Johnson, R. F. (1962). The prediction of lean percentage of pigs of bacon weight from carcass measurements. Animal Science, 4(1), 25-36. doi:10.1017/S0003356100034371.

Cabling, M. M., Kang, H. S., Lopez, B. M., Jang, M., Kim, H. S., Nam, K. C. and Seo, K. S. (2015). Estimation of genetic associations between production and meat quality traits in duroc pigs. Asian-Australasian Journal of Animal Sciences, 28(8), 1061-1065. doi:10.5713/ajas.14.0783.

Cai, J., Chen, Q., Wan, X., and Zhao, J. (2011). Determination of total volatile basic nitrogen (TVB-N) content and Warner–Bratzler shear force (WBSF) in pork using fourier transform near infrared (FT-NIR) spectroscopy. Food Chemistry, 126(3), 1354-1360. doi:10.1016/j.foodchem.2010.11.098.

Cameron, N. D. (1990). Genetic and phenotypic parameters for carcass traits, meat and eating quality traits in pigs. Livestock Production Science, 26(2), 119-135. doi:10.1016/0301-6226(90)90061-.

Cameron, N. D., Warriss, P. D., Porter, S. J., and Enser, M. B. (1990). Comparison of duroc and british landrace pigs for meat a and eating quality. Meat Science, 27(3), 227-247. doi:10.1016/0309-1740(90)90053-9.

Canadian Council on Animal Care. (1993). In Olfert, E.D., Cross, B.M. and McWilliams, A.A, (Ed.), Guide to the care and use of experimental animals Can Counc Anim Care, Ottawa, Ontario, Canada.

Cherel, P., Herault, F., Vincent, A., Le Roy, P., and Damon, M. (2012). Genetic variability of transcript abundance in pig skeletal muscle at slaughter: Relationships with meat quality traits. Journal of Animal Science, 90(3), 699-708. doi:10.2527/jas.2011-4198.

Cifuni, G., Amici, A., Contò, M., Viola, P., and Failla, S. (2014). Effects of the hunting method on meat quality from fallow deer and wild boar and preliminary studies for predicting lipid oxidation using visible reflectance spectra. European Journal of Wildlife Research, 60(3), 519-526. doi:10.1007/s10344-014-0814-3.

Ciobanu, D.C., Lonergan, S.M and Huff-Lonergan, E.J. (2011). Genetics of meat quality and carcass traits. In Rothschild, M.F and Ruvinsky, A (Ed.), The genetics of the pig (pp. 355-390) CAB International.

Clark, A. L., Slayden, O. D., Hettrich, K. and Brenner, R. M. (2005). Estrogen increases collagen I and III mRNA expression in the pelvic support tissues of the rhesus macaque. American

Journal of Obstetrics and Gynecology, 192(5), 1523-1529. doi:10.1016/j.ajog.2004.11.042.

Colgrave, M. L., Allingham, P. G., Tyrrell, K. and Jones, A. (2012). Multiple reaction monitoring for the accurate quantification of amino acids: Using hydroxyproline to estimate collagen content. Methods in Molecular Biology (Clifton, N.J.), 828, 291. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/22125153.

Correa, J. A., Faucitano, L., Laforest, J. P., Rivest, J., Marcoux, M. and Gariépy, C. (2006). Effects of slaughter weight on carcass composition and meat quality in pigs of two different growth rates. Meat Science, 72(1), 91-99. doi:10.1016/j.meatsci.2005.06.006.

Cross, H. R., Carpenter, Z. L., and Smith, G. C. (1973). Effects of intramuscular collagen and elastin on bovine muscle tenderness. Journal of Food Science, 38(6), 998-1003. doi:10.1111/j.1365-2621.1973.tb02133.x.

De Vries, A. G., van der Wal, P. G., Long, T., Eikelenboom, G., and Merks, J. W. M. (1994). Genetic parameters of pork quality and production traits in Yorkshire populations. Livestock Production Science, 40(3), 277-289. doi:10.1016/0301-6226(94)90095-7.

DeVol, D. L., McKeith, F. K., Bechtel, P. J., Novakofski, J., Shanks, R. D. and Carr, T. R. (1988). Variation in composition and palatability traits and relationships between muscle characteristics and palatability in a random sample of pork carcasses. Journal of Animal Science, 66(2), 385. doi:10.2527/jas1988.662385x.

Dikeman, M. E., Reddy, G. B., Arthaud, V. H., Tuma, H. J., Koch, R. M., Mandigo, R. W., and Axe, J. B. (1986). Longissimus muscle quality, palatability and connective tissue histological characteristics of bulls and steers fed different energy levels and slaughtered at four ages. Journal of Animal Science, 63(1), 92-101. doi:10.2527/jas1986.63192x.

Dransfield, E. (1977). Intramuscular composition and texture of beef muscles. Journal of the Science of Food and Agriculture, 28(9), 833-842. doi:10.1002/jsfa.2740280910.

Dransfield, E., Casey, J. C., Boccard, R., Touraille, C., Buchter, L., Hood, D. E. and Tinbergen, B. J. (1983). Comparison of chemical composition of meat determined at eight laboratories. Meat Science, 8(2), 79-92. doi:10.1016/0309-1740(83)90008-6.

Enfield, F. D., and Whatley, J. A., Jr. (1961). Heritability of carcass length, carcass backfat thickness and loin lean area in swine. Journal of Animal Science, 20(3), 631-634. doi:10.2527/jas1961.203631x.

Etherington, D. J., and Sims, T. J. (1981). Detection and estimation of collagen. Journal of the Science of Food and Agriculture, 32(6), 539-546. doi:10.1002/jsfa.2740320603.

Fan. F.Y. (2016). Fincal: Package for time value of money calculation, time series analysis and computational finance [computer software] Zenodo.

Fang, S. H., Nishimura, T. and Takahashi, K. (1999). Relationship between development of intramuscular connective tissue and toughness of pork during growth of pigs. Journal of Animal Science, 77(1), 120. doi:10.2527/1999.771120x.

Fernandez, X., Sante, V., Baeza, E., Lebihan-Duval, E., Berri, C., Remignon, H. and Astruc, T. (2001). Post mortem muscle metabolism and meat quality in three genetic types of turkey. British Poultry Science, 42(4), 462-469. doi:10.1080/00071660120070604.

Francisco Penagaricano, Bruno D Valente, Juan P Steibel, Ronald O Bates, Catherine W Ernst, Hasan Khatib, and Guilherme JM Rosa. (2015). Exploring causal networks underlying fat deposition and muscularity in pigs through the integration of phenotypic, genotypic and transcriptomic data. BMC Systems Biology, 9(1), 58. doi:10.1186/s12918-015-0207-6.

Fredeen, H. T., and Newman, J. A. (1962). Rib and vertebral numbers in swine.: I. variation observed in a large population. Canadian Journal of Animal Science, 42(2), 232-239. doi:10.4141/cjas62-036.

Freise, K., Brewer, S., and Novakofski, J. (2005). Duplication of the pale, soft, and exudative condition starting with normal postmortem pork. Journal of Animal Science, 83(12), 2843-2852. doi:10.2527/2005.83122843x.

García-Celdrán, M., Ramis, G., Manchado, M., Estévez, A., Navarro, A. and Armero, E. (2015). Estimates of heritabilities and genetic correlations of raw flesh quality traits in a reared gilthead sea bream (sparus aurata L.) population sourced from broodstocks along the spanish coasts. Aquaculture, 446, 181-186. doi:10.1016/j.aquaculture.2015.04.030.

Gilmour, A. R., Gogel, B. J., Cullis, B. R., Welham, S. J. and Thompson, R. (2015). ASReml user guide release 4.1 structural specification. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK, Retrieved from www.vsni.co.uk.

Gjerlaug-Enger, E., Aass, L., Ødegård, J. and Vangen, O. (2010). Genetic parameters of meat quality traits in two pig breeds measured by rapid methods. Animal, 4(11), 1832-1843.doi:10.1017/S175173111000114X.

Goodnight. C.J. (2010). Adaptive landscapes and optimality. In Michael D. Breed, Janice Moore (Ed.), Encyclopedia of animal behavior (pp. 24-29) Academic press. doi: https://doi.org/10.1016/B978-0-08-045337-8.00111-X. Retrieved from https://search.credoreference.com/content/entry/estab/adaptive_landscapes_and_optimality.

Gorjanc, G., Bijma, P., and Hickey, J. M. (2015). Reliability of pedigree-based and genomic evaluations in selected populations. Genetics, Selection, Evolution, 47(1), 65. doi:10.1186/s12711-015-0145-1.

Greaser, M.L and Guo, W. (2015). Proteins. In Leo M.L. Nollet, & Fidel Toldrá (Eds.), Handbook of food analysis (Third edition ed., pp. 357-369). Boca Raton, FL: CRC Press, Taylor & Francis Group. Retrieved from https://ebookcentral.proquest.com/lib/[SITE_ID]/detail.action?docID=3563647.

Gross J and Ligges U. (2015). Nortest: Tests for normality. R Package Version 1.0-4, Retrieved from https://CRAN.R-project.org/package=nortest.

Hamm, R. (1986). 4 - functional properties of the myofibrillar system and their measurements. In P.J. Bechtel (Ed.), Muscle as food (pp. 135-199) Elsevier Inc. doi:10.1016/B978-0-12-084190-5.50009-6.

Hamzah, A., Nguyen, N. H., Mekkawy, W., Ponzoni, R. W., Khaw, H. L., Yee, H. Y. and Mohd Nor, S. A. (2016). Flesh characteristics: Estimation of genetic parameters and correlated responses to selection for growth rate in the GIFT strain. Aquaculture Research, 47(7), 2139-2149. doi:10.1111/are.12667.

Health Canada. (2015). General food tips. safe internal cooking temperatures chart. Retrieved from Health Canada Website. Https://Www.Canada.Ca/En/Health-Canada/Services/General-Food-Safety-Tips/Safe-Internal-Cooking-Temperatures-Chart.Html.

Hermesch, S., Luxford, B. G., and Graser, H. -. (2000). Genetic parameters for lean meat yield, meat quality, reproduction and feed efficiency traits for australian pigs: 1. description of traits and heritability estimates. Livestock Production Science, 65(3), 239-248. doi:10.1016/S0301-6226(00)00150-0.

Heymann, H., Hedrick, H. B., Karrasch, M. A., Eggeman, M. K., and Ellersieck, M. R. (1990). Sensory and chemical characteristics of fresh pork roasts cooked to different endpoint temperatures. Journal of Food Science, 55(3), 613-617. doi:10.1111/j.1365-2621.1990.tb05189.x.

Hill, F. (1966). The solubility of intramuscular collagen in meat animals of various ages. Journal of Food Science, 31(2), 161-166. doi:10.1111/j.1365-2621.1966.tb00472.x.

Hill, W. G. (2001). Genetic correlation. In Sydney Brenner, Jefferey H. Miller (Ed.), Encyclopedia of genetics (pp. 823-825) Academic press. doi:https://doi.org/10.1006/rwgn.2001.1423. Retrieved from https://search.credoreference.com/content/entry/estbengen/genetic_correlation/0.

Hill, W. G., Visscher, P. M., and Wray, N. R. (2008). Heritability in the genomics era - concepts and misconceptions. Nature Reviews Genetics, 9(4), 255-266. doi:10.1038/nrg2322.

Hocquette, J., Botreau, R., Picard, B., Jacquet, A., Pethick, D. W., and Scollan, N. D. (2012). Opportunities for predicting and manipulating beef quality. Meat Science, 92(3), 197-209. doi:10.1016/j.meatsci.2012.04.007.

Hodgson, R. R., Davis, G. W., Smith, G. C., Savell, J. W., and Cross, H. R. (1991). Relationships between pork loin palatability traits and physical characteristics of cooked chops. Journal of Animal Science, 69(12), 4858-4865. doi:10.2527/1991.69124858x.

Honikel, K. O. (1998). Reference methods for the assessment of physical characteristics of meat. Meat Science, 49(4), 447-457. doi:10.1016/S0309-1740(98)00034-5.

Hovenier, R., Kanis, E., van Asseldonk, T., and Westerink, N. G. (1992). Genetic parameters of pig meat quality traits in a halothane negative population. Livestock Production Science, 32(4), 309-321. doi:10.1016/0301-6226(92)90002-L.

Hsiang, M. W. and Cole, R. D. (1978). Chapter 12 determination of the primary structures of histones. Methods in cell biology (pp. 189-228) Elsevier Science & Technology. doi:10.1016/S0091679X(08)60140-5. Retrieved from https://www.sciencedirect.com/science/article/pii/S0091679X08601405.

Huffman, K. L., Miller, M. F., Hoover, L. C., Wu, C. K., Brittin, H. C. and Ramsey, C. B. (1996). Effect of beef tenderness on consumer satisfaction with steaks consumed in the home and restaurant. Journal of Animal Science, 74(1), 91-97. doi:10.2527/1996.74191x.

Hugenschmidt, G., Hadorn, R., Guggisberg, D., Silacci, P., Scherrer, D., Haldimann, M., Scheeder, M. and Wenk, C. (2009). Physico-chemical characterisation of destructured zones in cooked hams. Fleischwirtschaft, 89(1), 86-91.

Jackson, S. R., Eckford, S. D., Abrams, P., Avery, N. C., Tarlton, J. F., and Bailey, A. J. (1996). Changes in metabolism of collagen in genitourinary prolapse. The Lancet, 347(9016), 1658-1661. doi:10.1016/S0140-6736(96)91489-0.

Jensen, P., Craig, H. B., and Robison, O. W. (1967). Phenotypic and genetic associations among carcass traits of swine. Journal of Animal Science, 26(6), 1252. Retrieved from http://jas.fass.org/cgi/content/abstract/26/6/1252.

Johansson, K. (1987). Evaluation of station testing of pigs. Acta Agriculturae Scandinavica, 37(1), 108-119. doi:10.1080/00015128709436548.

Johnson, Z. B., Chewning, J. J., and Nugent, R. A., 3rd. (1999). Genetic parameters for production traits and measures of residual feed intake in large white swine. Journal of Animal Science, 77(7), 1679. doi:10.2527/1999.7771679x.

Jones, H. E., Ramsey, C. B., Hines, R. C., and Hoes, T. L. (1980). Low temperature roasting of thawed or frozen pork loins. Journal of Food Science, 45(2), 178-181. doi:10.1111/j.1365-2621.1980.tb02571.x.

Jung, J., Shim, K., Na, C., and Choe, H. (2015). Studies on intramuscular fat percentage in live swine using real-time ultrasound to determine pork quality. Asian-Australasian Journal of Animal Sciences, 28(3), 318-322. doi:10.5713/ajas.14.0927.

Kempster, A. J., Dilworth, A. W., Evans, D. G., and Fisher, K. D. (1986). The effects of fat thickness and sex on pig meat quality with special reference to the problems associated with overleanness 1. butcher and consumer panel results. Animal Science, 43(3), 517-533. doi:10.1017/S0003356100002737.

Kim, T. W., Kim, C. W., Yang, M. R., No, G. R., Kim, S. W., and Kim, I. (2016). Pork quality traits according to postmortem pH and temperature in berkshire. Korean Journal for Food Science of Animal Resources, 36(1), 29-36. doi:10.5851/kosfa.2016.36.1.29.

Kristensen, L., Therkildsen, M., Riis, B., Sorensen, M. T., Oksbjerg, N., Purslow, P. P., and Ertbjerg, P. (2002). Dietary-induced changes of muscle growth rate in pigs: Effects on in vivo and postmortem muscle proteolysis and meat quality. Journal of Animal Science, 80(11), 2862. Retrieved from http://jas.fass.org/cgi/content/abstract/80/11/2862.

Lanari, M. C., and Cassens, R. G. (1991). Mitochondrial activity and beef muscle color stability. Journal of Food Science, 56(6), 1476-1479. doi:10.1111/j.1365-2621.1991.tb08619.x.

Larzul, C., Lefaucheur, L., Ecolan, P., Gogue, J., Talmant, A., Sellier, P. and Monin, G. (1997). Phenotypic and genetic parameters for longissimus muscle fiber characteristics in relation to growth, carcass, and meat quality traits in large white pigs. Journal of Animal Science, 75(12), 3126. doi:10.2527/1997.75123126x.

Le Bihan-Duval, E., Berri, C., Baéza, E., Santé, V., Astruc, T., Rémignon, H. and Fernandez, X. (2003). Genetic parameters of meat technological quality traits in a grand-parental commercial line of turkey. Genetics, Selection, Evolution: GSE, 35(6), 623-635. doi:2003043.

Lebret, B., Listrat, A. and Clochefert, N. (1998). Age-related changes in collagen characteristics of porcine loin and ham muscles. Paper presented at the 718-719.

Lee, J., Song, K., Lee, H., Cho, K., Park, H., and Park, K. (2015). Genetic parameters of reproductive and meat quality traits in korean berkshire pigs. Asian-Australasian Journal of Animal Sciences, 28(10), 1388-1393. doi:10.5713/ajas.15.0097.

Lilliefors, H. W. (1967). On the kolmogorov-smirnov test for normality with mean and variance unknown. Journal of the American Statistical Association, 62(317), 399. Retrieved from https://search.proquest.com/docview/1311791678.

Liu, A., Nishimura, T., and Takahashi, K. (1996). Relationship between structural properties of intramuscular connective tissue and toughness of various chicken skeletal muscles. Meat Science, 43(1), 43-49. doi:10.1016/0309-1740(95)00065-8.

Lo, L. L., McLaren, D. G., McKeith, F. K., Fernando, R. L., and Novakofski, J. (1992). Genetic analyses of growth, real-time ultrasound, carcass, and pork quality traits in duroc and landrace pigs: II. heritabilities and correlations. Journal of Animal Science, 70(8), 2387-2396. doi:10.2527/1992.7082387x.

Lonergan, S. M., Huff-Lonergan, E., Rowe, L. J., Kuhlers, D. L., and Jungst, S. B. (2001). Selection for lean growth efficiency in duroc pigs influences pork quality. Journal of Animal Science, 79(8), 2075. doi:10.2527/2001.7982075x.

Lonergan, S.M., Topel, D.G. and Marple, D.N. (2019). The science of animal growth and meat technology. (2nded.).US:AcademicPress.Retrievedfrom https://ebookcentral.proquest.com/lib/[SITE_ID]/detail.action?docID=5568971.

Loyd, E. J., and Hiner, R. L. (1959). Meat tenderness, relation between hydroxyproline of alkali-insoluble protein and tenderness of bovine muscle. Journal of Agricultural and Food Chemistry, 7(12), 860-862. doi:10.1021/jf60106a010.

Malmfors, B., and Nilsson, R. (1978). Meat quality traits in swedish landrace and yorkshire pigs with special emphasis on genetics. Acta Agriculturae Scandinavica, 28(1), 81-90. doi:10.1080/09064702.1978.11884472.

Marchi D.F., Beteto F.M., Santos G.R., Soares A.L., Ida E.I. and Shimokomaki M. (2011). Changes in collagen fractions during PSE meat (pale, soft, exudative) chicken installation. Paper presented at the 1-4.

Marschner, I. C. (2011). Glm2: Fitting generalized linear models with convergence problems. R Journal, 3(2), 12-15.

Mateescu, R. G., Garrick, D. J., Garmyn, A. J., VanOverbeke, D. L., Mafi, G. G., and Reecy, J. M. (2015). Genetic parameters for sensory traits in longissimus muscle and their associations with tenderness, marbling score, and intramuscular fat in angus cattle. Journal of Animal Science, 93(1), 21. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/25412744.

Miar, Y., Plastow, G. S., Moore, S. S., Manafiazar, G., Charagu, P., Kemp, R. A. and Wang, Z. (2014). Genetic and phenotypic parameters for carcass and meat quality traits in commercial crossbred pigs. Journal of Animal Science, 92(7), 2869. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/24778330.

Miyada, D. S., and Tappel, A. L. (1956). Colorimetric determination of hydroxyproline. Analytical Chemistry, 28(5), 909-910. doi:10.1021/ac60113a039.

Monin, G., and Sellier, P. (1985). Pork of low technological quality with a normal rate of muscle pH fall in the immediate post-mortem period: The case of the hampshire breed. Meat Science, 13(1), 49-63. doi:10.1016/S0309-1740(85)80004-8.

Mortimer, S. I., Van der Werf, J. H. J., Jacob, R. H., Hopkins, D. L., Pannier, L., Pearce, K. L. and Pethick, D. W. (2014). Genetic parameters for meat quality traits of Australian lamb meat. Meat Science, 96(2), 1016-1024. doi:10.1016/j.meatsci.2013.09.007.

Møller, A. J. (1981). Analysis of warner-bratzler shear pattern with regard to myofibrillar and connective tissue components of tenderness. Meat Science, 5(4), 247-260. doi:10.1016/0309-1740(81)90015-2.

Nakamura Y.N, Iwamoto H, Tabata S, Ono Y, Shiba N, and Nishimura, S. (2003). Comparison of collagen content, distribution and architecture among the pectoralis, iliotibialis lateralis and puboischiofemoralis muscles with different myofiber composition in silky cocks. Animal Science Journal, 74(2), 119-128. doi:10.1046/j.1344-3941.2003.00096.x.

Nakamura, Y. N., Iwamoto, H., Shiba, N., Miyachi, H., Tabata, S., and Nishimura, S. (2004). Developmental states of the collagen content, distribution and architecture in the pectoralis, iliotibialis lateralis and puboischiofemoralis muscles of male red cornish x new hampshire and normal broilers. British Poultry Science, 45(1), 31. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15115198.

Nakano, T., and Thompson, J. R. (1980). Age- and sex-associated changes in chemical composition of bovine triceps brachii intramuscular and epimysial connective tissue with emphasis on glycosaminoglycans. Canadian Journal of Animal Science, 60(3), 643-662. doi:10.4141/cjas80-075.

Naveena, B. M., Kiran, M., Reddy, K. S., Ramakrishna, C., Vaithiyanathan, S., and Devatkal, S. K. (2011). Effect of ammonium hydroxide on ultrastructure and tenderness of buffalo meat. Meat Science, 88(4), 727-732. doi:10.1016/j.meatsci.2011.03.005.

Neuman, R.E. and Logan, A.M. (1950). The determination of hydroxyproline. J. Biol. Chem, 185, 299-306.

Newcom, D. W., Baas, T. J., Mabry, J. W. and Goodwin, R. N. (2002). Genetic parameters for pork carcass components. Journal of Animal Science, 80(12), 3099. Retrieved fromhttp://jas.fass.org/cgi/content/abstract/80/12/3099.

Nishimura, T., Hattori, A., and Takahashi, K. (1999). Structural changes in intramuscular connective tissue during the fattening of Japanese black cattle: Effect of marbling on beef tenderization. Journal of Animal Science, 77(1), 93. doi:10.2527/1999.77193x.

Novakofski, J., Park, S., Bechtel, P. J., and Mckeith, F. K. (1989). Composition of cooked pork chops: Effect of removing subcutaneous fat before cooking. Journal of Food Science, 54(1), 15-17. doi:10.1111/j.1365-2621.1989.tb08556.x.

Odetti, P. R., Borgoglio, A., and Rolandi, R. (1992). Age-related increase of collagen fluorescence in human subcutaneous tissue. Metabolism, 41(6), 655-658. doi:10.1016/0026-0495(92)90059-J.

Official methods of analysis of AOAC international (1995). Official Methods of Analysis of AOAC International. Arlington, Va: AOAC International.

Oksbjerg, N., Petersen, J. S., Sørensen, I. L., Henckel, P., Vestergaard, M., Ertbjerg, P. and Støier, S. (2000). Long-term changes in performance and meat quality of danish landrace pigs: A study on a current compared with an unimproved genotype. Animal Science, 71(1), 81-92.doi:10.1017/S1357729800054916.

Patiyal, S. N., and Katoch, S. S. (2006). Tissue specific and variable collagen proliferation in swiss albino mice treated with clenbuterol. Physiological Research, 55(1), 97. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15857157.

R Core Team. (2018). R: Language for statistical computing. R foundation for statistical computing. Vienna, Austria: URL https://www.R-project.org/.

Raes, K., Balcaen, A., Dirinck, P., De Winne, A., Claeys, E., Demeyer, D., and De Smet, S. (2003). Meat quality, fatty acid composition and flavour analysis in belgian retail beef. Meat Science, 65(4), 1237-1246. doi:10.1016/S0309-1740(03)00031-7.

Roy, B. C., Oshima, I., Miyachi, H., Shiba, N., Nishimura, S., Tabata, S. and Iwamoto, H. (2007). Histochemical properties and collagen architecture of M. iliotibialis lateralis and M. puboischiofemoralis in male broilers with different growth rates induced by feeding at different planes of nutrition. British Poultry Science, 48(3), 312. doi:10.1080/00071660701370491.

Sakakibara, K., Tabata, S., Shiba, N., Gotoh, T., Nishimura, S. and Iwamoto, H. (2000). Myofibre composition and total collagen content in M. iliotibialis lateralis and M.

pectoralis of silkie and white leghorn chickens. British Poultry Science, 41(5), 570-574. doi:10.1080/713654983.

Sakuma, H., Saito, K., Kohira, K., Ohhashi, F., Shoji, N., and Uemoto, Y. (2017). Estimates of genetic parameters for chemical traits of meat quality in japanese black cattle. Animal Science Journal, 88(2), 203-212. doi:10.1111/asj.12622.

Scheper, J. (1978). Influence of environmental and genetic factors on meat quality. Acta Agriculturae Scandinavica, 28(1), 20-31. doi:10.1080/09064702.1978.11884465.

Sellier, P., and Monin, G. (1994). Genetics of pig meat quality: A review. Journal of Muscle Foods, 5(2), 187-219. doi:10.1111/j.1745-4573.1994.tb00530.x.

Shackelford, S. D., Wheeler, T. L., and Koohmaraie, M. (1999). Evaluation of slice shear force as an objective method of assessing beef longissimus tenderness. Journal of Animal Science, 77(10), 2693. doi:10.2527/1999.77102693x.

Shackelford, S. D., Wheeler, T. L., and Koohmaraie, M. (2004). Technical note: Use of belt grill cookery and slice shear force for assessment of pork longissimus tenderness. Journal of Animal Science, 82(1), 238. Retrieved from http://jas.fass.org/cgi/content/abstract/82/1/238.

Shearer, I. J., and Dunkin, A. C. (1968). Lactose utilisation by the growing pig. New Zealand Journal of Agricultural Research, 11(2), 465-476. doi:10.1080/00288233.1968.10431442.

Sionkowska, A. (2005). Current topics in polymer research. In K. R. Bregg (Ed.), New materials based on the blends of collagen and other polymers. pp. 125-168.

Sionkowska, A. (2011). Current research on the blends of natural and synthetic polymers as new biomaterials: Review. Progress in Polymer Science, 36(9), 1254-1276. doi:10.1016/j.progpolymsci.2011.05.003.

Strong, C. L. (1951). Standard methods of measuring and grading for pork carcass evaluation American Meat Science Association. Reciprocal Meat Conference Proceedings. pp 123-141.

Sun, X., Young, J. M., Liu, J. H. and Newman, D. J. (2017). Comparison of C and D65 illuminants of minolta colorimeter for assessing pork color. Paper presented at the Comparison of C and D65 Illuminants of Minolta Colorimeter for Assessing Pork Color. 68: 25-260.

Suzuki, K., Irie, M., Kadowaki, H., Shibata, T., Kumagai, M., and Nishida, A. (2005). Genetic parameter estimates of meat quality traits in duroc pigs selected for average daily gain, longissimus muscle area, backfat thickness, and intramuscular fat content. Journal of Animal Science, 83(9), 2058-2065. doi:10.2527/2005.8392058x.

Swatland, H. J. (1990). A note on the growth of connective tissues binding turkey muscle fibers together. Canadian Institute of Food Science and Technology Journal, 23(4-5), 239-241. doi:10.1016/S0315-5463(90)70251-9.

Swatland, H. J., and Findlay, C. J. (1997). On-line probe prediction of beef toughness, correlating sensory evaluation with fluorescence detection of connective tissue and dynamic analysis of overall toughness. Food Quality and Preference, 8(3), 233-239. doi:10.1016/S0950-3293(96)00053-5.

Thakur, D. P., Morioka, K., Itoh, Y., and Obatake, A. (2002). Influence of muscle biochemical constituents on the meat texture of cultured yellowtail (seriola quinqueradiata) at different anatomical locations. Journal of the Science of Food and Agriculture, 82(13), 1541-1550. doi:10.1002/jsfa.1227.

Therkildsen, M., Riis, B., Karlsson, A., Kristensen, L., Ertbjerg, P., Purslow, P. P. and Oksbjerg, N. (2002). Compensatory growth response in pigs, muscle protein turn-over and meat texture: Effects of restriction/realimentation period. Animal Science, 75(3), 367-377. doi:10.1017/S1357729800053145.

Underly, K. (2012). The art of beef cutting (1. Aufl. ed.) Wiley. Retrieved from http://ebooks.ciando.com/book/index.cfm/bok_id/508797.

Van Wijk, H. J., Arts, D. J. G., Matthews, J. O., Webster, M., Ducro, B. J., and Knol, E. F. (2005). Genetic parameters for carcass composition and pork quality estimated in a commercial production chain. Journal of Animal Science, 83(2), 324-333. Retrieved from: http://jas.fass.org/cgi/content/abstract/83/2/324.

Voutila, L., Mullen, A. M., Ruusunen, M., Troy, D., and Puolanne, E. (2007). Thermal stability of connective tissue from porcine muscles. Meat Science, 76(3), 474-480. doi:10.1016/j.meatsci.2006.12.012.

Wagner, C. T., Owens, R. T., Harper, J. R., and Mcquillan, D. J. (2009). 10 - human-derived acellular matrices for dermal replacement. Biomaterials for treating skin loss (pp. 142-173) Elsevier Ltd. doi:10.1533/9781845695545.2.142.

Wagner, CT, Owens, RT, Harper, JR, and McQuillan, DJ. (2009). Human-derived acellular matrices for dermal replacement. In Orgill, D and Blanco, C (Ed.), Biomaterials for treating skin loss (pp. 150) Woodhead Publishing Series.

Warner, K. F. (1952). Adventures in testing meat for tenderness. Proceedings of the Reciprocal Meat Conference, 5(156-160).

Wheeler, T. L., Shackelford, S. D., and Koohmaraie, M. (2000). Variation in proteolysis, sarcomere length, collagen content, and tenderness among major pork muscles. Journal of Animal Science, 78(4), 958. doi:10.2527/2000.784958x.

Wheeler, T.L., Shackelford, S.D., Johnson, L.P., Miller, M.F., Miller, R.K and Koohmaraie, M. (1997). A comparison of warner-bratzler shear force assessment within and among institutions. Journal of Animal Science, 75(9), 2423–2432. doi:https://doi.org/10.2527/1997.7592423x.

Woolley, L. D., Spivey, K. S., Martin, J. N., Johnston, J. E., Carmichael, R. N., Gredell, D. A. and Miller, M. F. (2016). A comparison of the foss foodscan and chemical analyses for proximate composition in fresh beef. Meat Science, 112, 151-152. doi:10.1016/j.meatsci.2015.08.113.

Yancey, J. W. S., and Kropf, D. H. (2008). Instrumental reflectance values of fresh pork are dependant on aperture size. Meat Science, 79(4), 734-739. doi:10.1016/j.meatsci.2007.11.006.

Zayas, J. F. (1997). Solubility of proteins. Functionality of proteins in food (pp. 6-33) Springer.

Chapter 3

Contributions of company of origin, sex and intrinsic pork characteristics to measures of loin physical, meat and collagen characteristics in a Canadian context

3.1 Introduction

Consumer acceptability of pork is a factor of significant importance to the success of pork products in the market. It is driven mainly by product appearance at retail or point of purchase and the subsequent satisfaction experienced upon consumption (Jeremiah et al., 1999). Yet producing pork at reduced cost by aiming for increased animal growth rates, using cheaper feed ingredients and increasing lean percent (Ngapo and Gariepy, 2008) with minor emphasis on product quality has been the focus of swine production over the past decades (Gjerlaug-Enger et al., 2010). Recently, shifts in consumer preferences suggest that pork market standing could be bolstered by putting additional weight on quality to enhance consumer product acceptance.

Indeed, pork quality in the last decade has received appreciable attention from industry players like retailers, producers, processors, packers and researchers (Newcom et al., 2004) due to the potential for consumer discontent with eating quality of pork from current genotypes with higher lean-to-fat ratios (Kempster et al., 1986). Based upon this, producing pork products tailored to meet demands of certain market niches and export markets may be critical to the long-term competitiveness of the Canadian pork industry on the export market.

Several factors come into play to determine pork quality. These can be of genetic origin like breed and sex or environmental factors like pre-slaughter handling, post-slaughter management and contemporary groups (Ngapo and Gariepy, 2008). Due to the fact that Canadian pork for the most part is obtained from crosses between Large White sows and Duroc boars, minimum differentiation among different populations in terms of loin physical and pork characteristics would be expected owing to the fact that selection is applied only to a defined number of swine breeds and is directed by grading systems that place premiums on lean percent (Zhang et al., 2016). However, that is usually not the case, as inconsistencies in pig meat products are a major challenge confronting the pig industry in many countries (Ellis et al., 1996). A stratification system generated from compositional or relatively easy to measure pork quality measurements can be useful to retailers as a greater degree of information could be provided to consumers with respect to the physical characteristic of a cooked product, thus allowing individuals to buy cuts with tailored levels of protein, fat, moisture, and predicted yields and losses.

Although several studies have been undertaken over the years, debates still exist on the effect of sex and location/origin/slaughter plant on pork quality. Indeed, significant differences in tenderness, juiciness and overall quality have been reported for pork from different locations in Australia under their present production and product processing schemes (Channon et al., 2000). Further, differences in intramuscular fat, color and tenderness attributes were found to be due to sex (Channon et al 2004) while Jeremiah et al (1999) reported the opposite. In general, a perusal of research on the influence of sex on quality attributes reveals differences in its effect on quality; while some studies report influence of sex on quality (Channon et al., 2000; Ellis et al., 1995), others do not (Jeremiah et al., 1999; Ellis et al., 1996). It is therefore necessary to explore the influence of these factors on Canadian pork quality attributes.

Tenderness is the most important palatability trait affecting pork acceptability (Suman, 2012) and a positive relationship between tenderness and collagen characteristics has been proposed in beef (Cross et al., 1973). Further, drip loss has been showed to be significantly associated with meat protein oxidation (Traore et al., 2011) and myofibrillar protein oxidation has been found to decrease beef tenderness (Rowe et al., 2004) hinting at a potential relationship between drip loss and tenderness. However, few studies have looked at the potential presence of these relationships in pork especially in the Canadian context.

Further, meat quality traits like tenderness tend to be of low to moderate heritability (Ciobanu et al., 2011) and are mostly difficult to measure on live animals, thus, there is increasing interest in the level of breeding effort to be allocated to these quality traits relative to the importance of crucial factors of pork production like sex, feeding regimen, slaughter plant, terminal sire genotype and other management practices which ultimately, also influence product quality (Ellis et al., 1996). Therefore, it is imperative to investigate the factors that predict and/or influence these traits and the degree of their effect. Thus, this study sought to investigate the relationship between company, sex, loin physical, meat quality and collagen characteristics of cross-bred pigs subjected to commercial finishing conditions. Specific hypotheses tested included: Drip loss influences Warner-Bratzler shear force values; tenderness of cooked pork is influenced more by myofibrillar proteins than by intramuscular fat content; collagen characteristics influence cooking loss percent and tenderness decreases with increased muscling. In addition, this study further assesses the relationship between sub-primal, meat quality and collagen characteristics when stratified into 4 subclasses based on compositional and quality measures (intramuscular fat (%), shear force values, pH and $L*$) to test the hypothesis that varying levels of intramuscular (%), shear force, pH and $L*$ values can be used to predict pork quality.

3.2 Materials and methods

3.2.1 Animals and husbandry

Data were from 500 pigs derived from 3-way crosses between Duroc sires and hybrid Large White × Landrace sows. They were collateral relatives (full and half sibs) obtained from 2 breeding populations. All animals were raised on farms located in 2 Canadian provinces under commercial growing conditions. Male piglets were neutered at 3 to 5 days post birth. Piglets were weaned at approximately 7.5 kg which was on average 21 days. The weanlings were subsequently housed in nursery pens for 5 weeks, subsequently raised in pre-grower barns for a pre-growing period of 4 weeks and then subjected to commercial finishing conditions in randomly allocated finishing units with *ad libitum* access to feed and water. The final body weight of the animals was approximately 115 kg. The pigs were transported to East 40 Packers (provincially inspected abattoir), Brandon, MB, Canada, on a weekly basis in groups of 20-25 pigs for animals from company B and 20-35 pigs for those from company A. They were rested in lairage overnight with *ab libitum* access to water and slaughtered the following morning. Guidelines recommended by the Government of Canada were adhered to in the slaughter of the animals. They were electrically stunned prior to exsanguination and their carcasses fabricated within 24 hours post-slaughter. They were on average 160 days old at slaughter with an average live weight of 124 kg at slaughter. Further descriptive information on the animals can be found in section 2.2.1.

3.2.2 Loin physical measurements

For a complete description of loin physical measurements see section 2.2.2. In brief, a 3 and 4 rib loin section from the right side of each carcass was weighed and recorded as the loin weight

(LWT). The loin eye muscle (longissimus thoracis) was removed and recorded as (LEW). The back fat was removed, weighed and recorded as thick fat weight (TFW). Bone weight (BWT) was obtained by weighing the loin bones.

3.2.3 Meat quality measurements

A complete description of meat quality and collagen characteristics measurements is found in section 2.2.3 and 2.2.4. Briefly, pH of the thawed muscles was measured using a glass electrode equipped pH meter after a 2-point calibration with 4.01 and 7.01 buffer solutions. The probe was inserted at 3 different sites for a total of 3 readings per loin. The average of the readings was used for statistical analysis. Drip loss was determined following the procedures elaborated by Honikel (1998). The loin chops to be used were cut across the muscle fiber direction. They were subsequently deboned and trimmed of excess fat and epimysium. Average weight after trimming was 81g± 9. Intramuscular pH of the chops was on average, 5.54 ± 0.19. The chops were weighed, and this weight was recorded as the initial weight. They were then suspended by hooks in inflated plastic bags ensuring that no other external forces are exerted on the samples except for gravity. Samples were stored at 4°C for 24 hours and afterwards gently blotted with soaker pads and re-weighed and this weight recorded as the final weight. Percent drip loss was subsequently calculated with the following formula: $\frac{Initial\ weight - Final\ weight}{Initial\ weight} \times 100.$

Cooking loss (CL) was determined by cooking approximately 192g± 12 of loin roast in a 73°C water bath until an internal roast temperature of 71°C was reach. Cooking loss was calculated as a percentage of the roast weight before cooking.

Minolta L^*, a^*, and b^* measurements were taken with a Konica Minolta CR 400 (Konica Minolta Sensing Inc., Japan) set at CIE standard illuminant D65. The average of 3 readings was used for statistical analysis. Shear force measurements were taken on six 1cm^2 rectangular cores using a Lloyd material testing machine (Lloyd Instrument Ltd, Surrey, UK) fitted with a Warner-Bratzler-like shear blade. Cores were cut at a 200mm/min shear speed and force exerted was recorded with NEXYGEN software (NEXYGEN Corp. USA). Moisture content (MC) was determined by expressing weight loss after freeze drying as a percentage of initial weight.

A Soxtec™ 2050 Automatic Extraction apparatus (FOSS Analytical AB, Höganäs, Sweden) was using for intramuscular fat content determinations. Two grams of ground lyophilized loin muscle were weighed into pre-weighed cellulose extraction thimbles for the analysis. Petroleum ether was used as the extraction solvent for the procedure. All determinations were made in duplicate and the average used for statistical analysis.

3.2.4 Collagen characteristics

A complete description of collagen solubility analysis, acid hydrolysis and hydroxyproline content determination is found in Section 2.2.4. Sample preparation and solubility analysis were undertaken as described by Hill (1966) while hydroxyproline content in the soluble and insoluble fractions were determined with the colorimetric assay of Neuman and Logan (1960). Regression equations obtained from trans-4-hydroxy-L-proline (Sigma Aldrich, MO, USA) standards were used to predict hydroxyproline content of the samples based on their absorbance readings at 550nm. Hydroxyproline content was subsequently converted to collagen by multiplying by the conversion factor 7.14.

3.2.5 Stratification design

Loin physical, meat quality and collagen characteristics data were stratified into 4 subclasses based on their intramuscular fat content, shear force, intramuscular pH, and Minolta $L*$ values with group 1 having the lowest and group 4 having the highest values (De Vol et al. 1987). For IMF groupings, group 1 contained individuals with levels ranging between 2.4-4.99% which were the low IMF individuals (De Vol et al., 1987), groups 2 and 3 (5.01-7.99% and 8.01-10.98%, respectively) were allocated the next two 2.98% increases in IMF, and group 4 whose range was 11.00-22.09% were the greater than 11% IMF animals. For the shear force group, group 1 encompassed individuals with relatively tender pork (Hodgson et al., 1991) with values ranging between 21.62-39.89N, and groups 2 and 3 had the next two 10 N ranges of WBSF values of 40.01-49.01N and 50.01-60.99N, respectively, while group 4 contained individuals with tough pork (Oksbjerg et al., 2001) with WBSF values ranging from 61.49-84.66 N. With respect to intramuscular pH groupings, group 1 consisted of individuals with potentially exudative pork with very low pH values ranging from pH 5.20-5.39, group 2 contained the loins considered to have normal pH values ranging from 5.40-5.68, group 3 contained the high normal pH loins (pH 5.69-5.89) and group 4 had the loins with pH values equal to and greater than 5.90 (pH 5.90-6.23) that were potentially dark, firm and dry (Honkavaara, 1988). Lastly, for the L^* groups, group 1 accommodated individuals with pork color that would be considered dark purplish red to dark reddish pink (Friese et al., 2005) with an L^* range of 33.74-41.97, group 2 had pork considered dark reddish pink with an L^* the range of 41.99-44.99, group 3 had a color considered reddish pink with L^* values ranging from 45.01-50.89, and group 4 contained pork considered pink to grayish pink with L^* values ranging from 51.00-56.85 (Friese et al., 2005).

3.2.6 Statistical analysis

Data were analyzed as a 2×2 factorial design in R version 3.5.2 software (R Core Team, 2017) with company (company A vs company B), sex (barrow vs gilt) and their 2-way interactions as the sources of variation. Least-squares means for specified factors and factor combinations were obtained with the lsmeans package version 2.27-62 (Lenth, 2016). Mean separation analysis was undertaken using Tukey multiple comparisons to compare treatment means at an alpha level of 0.05 with the Agricolae package version 1.2-8 (Mendiburu, 2017)

Pearson product-moment correlations were used to explore the linear relationships between and among the loin physical, meat quality traits and collagen characteristics using the rcorr function in the Harrell Miscellaneous (Hmisc) package version 4.2-0 (Harrell et al., 2019) in R to compute matrices of Pearson's r and p-values for all possible pair of traits, based on the hypothesis that no correlation (zero) exists between any 2 traits under consideration. Pearson correlations coefficients are calculated using the following formula: $r_{trait1,trait2}=\frac{covariance(trait1,trait2)}{standard\ deviation\ trait1 \times standard\ deviation\ trait2}$ and standard error (S.E) for the correlation coefficient is: S.E=$\sqrt{\frac{1-r^2}{n-2}}$ where n= sample size, r= Pearson correlation coefficient. The t-test for Pearson's r =$\frac{r-\rho}{S.E}$ and since the null hypothesis is that the correlation between the variables is zero, the ρ term will be dropped out and thus, the t-statistic is essentially Pearson's r divided by its standard error. Bonferroni multiple-comparison correlation was used to minimize probability of type 1 error (false positives) results. Thus, because 31 comparisons were made at an alpha level of 0.05, significant correlations were determined as follows: 0.05/31=0.002, therefore correlation coefficients with p<0.002 were reported as significant.

In order to ascertain statistical relationships among the variables in this study, multiple regression analyses were performed to fit models to predict/estimate loin weight, thick fat, loin eye weight, bone weight, pH, drip loss, cooking loss, L^*,a^*,b^*, moisture content, Warner-Bratzler shear force, intramuscular fat content and insoluble collagen using other loin physical, meat quality traits and collagen characteristics as predictors/independent variables (X) to generate regression models with the best regression coefficient (R^2) for the regressands (Y) in R statistical computing environment.

The fitted models were of the form: $\widehat{Y_i} = \widehat{\beta_0} + \widehat{\beta_1}X_{1i} + \widehat{\beta_2}X_{2i} + \cdots + \widehat{\beta_k}X_{ki} + e_i$

Where: $\widehat{Y_i}$= response variable

β_0=population intercept/mean

$\widehat{\beta_1}, \widehat{\beta_2}, \ldots \widehat{\beta_k}$= regression coefficients

$X_{1i}, X_{2i} \ldots X_{ki}$=predictors

e_i= error term with expectation E ($\varepsilon | X_{1i}, X_{2i} \ldots X_{ki}$)=0

Correlation among independent variables was tested using the VIF function in car package version 3.0-2 (Fox and Weisberg, 2011), which computes variance inflation factor (VIF) for linear models and variables with VIF's greater than 5 were removed. Results from the Pearson correlations were further used to check for significant relationships among the variable.

The step function in the stats package (R Core Team, 2018) was used for model selection based on their Akaike information criterion (AIC) values. Backward elimination method was used for variable selection in the regression models. The method starts with a model including all the predictors (full model). Predictors with the least contribution to decline in error sum of squares or increase in R^2 were deleted. This process continued until deletion of any predictor resulted in substantial decline in R^2, thus achieving a parsimonious but best model. Pearson correlation coefficients of the independent variables were examined to ensure that variables in the various models were not correlated to each other.

3.3 Results

3.3.1 Effect of company of origin and sex on loin physical, meat quality traits and collagen characteristic

Results for treatments (company and sex) on the traits considered are presented in Tables 3.1-3.3. The results obtained showed that company had a significant effect ($p<0.01$) on the loin weight (LWT), loin eye weight (LEW) and thick fat weight (TFW) of the populations with the mean values of company A being significantly ($p<0.01$) greater than company B. There was however no significant difference ($p>0.05$) between barrows and gilts for loin physical traits. Pertaining to intramuscular collagen characteristics, soluble collagen percent was significantly ($p<0.01$) higher in company B compared to company A while for insoluble collagen percent, individuals from company A had significantly ($p<0.01$) higher mean values relative to company B. The effect of sex on collagen characteristics was however not significant ($p>0.05$). Total collagen was also statistically not significant ($p>0.05$) regardless of company of origin. Intramuscular pH and IMF were significantly influenced by company with animals from company A having significantly ($p<0.01$) higher pH values. Sex's influence on pH and IMF were however not significant ($p>0.05$). Cooking loss (%) was significantly ($p<0.01$) higher in company B compared to company A but was not significant ($p>0.05$) with respect to sex. The Minolta color traits (*L*, a*, b**) were not affected by company of origin, sex or their interaction ($p>0.05$), nor were moisture content and shear force.

3.3.2 Correlation analysis

Pearson product-moment correlation coefficient results for loin physical traits, meat quality traits and collagen characteristics are presented in Tables 3.3-3.6.

Loin weight (LWT) was highly significantly related with loin eye weight (LEW) (r = 0.73, p<0.0001), meat trim weight (MTW) (r = 0.60, p<0.0001), rib trim weight (RTW) (r = 0.72, p<0.0001) and moderately correlated fat trim weight (FTW) (r = 0.40, p<0.0001), and loin eye percent (LEP) (r = -0.35, p<0.0001). Loin eye weight on the other hand was not highly correlated with any of the loin physical traits but had low-moderate correlations. It was moderately correlated with MTW (r = 0.56, p<0.0001), RTW (r = 0.50, p<0.0001), bone weight (BWT) (r = 0.43, p<0.0001), and LEP (r = 0.37, p<0.0001) and lowly correlated with bone percent (BP) (r = -0.20, p<0.001) and TFW (r = 0.26, p<0.001).

Pertaining to TFW, it was highly negatively correlated with LEP (r = -0.70, p<0.0001) but positively correlated with thick fat percent (TFP) (r = 0.90, p<0.0001) as anticipated. It was further moderately associated with FTW (r = 0.39, p<0.0001), RTW (r = 0.39, p<0.0001), RTP (r = -0.32, p<0.0001) and BP (r = -0.37, p<0.0001) and lowly related with MTW (r = 0.18, p<0.01) and BWT (r = 0.28, p<0.0001). Rib trim weight, BWT and RTP were significantly correlated with MTW with correlation coefficients of 0.77, 0.50 and 0.42 respectively. Fat trim weight (FTW) was positively correlated with RTW (r = 0.63, p<0.0001), TFP (r = 0.28, p<0.0001) and RTP (r = 0.43, p<0.0001) but negatively correlated with LEP (r = -0.41, p<0.0001) and BP (r = -0.21, p<0.0001). Rib trim weight had low to moderate correlations with LEP (r = -0.28, p<0.0001), BW (r = 0.48, p<0.0001) and RTP (r = 0.59, p<0.0001). An expected high but negative correlation was obtained between TFP and LEP (r = -0.77, p<0.0001). Thick fat percent (TFP) was further negatively correlated with RTP (r = -0.36, p<0.0001) and BP (r = -0.34, p<0.0001).

Correlation coefficients for meat quality traits and collagen characteristics are shown in Table 3.5. Muscle pH was negatively correlated with $L*$ (r = -0.29, p<0.0001), $b*$ (r = -0.36, p<0.0001) and Hue (r = -0.39, p<0.0001) but positively correlated with moisture content (MC) (r = 0.36, p<0.0001). Drip loss (DL) was positively associated with CL (r = 0.23, p<0.0001) and WBSF (r = 0.39, p<0.0001) but was not significantly related to any other meat quality trait. Total cooking time (TCT) had low to moderate correlation with the Minolta color traits ranging from r = 0.20, p<0.0001 for *a** to r = -0.36, p<0.0001 for Hue. Total cooking time was further positively correlated with cooking loss (%) (r = 0.43, p<0.0001). Cooking loss percent (CL) on the other hand, was negative related with all the Minolta color traits except with LOINA (r = 0.31, p<0.0001) and its correlations with LOINL, LOINLB and LOINH were -0.34, -0.27 and -0.41 respectively. Cooking loss percent further had a low but positive correlation with WBSF (r = 0.27, p<0.001).

Minolta color traits were generally moderately to highly collinearly related amongst themselves with correlation coefficients ranging from 0.40 between LOINB and LOINC to 0.91 between LOINA and LOINC, although LOINL was lowly correlated with LOINC (-0.26). Moisture content as anticipated, was moderately but negatively correlated with fat traits; its correlation with CF and IMF were r = -0.36, p<0.0001 and r = -0.59, p<0.0001, respectively. Furthermore, its relationship with FOSS crude protein (FOP) (0.30) and FOSS crude moisture (FOM) (0.38) were also moderate. Warner-Bratzler shear force (WBSF) had a significant but low positive correlation with FOM (r = 0.25, p<0.001). There was strong correlation among the traits measured with the commercial meat analyzer namely Foss crude fat (FOF), FOP and FOM ranging from 0.80 between FOP and FOM to -0.98 between FOF and FOM. FOSS crude fat was positively correlated with intramuscular fat (IMF) (r = 0.45, p<0.0001) while FOM (r = -0.42, p<0.0001) and FOP (r = -0.41, p<0.0001) had negative correlations with IMF. With regard to collagen characteristics, soluble collagen percent (SOLC) had a low negative correlation (r = -

0.30) with total collagen (TSOL) while insoluble collagen percent's (ISOLC) correlation with TSOLC was positive (0.30).

Pearson correlation coefficients of sub-primal traits with meat quality traits and collagen characteristics are shown in Table 3.6. Significant correlation coefficients of sub-primal variables with the meat quality traits and collagen characteristics were generally low to moderate except for correlations for TFP with FOM ($r = -0.60$, $p<0.0001$) and FOF ($r = 0.62$, $p<0.0001$) which were high. Loin weight was moderately correlated with pH (0.30) but lowly related to LOINL (-0.22), LOINH (-0.21), FOF (0.24), FOP (-0.27), FOM (-0.21). Thick fat weight was moderately correlated with FOF (0.54), FOP (-0.50) and FOM (-0.51) and IMF (0.36). Bone weight had a low correlation with MC (0.23). Loin eye percent was moderately correlated with FOF (-0.55), FOP (0.42), FOM (0.57) and IMF (-0.41). Thick fat percent on the other hand had moderate relations with FOP (-0.54) and IMF (0.46). Significant correlations of RTP and BP with meat quality traits and collagen characteristics were all low. No significant associations were obtained between sub-primal variables and the collagen characteristics.

3.3.3 Regression analysis

Presented in Table 3.7 and 3.8 are the significant multiple linear regression analyses between loin physical traits, meat quality trait and collagen characteristics.

The multiple regression analysis for LWT was performed with, LEW ($p<0.001$), DL (p=<0.05), a^* ($p<0.001$) and MC. Fifty three percent of the variation in loin weight was explained by variation in loin eye weight. Sixty one percent of the variation in TFW was explained by the following variables: LWT ($p<0.001$), DL ($p<0.05$), a^* ($p<0.05$) and ISOLC ($p<0.001$). Model for LEW included, LWT ($p<0.001$), DL ($p<0.001$), and a^* ($p<0.01$) and they explained 56% of the variation in loin eye weight. The statistical significance of the p-values showed that DL and a^* play vital roles in prediction of the regressands above.

Regression equations for loin physical regressands were:

LWT= 0.25 + 1.94 ×(Loin eye weight) - 0.01× (Drip loss) + 0.02× (Minolta a^*)

TFW= -0.35 + Loin weight × (0.37) - 0.00× (Drip loss) - 0.01× (Minolta a^*) + 0.00× (Insoluble collagen percent)

LEW= 0.15 + 0.28× (Loin weight) + 0.00× (drip loss) – 0.01× (Minolta a^*)

Summaries of regressions for meat quality regressands are presented in Table 3.8. For intramuscular pH, 12% of its variation were explained by moisture content while L^* and Thick fat weight explained 9% and 8% respectively. Loin eye percent explained only 4 % of the variations in drip loss. For CL, the regression analysis retained total cooking time (TCT) ($p<0.001$), Minolta chroma ($p<0.001$), and SOLC ($p<0.001$) and intramuscular fat content (%) and they described 25% of the variation in cooking loss. Twenty-six percent of the variation in WBSF was model by DL ($p<0.001$), FOF ($p<0.001$) and Minolta chroma ($p<0.001$) with DL explaining 15% of the variation in WBSF. Minolta L^* was best modeled with pH ($p<0.01$), and a^* ($p<0.001$), and they explained 37% of the variation in L^*. The backward selection retained TFW ($p<0.01$), WBSF ($p<0.001$), and L^* ($p<0.001$) in the multiple regression model of Minolta a^*. Minolta b^* was best modelled by pH and chroma as they explained 13 and 16% of its variation respectively. Stepwise regression to assess the contribution various independent variables to variations in insoluble collagen percent selected intramuscular pH, total collagen (mg/g raw meat) and intramuscular fat and these variables predicted 12% of its variation.

With reference to MC, the stepwise approach retained pH ($p<0.001$) and IMF ($p<0.001$) and described 50% of the variation in moisture content. P-values for TFW ($p<0.001$), MC ($p<0.001$), and ISOLC ($p<0.05$) partial regression coefficients were significant versus IMF and explained 44% of the variation in intramuscular fat content. Cooking time explained 18% of the variance in CL while a^* explained the most variation in L^* (28%). IMF on the other hand, explained most of the variation in MC, explaining 35% of the variation.

Regression equations for cooking loss (%), pH and shear force (N) were:

CL= 16.23 + 0.09 ×(cooking time) +0.48× (Minolta chroma) + 0.08× (soluble collagen (%))

pH=0.95 + 0.56× (Thick fat weight)-0.01× (Minolta L^*) + 0.07× (Moisture content)

WBSF= 58.80 + 1.46 ×(Drip loss) - 0.30× (FOSS crude fat) - 1.61× (Minolta chroma)

3.3.4 Stratification analysis

Data obtained from the 500 loins were stratified into 4 groups based on their intramuscular fat content, shear force, pH and Minolta L^* values. Mean separation analysis for selected physical and meat quality measurements stratified according to their ether extractable intramuscular fat content are presented in Table 3.9, those stratified by Warner-Bratzler shear force are in Table 3.10 while Tables 3.10 and 3.11 represent those of pH and L^* respectively. The stratification system effectively partitioned the loins into groups that differed in physical, meat quality and collagen characteristics. Stratification using IMF level or shear force could not successfully explain variation in pH, stratification by L^* however achieved significant differences in pH. Stratification based on IMF content successfully explained variations in back fat weight, loin eye percent, back fat percent, moisture content, shear force and FOSS protein. Stratification based on

WBSF successfully explained variations in loin eye percent, back fat percent, drip loss, cooking loss and FOM and FOM, but could not explain variation in back fat weight, moisture content, and soluble collagen percent. Stratification by pH on the other hand explained differences in back fat weight, loin eye weight, a^*, L^*, cooking loss, moisture content and soluble collagen percent. Groupings based on L^* explained dissimilarities in pH, loin eye weight, a^*, IMF, CL, FOSS protein and total collagen.

Specifically, intramuscular fat groups 1 and 2 had significantly ($p<0.01$) higher loin eye percent and moisture content but lower back fat weight and back fat percentages. Intramuscular fat group 4 (which contained the high IMF individuals) on the other hand, had the lowest ($p<0.01$) moisture content of the 4 IMF groups as well as the highest backfat percent. Shear force group 1 had significantly ($p<0.01$) lower drip loss and cooking loss (%). Samples in shear force group 4 had the highest ($p<0.01$) loin eye percent, FOSS moisture content and lowest back fat percent although not significantly different from group 2 and 3. For the pH groups, groups 1 and 2 had significantly ($p<0.01$) lower backfat weight and loin eye weight but higher a^*. Group 1 further had the lowest ($p<0.01$) moisture content of the 4 pH groups. For pH group 4, it had the lowest a^*, L^*, cooking loss, although not significantly different from group 3. Intramuscular pH group 4 further had the lowest soluble collagen percent although not significantly different from groups 2 and 3. Animals in L^* group 1 had significantly ($p<0.01$) lower IMF but higher loin eye weight, pH and moisture content of the L^* groups while those in group 4 had the lowest ($p<0.01$) a^* and cooking loss. Total collagen was significantly lower ($p<0.01$) for group 1 although not significantly different from group 2.

3.4 Discussion

The regression coefficient of the LWT model indicated that LEW is the most important variable to variations in loin weight. Regression analysis by Lisiak et al. (2015) and Wilson et al. (2016) for loin primals and loin respectively however both retained back fat in the final models. The present study did not include backfat (TFW) in the LWT models due to issues with multicollinearity.

Cooking time being the most important factor predicting cooking loss in the present study is not surprising as Bouton et al. (1976) indeed obtained higher cooking loss with increasing cooking time. Products with higher fluid losses upon cooking are also known to have lower juiciness ratings (Channon et al., 2016) thus, making cooking loss important to eating quality. A key variable influencing variations in pork quality is pH. The pH accounted for variation in $L*$ (10%) and MC (12%) in this study and it was also among the traits that predicted variations in insoluble collagen percent. This is expected as the quality defects PSE and DFD are intimately related to these traits. Muscle pH contributions to variations in $L*$ reported by Boler et al. (2010) were 28%, evidently higher than the estimate obtained in this study. These differences could be due to differences in postmortem treatment of the samples. For instance, Boler et al. (2010) stored their samples at 4℃ for 21 days before taking quality measurements while this current study's samples were stored at -20℃ and thawed for 61hrs at 4℃ before measurements. Dransfield et al. (1995) reported that pH accounted for as high as 53% of the variations in $L*$. However, it must be noted that their $L*$ measurements were taken with a Hunter D25 color difference meter with a sample size of 64 pigs while this current study employed a Minolta chromameter with a sample size of 500 pigs. The contribution of pH to variations in the meat quality traits under consideration in this study indicate that for frozen-thawed samples, other traits in addition to ultimate pH is needed to accurately predict pork quality. The fact that intramuscular fat content (lipid content) explained 35% of the variation in moisture content while moisture content also explained 35% of the variation in intramuscular fat content confirms the already established relationship between those two traits for predicting variations in each other. Indeed, a strong genetic relationship was obtained between those two traits in study 2.

A prediction equation for Warner Bratzler shear force by DeVol et al (1988) also retained fat percentage as a variable contributing to variability of shear force, which agrees with the finding of this study. Intramuscular fat may have contributed to variation in insoluble collagen percent as explained by Nishimura (2010), who suggested that deposition of fat in the perimysium results in remodeling of the extracellular matrix and reduction in the mechanical strength of the intramuscular connective tissue through disruption of the collagen fibers' ability to form longterm crosslinks.

Freezing is a technology extensively used in the meat industry to preserve meat and to ensure long term usability (Estévez et al., 2011). However, in the course of freezing pork for storage, its myofibrillar proteins undergo oxidative reactions resulting in the formation of inter and intramolecular crosslinks, carbonylation of specific amino acids, modification of side chains, peptide scission and loss of functional groups (Xiong, 2000; Estévez et al., 2011). Indeed, studies by Estévez et al. (2011) on the effect of frozen-thawed storage on protein carbonylation confirmed that myofibrillar proteins of porcine *m. longissimus dorsi* undergo oxidative reactions during postmortem frozen storage, leading to the formation of α-aminoadipic and γ-glutamic semialdehydes from certain amino acids namely: arginine, proline and lysine. This oxidation of myofibrillar proteins has been found to significantly decrease water holding capacity (Lu et al., 2017; Bao and Ertbjerg, 2018) and porcine longissimus muscle with higher drip loss also tend to have higher protein oxidation as shown in the results of Traore et al. (2012). Rowe et al. (2004) further found oxidation conditions to decrease beef tenderization through μ-calpain inactivation. Indeed, m and μ-calpain possess oxidizable cysteine residues at their active sites and thus oxidizing conditions inhibit their proteolytic activity (Guttmann, 1997). It is therefore not surprising that drip loss predicted most of the variation in tenderness in the present study which goes on to suggests that pork samples in the present study may have gone extensive myofibrillar protein oxidation during storage.

Pork producers are always looking for ways to improve production efficiency and profitability through the use of the best animals for breeding and the fine tuning of production practices. The finding that sex had no influence on loin weight and loin eye weight agree with the results obtained by Bertol et al. (2015) and Cisneros et al. (1996). Ramirez and Cava (2007) however obtained statistically higher loin weights in barrows compared to gilts. Their measurements were however on whole loin primals while the present study took measurements on sub-primals. Cisneros et al. (1996) further reported no significant differences in backfat thickness (cm) measured at the 1st rib between barrows and gilts, however for the measurement taken at the 10th rib barrows had a significantly higher backfat thickness (cm). Lattore et al. (2004), Ramirez et al. (2007) and Kim et al. (2018) also reported significantly higher backfat (mm) in barrows compared to gilts which disagrees with results of this study as no significant differences were obtained among the sexes although it must to stated that in the current study, sub-primal backfat weight was measured rather than backfat depth.

The results from the stratification analysis suggest that samples with lower IMF levels tend to be tougher and have higher moisture content, lean percent, and cooking losses while vice versa can be said for high IMF samples. These results agree with the results obtained by Hodgson et al.

(1991) after that study stratified samples into 10 marbling groups. Hodgson et al. (1991) further reported an increase in protein percent and moisture percent but a decrease in fat percent for samples in their high shear force groups which indeed agrees with the results reported in the present study.

Moisture content in meat plays a crucial role in product shelf life, palatability and functionality (Branden, 2013). Indeed, approximately 75% of muscle composition is water (Voyle, 1979). However, after slaughter, alterations in homeostatic processes causes an increase in lactic acid concentration leading to a decline in meat pH (Braden, 2013). This causes changes in water holding capacity and consequently, moisture content. Thus, water holding capacity and moisture content decreases as muscle pH approach its isoelectric point (minimum hydration). Indeed, the major muscle proteins, myosin and actin have their isoelectric points at 5.3 and 4.8 respectively (Rusell, 2000) which suggest that myosin's ability to hold on to water molecules will be minimal at the aforementioned pH. This decline in pH can lead to muscle defects like PSE condition resulting in economic losses. It is therefore not surprising to observe that, animals that fell into the high pH group (group 4) had significantly higher ($p<0.01$) moisture content while those in group 1 had the lowest means. The stratification based on pH further suggested that animals with higher pH tend to also have significantly higher backfat but lower $L*$, drip loss, cooking loss, and soluble collagen percent, this result sheds further light on the potential of stratification by pH to predict certain quality attributes. Results from the $L*$ stratification suggests that animal with lower luminosity values also tend to have higher pH, lower IMF and total collagen, but higher loin eye muscle weight and moisture content.

Meat appearance on retail shelves has tremendous influences on initial consumer perceptions of product quality. Latorre et al. (2004), Kim et al. (2018) and Zemra et al. (2015) reported no significant differences in Minolta color traits regardless of sex. These results are in agreement with those of this study and thus suggests that pork color traits are not significantly influenced by animal sex. One important indicator of pork quality is its ability to retain moisture (Huff-Lonergan and Lonergan, 2005). Muscle pH and drip loss are indirect indicators of moisture retention potential. The finding that irrespective of sex, muscle pH and drip loss were similar between barrows and gilts agrees with reports by Ramirez and Cava (2007), Cisneros et al. (1996) and Franco et al. (2014). Indeed Barton-Gade (1987) in an investigation of meat quality in castrates and gilts from 3 breed combination: Large White×(Large White× Landrace), Duroc×(Large White× Landrace) and Hampshire×(Large White× Landrace) concluded that sex had no significant effect on the traits that reflect the PSE/DFD defect in their study's carcasses.

Castrated males in the studies of Franco et al. (2014) and Alonso et al. (2009) had higher intramuscular fat contents compared to entire females. Also, studies in Quebec by Correa et al. (2006) of pigs from similar breed combination as this study (Duroc× (Landrace× Large White) revealed significantly higher IMF in barrows. These differences with the present study could be due to population variations and differences in experimental design. It is, however, worth noting that barrows in this study on average, had higher IMF although not statistically significant ($p>0.05$). Ramirez and Cava (2007), Kim et al. (2018) and Sundrum et al. (2011) however found no effect of sex on intramuscular fat content, which agrees with the results of the present study. Although, it is also worth noting that in all those studies, castrated males had numerically higher intramuscular fat content that was not significant statistically.

Meat tenderness is a highly ranked quality attribute in meat products (Williams et al., 1986). Warner Bratzler shear force test is a method established as an objective measure of meat tenderness. Shear force was not significant ($p>0.05$) between sex in the study of Magowan et al.

(2011) and Kim et al. (2018), which agrees with the findings of this study. Barton-Gade (1987) however reported a 3N difference between gilts and barrows with gilts having higher estimates on average though not statistically significant (p>0.05). Sex, however, had a significant effect on cooking loss as reported by Kim et al. (2018), Magowan et al. (2011) and Latorre et al. (2004) which contradicts the findings of the present study. These differences could, however, be due to several factors such as statistical modeling and differences in data collection. As an instance, Kim et al. (2018) cooked samples at 80℃ for 30min while Magowan et al. (2011) cooked samples at 70℃ for 50min. However, in the present study, samples were cooked to an internal temperature of 71℃ as monitored by a probe and therefore, resident time in the water bath varied. Other investigators who have studied the effect of sex on cooking loss, however, reported no significant (p>0.05) influence of sex on cooking loss (Cisneros et al., 1996; Beattie et al., 1999 and Ramirez and Cava, 2007). With respect to collagen characteristics, sex had no influence on intramuscular collagen characteristics in the study of Correa et al. (2006) which agrees with the results of the present study. The results of the present study generally agree with the conclusions drawn by Correa et al. (2006) that sex has no significant effect on pork quality traits.

Pearson correlation is used to give an indication of the strength and direction of the linear relationship between 2 variables. The high correlation of LWT with LEW and TFW indicate that samples with heavier loins were likely to also have heavier loin eye's and backfat. The negative association of LEP with TFW suggests that heavily muscled loins tend to however have lower backfat contents. Furthermore, the moderate-high correlation of loin percent with crude fat, crude protein, and crude moisture indicates that highly muscled samples tend to have lower fat content but higher protein and moisture contents.

Brewer et al. (2001) and Van Laack and Kauffman (1999) obtained a high negative correlation between pH and $L*$ while the degree of association in this study was low. Hambrecht et al. (2003) however obtained similar associations of pH and $L*$ (-0.33) as this study even though that study measured pH at 18hrs. Correlation between shear force and drip loss was low and not significant in the study of Cannata et al. (2010). However, the present study obtained a significant moderate correlation between those two traits. These differences could be due to several factors such as sample size and trait measurement differences as Cannata used a sample size of 53 and measure slice shear force with a crosshead speed of 500 mm/min. In fact, crosshead speed has been found to influence shear force values (Wheeler et al., 1997).

Cooking loss is a trait of appreciable importance in fresh as well as processed meat products as the ability of a product to retain its moisture during cooking enhances juiciness for the consumer and profitability for the processor (Channon et al., 2016). Cooking rate (Boles and Swan, 2002), cooking temperature (Shin et al., 1992) and end-point temperature (Fjelkner-Modig, 1986) are some factors affecting cooking loss. The moderate positive correlation of cooking time with cooking loss indicates that steaks that take longer to reach an internal temperature of 71℃ also tend to have more fluid losses associated with it. The low positive correlation of drip loss with cooking loss obtained in this study agrees with the results of Watanabe et al. (2018). The positive correlation of shear force with cooking loss agrees with the results of Bouton et al. (1975) and Li et al. (2013). Thus, samples that loose more fluids during cooking tend to be tougher. Since a significant proportion of muscle water can be found between and within myofibrils, and between muscle bundles, heat application will cause a release of loosely bound water molecules resulting in an increase in fiber density and ultimately a tougher product.

The high association of crude fat with crude protein and moisture reported in this study agrees with the results of Hodgson et al. (1991). Hodgson et al. (1991) however reported a moderate correlation of moisture percent and protein percentage while correlation obtained in this study was high. Further, Watanabe et al. (2018) also obtained a high negative correlation of IMF with moisture content but not with cooking loss or drip loss in their study with commercial Japanese hybrid (Large White × Landrace) × Duroc pigs which agrees with results obtained in the present study. Matured adipose cells tend to have very sparse cytoplasm with approximately 85% of its volume being filled with triglyceride (Swatland, 1994) and as a consequence, increased deposition of intramuscular fat results in a reduction in moisture content.

3.5 Conclusion

Although the debate on the role of collagen fiber state on fluid losses from cooked meat may persist in the meat science community, results from the present study indicated that collagen characteristics do indeed influence variations in cooking loss. This study further indicated that Warner-Bratzler shear force values may be driven more by denaturation of myofibrillar protein native structure than by intramuscular fat content. Mean separation analysis also showed WBSF to increase with increased loin eye muscle weight and reduced backfat which suggests that selection for rapid growth rate with its associated reduction in calpain activity may increase pork toughness. This study further implicated pH and intramuscular fat content as variables influencing insoluble collagen percent, indicating that deposition of fat in the perimysium may be affect the level and/or amount of crosslink formation. The stepwise regression further suggested that pH is not a reliable sole predictor of meat quality. The present study also confirmed that high lean or muscle content tended to be associated with high moisture but lower fat content which suggests that lean sub-primals will also tend to have low fat content which indirectly affect eating quality.

3.6 Tables

Table 3. 1: Effect of company and sex on collagen characteristics of porcine m. longissimus dorsi

Traits	Factors				P-value		
	Company		Sex				
	Company A	Company B	Barrow	Gilt	Company	Sex	Company× Sex
Soluble collagen (%)	16.83 ±0.44	19.10 ±0.57	17.83 ±0.48	18.15 ±0.53	<0.01	0.43	0.18
Insoluble collagen (%)	83.21 ±0.44	80.89 ±0.57	82.65 ±0.48	81.94 ±0.53	<0.01	0.43	0.18
Total collagen (mg/g raw meat)	3.00 ±0.07	3.17 ±0.09	3.06 ±0.07	3.07 ±0.08	0.14	0.94	0.52

Table 3. 2: Effect of company and sex on loin physical traits of porcine m. longissimus dorsi

Traits	Factors				P-value		
	Company		Sex				
	Company A	Company B	Barrow	Gilt	Company	Sex	Company× Sex
Loin weight (kg)	1.46 ±0.01	1.30 ±0.01	1.40 ±0.01	1.39 ±0.01	<0.01	0.85	0.61
Loin eye weight (kg)	0.54 ±0.01	0.50 ±0.01	0.53 ±0.01	0.52 ±0.01	<0.01	0.52	0.89
Thick fat weight (kg)	0.36 ±0.01	0.26 ±0.01	0.32 ±0.01	0.32 ±0.01	<0.01	0.55	0.39

Table 3. 3: Effect of company and sex on meat quality traits of porcine m. longissimus dorsi

Traits	Factors				P-value		
	Company		Sex				
	Company A	Company B	Barrow	Gilt	Company	Sex	Company × Sex
PH	5.61±0.01	5.50±0.01	5.56±0.01	5.57±0.01	<0.01	0.41	0.56
Drip loss (%)	6.48±0.20	7.26±0.26	6.80±0.22	6.74±0.24	0.02	0.72	0.46
Cooking loss (%)	24.21±0.24	26.45±0.31	25.10±0.25	25.00±0.28	<0.01	0.50	0.92
Minolta $L*$	45.26±0.24	45.39±0.31	45.25±0.26	45.38±0.28	0.75	0.75	0.65
Minolta $a*$	7.59±0.10	7.64±0.12	7.53±0.10	7.70±0.11	0.75	0.28	0.46
Minolta $b*$	3.36±0.08	3.39±0.10	3.32±0.09	3.43±0.09	0.79	0.39	0.94
Moisture content (%)	72.26±0.06	72.19±0.08	72.21±0.07	72.25±0.07	0.49	0.64	0.28
Warner-Bratzler Shear force (N)	47.32±0.83	47.93±1.07	48.47±0.90	46.40±0.99	0.64	0.10	0.15
Intramuscular fat	8.35±0.20	7.51±0.26	8.10±0.22	7.95±0.24	0.01	0.78	0.90

Table 3. 4: Pearson correlation coefficients between loin physical traits of porcine m. longissimus dorsi

Trait	LEW	TFW	MTW	FTW	RTW	BWT	LEP	TFP	RTP	BP
LWT[1]	.73*	.76*	.60*	.40*	.72*	.53*	-.35*	.42*	-.11	-.30*
LEW[2]	1.00	.26*	.56*	.10	.50*	.43*	.37*	-.12	-.14	-.20*
TFW[3]		1.00	.18*	.39*	.39*	.28*	-.70*	.90*	-.32*	-.37*
MTW[4]			1.00	-.01	.77*	.50*	-.02	-.12	.42*	.02
FTW[5]				1.00	.63*	.14	-.41*	.28*	.42*	-.21*
RTW[6]					1.00	.48*	-.28*	.09	.59*	-.12
BWT[7]						1.00	-.16	.04	.03	.63*
REP[8]							1.00	-.77*	0.00	.12
TFP[9]								1.00	-.36*	-.34*
RTP[10]									1.00	.14
BP[11]										1.00

1-Whole loin Weight; 2- Loin eye Weight; 3- Thick fat weight; 4- Meat trim weight; 5- Fat trim weight; 6- Rib trim weight; 7-Bone weight; 8- Loin eye percent; 9- Thick fat percent; 10- Rib trim percent; 11- Bone percent *P<0.002.

Table 3. 5: Pearson correlation coefficients between and meat quality traits and collagen characteristics of porcine m. longissimus dorsi

Trait	DL	TCT	CL	_L_*	_a_*	_b_*	hue	chr	MC	WBSF	FOF	FOP	FOM	SOLC	ISOLC	TCOL	IMF
PH	.07	.12	-.06	-.29*	.00	-.36*	-.34*	-.10	.36*	.10	.10	-.11	-.05	-.09	.09	-.14	.07
DL[1]	1.00	-.11	.23*	.12	-.12	.09	.12	-.08	.12	.39*	-.14	.21*	.14	.08	-.08	.05	-.11
TCT[2]		1.00	.43*	-.30*	.20*	-.29*	-.36*	.07	.05	.00	.02	-.17	.04	.00	.00	-.12	-.05
CL[3]			1.00	-.34*	.31*	-.27*	-.41*	.15	.00	.27*	-.06	-.12	.12	.13	-.13	-.02	-.12
_L_[4]				1.00	-.53*	.68*	.89*	-.26*	-.11	-.07	-.06	.26*	-.05	.04	-.04	.18	.08
_a_*[5]					1.00	.03	-.45*	.91*	-.28*	-.18	.26*	-.34*	-.21*	.04	-.04	-.01	.26*
_b_*[6]						1.00	.86*	.40*	-.38*	-.21*	.13	.10	-.24*	.03	-.03	.23*	.30*
Hue[7]							1.00	-.10	-.19	-.11	-.03	.27*	-.09	.00	.00	.22*	.13
Chr[8]								1.00	-.38*	-.25*	.28*	-.26*	-.28*	.04	-.04	.07	.34*
MC[9]									1.00	.17	-.36*	.30*	.38*	-.08	.08	-.05	-.59*
WBSF[10]										1.00	-.22*	.17	.25*	-.05	.05	-.09	-.12
FOF[11]											1.00	-.88*	-.98*	-.02	.02	.02	.45*
FOP[12]												1.00	.80*	.01	-.01	.05	-.41*
FOM[13]													1.00	.03	-.03	-.06	-.42*
SOLC[14]														1.00	-1.00*	-.30*	.09
ISOC[15]															1.00	.30*	-.09
TCOL[16]																1.00	.02
IMF[17]																	1.00

1- Drip loss; 2- Total cooking time; 3- Cooking loss (%); 4-Minolta _L_* ; 5-Minolta _a_* ; 6-Minolta _b_* ; 7-Minolta hue ; 8-Minolta chroma ; 9-Moisture content ; 10- Warner-Bratzler shear force; 11-FOSS crude fat ; 12-FOSS crude protein ; 13-FOSS crude moisture ; 14-soluble collagen percent ; 15-Insoluble collagen percent ; 16-Total collagen (mg/g raw meat); 17- Intramuscular fat; *P<0.002

Table 3. 6: Pearson correlation coefficients between loin physical traits, meat quality traits and collagen characteristics of porcine m. longissimus dorsi

Trait	LWT[1]	LEW[2]	TFW[3]	MTW[4]	FTW[5]	RTW[6]	BWT[7]	LEP[8]	TFP[9]	RTP[10]	BP[11]
PH	.30*	.28*	.29*	.13	.10	.16	.11	-.01	.20*	-.10	-.14
DL[12]	-.01	.13	-.12	.03	.04	.04	.06	.19	-.17	.04	.05
TCT[13]	.16	.25*	.06	.10	-.04	.05	.01	.15	-.02	-.07	-.12
CL[14]	.12	.22*	-.07	.16	-.11	.06	-.04	.19*	-.16	.00	-.12
L*[15]	-.22*	-.29*	-.13	-.09	.08	-.02	.00	-.13	-.05	.18*	.17
a*[16]	.14	-.04	.23*	-.05	.02	-.03	-.12	-.21*	.26*	-.17	-.23*
b*[17]	-.14	-.35*	.01	-.16	.17	-.02	-.02	-.32*	.12	.10	.09
Hue[18]	-.21*	-.31*	-.11	-.12	.14	-.01	.04	-.18*	-.03	.18*	.21*
Chr[19]	.09	-.14	.23*	-.11	.08	-.03	-.11	-.31*	.29*	-.13	-.18*
MC[20]	.11	.35*	-.14	.30*	-.02	.22*	.23*	.32*	-.28*	.15	.14
WBSF[21]	-.04	.16	-.13	.08	-.21*	-.07	.06	.26*	-.19*	-.07	.08
FOF[22]	.24*	-.17	.54*	-.34*	.55*	.09	-.09	-.55*	.62*	-.12	-.31*
FOP[23]	-.27*	.05	-.50*	.24*	-.37*	-.05	.04	.42*	-.54*	.19*	.28*
FOM[24]	-.21*	.21*	-.51*	.35*	-.57*	-.09	.10	.57*	-.60*	.08	.30*
SOLC[25]	-.08	-.03	-.16	.02	.06	.05	.00	.07	-.15	.16	.05

ISOLC[26]	.08	.03	.16	-.02	-.06	-.05	.00	-.07	.15	-.16	-.05
TCOL[27]	-.05	-.14	-.02	-.03	.16	.08	-.06	-.12	-.01	.14	-.01
IMF[28]	.11	-.20*	.36*	-.16	.20*	.00	-.09	-.41*	.46*	-.10	-.19*

1-Whole loin weight; 2- Loin eye weight; 3- Thick fat weight 4-Meat trim weight; 5- Fat trim weight; 6- Rib trim weight; 7-Bone weight; 8- Loin eye percent; 9-Thick fat percent total cooking time; 10- Rib trim percent Cooking loss; 11- Bone percent ; 12- Drip loss; 13- Total cooking time; 14- Cooking loss (%); 15-Minolta L^* ; 16-Minolta a^* ; 17-Minolta b^* ; 18-Minolta hue ; 19-Minolta chroma ; 20-Moisture content ; 21- Warner-Bratzler shear force; 22-FOSS crude fat ; 23-FOSS crude protein ; 24-FOSS crude moisture ; 25-soluble collagen percent ; 26-Insoluble collagen percent ; 27-Total collagen (mg/g raw meat); 28-Intramuscular fat; *$P<0.002$.

Table 3. 7: Multiple linear regression analysis of loin weight, thick fat and bone weight using other loin physical, meat and collagen characteristics.

Dependent Variable	R^2	S. E	Independent variables	Regression coefficient	Partial R^2	P-value
Loin Weight	0.56	0.11	Constant	0.25	-	0.0001
			Loin eye weight	1.94	0.5314	<0.0001
			Drip loss	-0.01	0.0002	0.0128
			Minolta *a**	0.02	0.0198	<0.0001
Thick fat	0.61	0.06	Constant	-0.35	-	<0.0001
			Loin Weight	0.37	0.5731	<0.0001
			Drip loss	-0.00	0.0134	0.0184
			Minolta *a**	-0.01	0.0507	0.0013
			Insoluble collagen (%)	0.00	0.0240	0.0069
Loin Eye Weight	0.56	0.04	Constant	0.15	-	<0.0001
			Loin weight	0.28	0.5314	<0.0001
			Drip loss	0.00	0.0174	0.0007
			Minolta *a**	-0.01	0.0013	0.0008

R^2 = coefficient of determination (correlation coefficient square); SE = standard error of estimates

All p-values for R^2 were significant $p<0.05$

Table 3. 8: Multiple linear regression analysis of meat quality traits using loin physical, other meat quality traits and collagen characteristics.

Dependent Variable	R^2	S. E	Independent variables	Regression coefficient	Partial R^2	P-value
Intramuscular pH	0.29	0.14	Constant	0.95	-	0.1
			Thick fat weight	0.56	0.0821	<0.0001
			Minolta *L**	-0.01	0.0864	<0.0001
			Moisture content	0.07	0.1269	<0.0001
Drip loss	0.04	2.86	Constant	-3.10	-	0.1
			Loin eye percent	-4.74	0.0355	<0.0001
Cooking Loss	0.25	3.05	Constant	16.23	-	<0.0001
			Cooking time	0.09	0.1888	<0.0001
			Minolta chroma	0.48	0.0235	0.001
			Soluble collagen percent	0.08	0.0178	0.004
			Intramuscular fat content (%)	-0.21	0.0136	0.001
Warner-Bratzler Shear force (N)	0.26	10.24	Constant	58.80	-	<0.0001
			Drip loss	1.46	0.1542	<0.0001
			Crude fat	-0.30	0.0494	0.02
			Minolta chroma	-1.61	0.0608	<0.0001
Minolta *L**	0.37	2.65	Constant	88.55	-	<0.0001
			pH	-5.99	0.0864	0.0009
			Minolta *a**	-1.28	0.2830	<0.0001
Minolta *a**	0.35	1.09	Constant	18.01	-	<0.0001
			Thick fat weight	1.98	0.0508	0.0055
			Minolta *L**	-0.22	0.2830	<0.0001
			Warner-Bratzler shear force	-0.22	0.0323	<0.0001
Minolta *b**	0.27	1.01	Constant	13.46	-	<0.0001
			pH	-2.30	0.1323	<0.0001
			Minolta Chroma	0.32	0.1613	<0.0001
Moisture Content	0.50	0.64	Constant	61.56	-	<0.0001
			pH	2.19	0.1269	<0.0001
			Intramuscular fat	-0.19	0.3523	<0.0001

Intramuscular fat	0.44	2.11	Constant	134.14	-	<0.0001
			Thick fat weight	9.69	0.1314	<0.0001
			Moisture content	-1.73	0.3525	<0.0001
			Insoluble collagen percent	-0.04	0.0086	0.0269
Insoluble collagen percent	0.12	6.00	Constant	46.93	-	<0.0001
			pH	5.55	0.0088	0.01
			Total collagen (mg/g raw meat)	2.06	0.0904	<0.0001
			Intramuscular fat content	-0.23	0.0086	0.04

R^2 = coefficient of determination (correlation coefficient square); SE = standard error of estimates; All p-values for R^2 were significant $p<0.05$.

Table 3. 9: Mean separation analysis for loin physical and meat quality measurements stratified according to their ether extractable intramuscular fat content (%)

Intramuscular fat (%) range	Group	n	Backfat weight (kg)	Loin eye (%)	Backfat (%)	pH	Drip loss (%)	Cooking loss (%)	Moisture content (%)	Shear force (N)	FOSS protein (%)
2.4-4.99	1	57	0.28 ±0.01^{b}	40.89 ±0.52^{a}	20.73 ±0.67^{c}	5.58 ±0.02	7.56 ±0.46	25.15 ±0.57	72.81 ±0.12^{a}	49.52 ±1.84^{ab}	17.80 ±0.20^{a}
5.01-7.99	2	193	0.30 ±0.01^{b}	39.64 ±0.27^{a}	21.87 ±0.35^{c}	5.56 ±0.01	6.79 ±0.24	25.20 ±0.30	72.57 ±0.06^{a}	49.86 ±0.96^{a}	17.15 ±0.10^{b}
8.01-10.98	3	148	0.35 ±0.01^{a}	37.75 ±0.33^{b}	24.88 ±0.42^{b}	5.55 ±0.01	6.55 ±0.29	25.12 ±0.36	71.98 ±0.07^{b}	44.44 ±1.17^{b}	16.38 ±0.12^{c}
11.00-22.09	4	66	0.39 ±0.01^{a}	36.50 ±0.49^{b}	27.35 ±0.63^{a}	5.61 ±0.02	6.60 ±0.43	23.98 ±0.54	71.19 ±0.11^{c}	45.70 ±1.74^{ab}	15.87 ±0.19^{c}
P-value			<0.01	<0.01	<0.01	0.22	0.31	0.24	<0.01	<0.01	<0.01

$^{a, b, c}$ Means without a common superscript letter within a column are significantly different ($P < 0.05$); n: sample size.

Table 3. 10: Mean separation analysis for loin physical and meat quality measurements stratified according to their Warner-Bratzler shear force (WBSF) value (N)

WBSF (N)	Group	n	Back-fat weight (kg)	Loin eye (%)	Back-fat (%)	pH	Drip loss (%)	Cook-ing loss (%)	Moisture content (%)	FOSS fat (%)	FOSS moisture (%)	FOSS protein (%)	Soluble collagen (%)
21.62-39.86	1	149	0.33 ±0.01	37.81 ±0.35^{b}	24.44 ±0.47^{a}	5.55 ±0.01	4.98 ±0.27^{b}	23.69 ±0.36^{b}	72.12 ±0.09	25.80 ±0.47^{a}	55.88 ±0.36^{b}	16.51 ±0.14	17.50 ±0.65
40.01-49.01	2	193	0.32 ±0.01	38.58 ±0.36^{ab}	23.17 ±0.48^{ab}	5.56 ±0.01	7.34 ±0.28^{a}	25.13 ±0.36^{a}	72.14 ±0.09	24.76 ±0.48^{ab}	56.86 ±0.36^{ab}	16.83 ±0.14	18.57 ±0.66
50.01-60.99	3	153	0.31 ±0.01	39.43 ±0.35^{a}	23.26 ±0.47^{ab}	5.59 ±0.01	7.61 ±0.27^{a}	25.47 ±0.36^{a}	72.34 ±0.09	24.08 ±0.47^{ab}	57.39 ±0.36^{a}	17.01 ±0.14	17.11 ±0.65
61.49-84.66	4	66	0.31 ±0.01	40.04 ±0.53^{a}	21.68 ±0.72^{b}	5.58 ±0.02	7.82 ±0.41^{a}	26.67 ±0.54^{a}	72.44 ±0.14	23.11 ±0.71^{b}	58.28 ±0.55^{a}	17.06 ±0.21	17.37 ±0.99
P-value			0.29	0.03	0.01	0.30	<0.01	<0.01	0.11	<0.01	<0.01	0.05	0.43

$^{a,\,b}$ Means without a common superscript letter within a column are significantly different ($P < 0.05$); n: sample size.

Table 3. 11: Mean separation analysis for loin physical and meat quality measurements stratified according to their pH values

pH	Group	n	Back-fat weight (kg)	Loin eye weight (kg)	a^*	L^*	Drip loss (%)	Cooking loss (%)	Moisture content (%)	FOSS fat (%)	FOSS moisture (%)	FOSS protein (%)	Soluble collagen (%)
5.20-5.39	1	66	0.31 ±0.01^{b}	0.52 ±0.01^{b}	7.80 ±0.15^{a}	46.39 ±0.35^{a}	6.86 ±0.31	25.14 ±0.40^{a}	71.60 ±0.08^{c}	23.81 ±0.54	57.53 ±0.41	16.99 ±0.14	19.88 ±0.87^{a}
5.40-5.68	2	331	0.32 ±0.01^{b}	0.53 ±0.01^{b}	7.70 ±0.08^{a}	45.74 ±0.19^{a}	6.72 ±0.21	24.91 ±0.19^{a}	72.05 ±0.04^{b}	24.47 ±0.26	56.94 ±0.21	16.93 ±0.08	17.99 ±0.35^{ab}
5.69-5.89	3	98	0.36 ±0.02^{a}	0.57 ±0.02^{a}	7.12 ±0.16^{b}	45.10 ±0.40^{ab}	6.86 ±0.32	24.00 ±0.39^{ab}	72.51 ±0.11^{a}	24.44 ±0.51	57.11 ±0.38	16.90 ±0.16	17.26 ±0.70^{ab}
5.90-6.23	4	26	0.38 ±0.02^{a}	0.59 ±0.02^{a}	7.01 ±0.28^{b}	43.65 ±0.72^{b}	6.41 ±0.53	22.11 ±0.93^{b}	72.89 ±0.14^{a}	24.61 ±0.98	57.15 ±0.78	16.60 ±0.25	15.62 ±1.46^{b}
P-value			<0.01	<0.01	<0.01	<0.01	0.78	<0.01	<0.01	0.77	0.70	0.72	0.01

$^{a, b, c}$ Means without a common superscript letter within a column are significantly different ($P < 0.05$); n: sample size.

Table 3. 12: Mean separation analysis for loin physical and meat quality measurements stratified according to their *L** values

*L**	Group	n	pH	Loin eye weight (kg)	*a**	IMF (%)	WBSF (N)	Cooking loss (%)	Moisture content (%)	FOSS fat (%)	FOSS moisture (%)	FOSS protein (%)	Total collagen (mg/g raw meat)	Soluble collagen (%)
33.74-41.97	1	71	5.68 ±0.01^{a}	0.57 ±0.01^{a}	8.40 ±0.15^{a}	6.96 ±0.32^{b}	48.87 ±1.36	24.89 ±0.42^{ab}	72.62 ±0.09^{a}	23.70 ±0.61	58.00 ±0.46	16.73 ±0.15^{b}	2.72 ±0.12^{b}	16.65 ±0.88
41.99-44.99	2	189	5.54 ±0.01^{b}	0.53 ±0.01^{b}	8.19 ±0.08^{a}	8.13 ±0.19^{a}	48.42 ±0.85	25.68 ±0.21^{a}	72.06 ±0.05^{b}	24.55 ±0.34	57.17 ±0.26	16.67 ±0.08^{b}	3.09 ±0.07^{ab}	17.93 ±0.45
45.01-50.89	3	220	5.57 ±0.01^{b}	0.53 ±0.01^{b}	7.12 ±0.09^{b}	8.44 ±0.24^{a}	46.43 ±0.77	24.26 ±0.25^{b}	72.03 ±0.06^{b}	24.62 ±0.31	56.79 ±0.24	16.93 ±0.09^{b}	3.13 ±0.08^{a}	18.45 ±0.47
51.00-56.85	4	51	5.54 ±0.02^{b}	0.55 ±0.01^{ab}	6.00 ±0.13^{c}	8.45 ±0.51^{a}	45.69 ±0.61	21.62 ±0.52^{c}	72.14 ±0.16^{b}	23.51 ±0.80	56.63 ±0.64	18.01 ±0.32^{a}	3.35 ±0.12^{a}	18.72 ±0.84
	P-value		<0.01	<0.01	<0.01	<0.01	0.15	<0.01	<0.01	0.28	0.09	<0.01	<0.01	0.24

$^{a, b, c}$ Means without a common superscript letter within a column are significantly different ($P < 0.05$); n: sample size.

3.7 References

Alonso, V., Campo, M. d. M., Español, S., Roncalés, P. and Beltrán, J. A. (2009). Effect of crossbreeding and gender on meat quality and fatty acid composition in pork. Meat Science, 81(1), 209-217. doi:10.1016/j.meatsci.2008.07.021.

Bao, Y., and Ertbjerg, P. (2018). Effects of protein oxidation on the texture and water-holding of meat: A review. Critical Reviews in Food Science and Nutrition. 1-15. doi:10.1080/10408398.2018.1498444.

Beattie, V. E., Weatherup, R. N., Moss, B. W. and Walker, N. (1999). The effect of increasing carcass weight of finishing boars and gilts on joint composition and meat quality. Meat Science, 52(2), 205-211. doi:10.1016/S0309-1740(98)00169-7.

Bertol, T. M., Oliveira, E. A., Coldebella, A., Kawski, V. L., Scandolera, A. J., and Warpechowski, M. B. (2015). Meat quality and cut yield of pigs slaughtered over 100 kg live weight. Arquivo Brasileiro De Medicina Veterinária E Zootecnia, 67(4), 1166-1174. doi:10.1590/1678-4162-8113.

Boler, D. D., Dilger, A. C., Bidner, B. S., Carr, S. N., Eggert, J. M., Day, J. W. and Killefer, J. (2010). Ultimate ph explains variation in pork quality traits. Journal of Muscle Foods, 21(1), 119-130. doi:10.1111/j.1745-4573.2009.00171.x.

Boles, J. A. and J. E. Swan. (2002). Heating method and final temperature affect processing characteristics of beef semimembranosus muscle . Meat Science. 62: 107 – 112.

Bouton, P. E., Ford, A. L., Harris, P. V. and Ratcliff, D. (1975). Objective-subjective assessment of meat tenderness. Journal of Texture Studies, 6(3), 315-328. doi:10.1111/j.1745-4603.1975.tb01128.x.

Bouton, P. E., Harris, P. V., and Shorthose, W. R. (1976). Factors influencing cooking losses from meat. Journal of Food Science, 41(5), 1092-1095. doi:10.1111/j.1365-2621.1976.tb14394.x.

Braden, K. W. (2013). Converting muscle to meat: The physiology of rigor. In C.R. Kerth (Ed.), The science of meat quality (pp. 79-99) Retrieved from https://library.biblioboard.com/viewer/c2dff0ee-f7e9-48bf-a909-3deb6365a504.

Brewer, M.S. Zhu, L.G. Bidner, B. Meisinger, D.J. and McKeith F.K. (2001). Measuring pork color effects of bloom time, muscle, pH, and relationship to instrumental parameters. Meat Science, 57(2), 169-176. Retrieved from https://doi.org/10.1016/S0309-1740(00)00089-9.

Cameron, N. D., Warriss, P. D., Porter, S. J., and Enser, M. B. (1990). Comparison of duroc and british landrace pigs for meat a and eating quality. Meat Science, 27(3), 227-247. doi:10.1016/0309-1740(90)90053-9.

Cannata, S., Engle, T. E., Moeller, S. J., Zerby, H. N., Radunz, A. E., Green, M. D. and Belk, K. E. (2010). Effect of visual marbling on sensory properties and quality traits of pork loin. Meat Science, 85(3), 428-434. doi:10.1016/j.meatsci.2010.02.011.

Channon, H. A., Kerr, M. G., and Walker, P. J. (2004). Effect of duroc content, sex and ageing period on meat and eating quality attributes of pork loin. Meat Science, 66(4), 881-888. doi:10.1016/j.meatsci.2003.08.010.

Channon, H. A., Payne, A. M., Kerr, M. G., Weston, P. A., Hofmeyr, C. D., and Baud, S. R. (2000). Variability in eating quality attributes of Australian pork. In: Proceedings 46th International Congress of Meat Science and Technology, 27 August–1 September, Buenos Aires, Argentina, 596–597.

Channon, H. A., D'Souza, D. N., and Dunshea, F. R. (2016). Developing a cuts-based system to improve consumer acceptability of pork: Impact of gender, ageing period, endpoint temperature and cooking method. Meat Science, 121, 216-227. doi: 10.1016/j.meatsci.2016.06.011.

Ciobanu, D.C., Lonergan, S.M and Huff-Lonergan, E.J. (2011). Genetics of meat quality and carcass traits. In Rothschild, M.F and Ruvinsky, A (Ed.), The genetics of the pig (pp. 355-390) CAB International.

Cisneros, F., Ellis, M., McKeith, F. K., McCaw, J., and Fernando, R. L. (1996). Influence of slaughter weight on growth and carcass characteristics, commercial cutting and curing yields, and meat quality of barrows and gilts from two genotypes. Journal of Animal Science, 74(5), 925. doi:10.2527/1996.745925x.

Conner, J. K., and Hartl, D. L. (2004). A primer of ecological genetics. Sunderland, Mass: Sinauer. Retrieved from http://www.loc.gov/catdir/toc/ecip0410/2003022664.html.

Correa, J. A., Faucitano, L., Laforest, J. P., Rivest, J., Marcoux, M., and Gariépy, C. (2006). Effects of slaughter weight on carcass composition and meat quality in pigs of two different growth rates. Meat Science, 72(1), 91-99. doi:10.1016/j.meatsci.2005.06.006.

Cross, H. R., Z. L. Carpenter and G. C. Smith. 1973. Effects of intramuscular collagen and elastin on bovine muscle tenderness. J. Food Sci. 38:998.

DeVol, D. L., McKeith, F. K., Bechtel, P. J., Novakofski, J., Shanks, R. D., and Carr, T. R. (1988). Variation in composition and palatability traits and relationships between muscle characteristics and palatability in a random sample of pork carcasses. Journal of Animal Science, 66(2), 385. doi:10.2527/jas1988.662385x.

Dransfield, E., Nute, G. R., Mottram, D. S., Rowan, T. G., and Lawrence, T. L. J. (1985). Pork quality from pigs fed on low glucosinate rapeseed meal: Influence of level in the diet, sex and ultimate pH. Journal of the Science of Food and Agriculture, 36(7), 546-556. doi:10.1002/jsfa.2740360705.

Estévez, M., Ventanas, S., Heinonen, M., and Puolanne, E. (2011). Protein carbonylation and water-holding capacity of pork subjected to frozen storage: Effect of muscle type, premincing, and packaging. Journal of Agricultural and Food Chemistry, 59(10), 5435-5443. doi:10.1021/jf104995j

Fjelkner-Modig, S. (1986). Sensory properties of pork, as influenced by cooking temperature and breed. Journal of Food Quality 9: 89 – 105.

Fox, J., and Weisberg, S. (2011). Anœ R companion to applied regression (2. ed. ed.). Los Angeles, Calif. [u.a.]: Sage. Retrieved from http://bvbr.bib-bvb.de:8991/F?func=service&doc_library=BVB01&local_base=BVB01&doc_number=021186123&sequence=000001&line_number=0001&func_code=DB_RECORDS&service_type=MEDI.

Franco, D., Vazquez, J.A. and Lorenzo, J. M. (2014). Growth performance, carcass and meat quality of the Celta pig crossbred with duroc and landrace genotypes.96(1), 195-202. doi:http://dx.doi.org/10.1016/j.meatsci.2013.06.024.

Freise, K., Brewer, S., and Novakofski, J. (2005). Duplication of the pale, soft, and exudative condition starting with normal postmortem pork. Journal of Animal Science, 83(12), 2843-2852. doi:10.2527/2005.83122843x.

Gjerlaug-Enger, E., Aass, L., Ødegård, J. and Vangen, O. (2010). Genetic parameters of meat quality traits in two pig breeds measured by rapid methods. Animal, 4(11), 1832-1843.doi:10.1017/S175173111000114X.

Guttmann, R. P., J. S. Elce, P. D. Bell, J. C. Isbell, and G. V. W.Johnson. (1997). Oxidation inhibits substrate proteolysis by calpain I but not autolysis. Journal of Biological Chemistry. 272:2005–2012.

Hambrecht, E., Eissen, J. J., and Verstegen, M. W. A. (2003). Effect of processing plant on pork quality. Meat Science, 64(2), 125-131. doi:10.1016/S0309-1740(02)00166-3

Hocquette, J., Botreau, R., Picard, B., Jacquet, A., Pethick, D. W., and Scollan, N. D. (2012). Opportunities for predicting and manipulating beef quality. Meat Science, 92(3), 197-209. doi:10.1016/j.meatsci.2012.04.007.

Honkavaara M. (1988). Influence of PSE pork on the quality and economics of cooked, cured ham and fermented dry sausage manufacture. Meat Science. 24 (3):201-207.https://doi.org/10.1016/0309-1740(88)90078-2.

Huff-Lonergan, E., and Lonergan, S. M. (2005). Mechanisms of water-holding capacity of meat: The role of postmortem biochemical and structural changes. Meat Science, 71(1), 194-204. doi:10.1016/j.meatsci.2005.04.022.

Hugenschmidt, G., Hadorn, R., Guggisberg, D., Silacci, P., Scherrer, D., Haldimann, M., Scheeder, M. and Wenk, C. (2009). Physico-chemical characterization of destructured zones in cooked hams. Fleischwirtschaft, 89(1), 86-91.

Jeremiah, L. E., Gibson, L. L., Gibson, J. P., Ball, R. O., Aker, C., and Fortin, A. (1999). The influence of breed, gender, and PSS (halothane) genotype on meat quality, cooking loss, and palatability of pork. Food Research International, 32(1), 59-71. doi:10.1016/S0963-9969(99)00077-0.

Kempster, A. J., Dilworth, A. W., Evans, D. G., and Fisher, K. D. (1986). The effects of fat thickness and sex on pig meat quality with special reference to the problems associated with over leanness 1. butcher and consumer panel results. Animal Science, 43(3), 517-533. doi:10.1017/S0003356100002737.

Kim, Y. M., Choi, T. J., Ho Cho, K., Cho, E. S., Lee, J. J., Chung, H. J. and Jeong, Y. D. (2018). Effects of sex and breed on meat quality and sensory properties in three-way crossbred pigs sired by duroc or by a synthetic breed based on a Korean native breed. Korean Journal for Food Science of Animal Resources, 38(3), 544-553. doi:10.5851/kosfa.2018.38.3.544.

Latorre, M. A., Lázaro, R., Valencia, D. G., Medel, P., and Mateos, G. G. (2004). The effects of gender and slaughter weight on the growth performance, carcass traits, and meat quality characteristics of heavy pigs1. Journal of Animal Science, 82(2), 526-533. doi:10.1093/ansci/82.2.526.

Lenth, R. V. (2016). Least-squares means: The R package lsmeans. Journal of Statistical Software, 69(1), 1-33. doi:10.18637/jss.v069.i01.

Li, Y. X., Cabling, M. M., Kang, H. S., Kim, T. S., Yeom, S. C., Sohn, Y. G. and Seo, K. S. (2013). Comparison and correlation analysis of different swine breeds meat quality. Asian-Australasian Journal of Animal Sciences, 26(7), 905-910. doi:10.5713/ajas.2012.12622.

Lisiak, D., Duziński, K., Janiszewski, P., Borzuta, K., and Knecht, D. (2015). A new simple method for estimating the pork carcass mass of primal cuts and lean meat content of the carcass. Animal Production Science, 55(8), 1044-1050. doi:10.1071/AN13534.

Lonergan, S. M., Huff-Lonergan, E., Rowe, L. J., Kuhlers, D. L., and Jungst, S. B. (2001). Selection for lean growth efficiency in duroc pigs influences pork quality. Journal of Animal Science, 79(8), 2075. doi:10.2527/2001.7982075x.

Lu, H., Wang, H., and Luo, Y. (2017). Changes in protein oxidation, water-holding capacity, and texture of bighead carp (aristichthys nobilis) fillets under chilled and partial frozen storage. Journal of Aquatic Food Product Technology, 26(5), 566-577. doi:10.1080/10498850.2016.1238860.

Magowan, E., Moss, B., Fearon, A. and Ball. E. (2011). Effect of breed, finish weight and sex on pork meat and eating quality and fatty acid profile. Agricultural Research Institute of Northern Ireland, 1-22. Retrieved from www.afbini.gov.uk

Miar, Y., Plastow, G. S., Moore, S. S., Manafiazar, G., Charagu, P., Kemp, R. A. and Wang, Z. (2014). Genetic and phenotypic parameters for carcass and meat quality traits in commercial crossbred pigs. Journal of Animal Science, 92(7), 2869. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/24778330.

Nishimura, T. (2010). The role of intramuscular connective tissue in meat texture. Animal Science Journal, 81(1), 21-27. doi:10.1111/j.1740-0929.2009.00696.x.

R core team. (2018). R: A language and environment for statistical computing. doi:10.1007/978-3-540-74686-7

Ramírez, R., and Cava, R. (2007). Carcass composition and meat quality of three different iberian × duroc genotype pigs. Meat Science, 75(3), 388-396. doi:10.1016/j.meatsci.2006.08.003.

Rowe, L. J., Maddock, K. R., Lonergan, S. M., and Huff-Lonergan, E. (2004). Oxidative environments decrease tenderization of beef steaks through inactivation of mu-calpain.

Journal of Animal Science, 82(11), 3254. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15542472.

Rusell, S. M. (2000). Functional properties of muscle proteins in processed poultry products. Poultry meat processing (pp. 191-204) CRC Press. doi:10.1201/9781420042177-14 Retrieved from https://doi.org/10.1201/9781420042177-14.

Shin, H. K., Abugroun, H. A., Forrest, J. C., Okos, M. R. and Judge, M. D. (1992). Effect of heating rate on palatability and associated properties of pre - and postrigor muscle. Journal of Animal Science 71: 939 – 945.

Sionkowska, A. (2005). Current topics in polymer research. In K. R. Bregg (Ed.), New materials based on the blends of collagen and other polymers (pp. 125-168)

Sundrum, A., Aragon, A., Schulze-Langenhorst, C., Bütfering, L., Henning, M., and Stalljohann, G. (2011). Effects of feeding strategies, genotypes, sex, and birth weight on carcass and meat quality traits under organic pig production conditions. NJAS - Wageningen Journal of Life Sciences, 58(3), 163-172. doi:10.1016/j.njas.2011.09.006.

Swatland, H. J. (1990). A note on the growth of connective tissues binding turkey muscle fibers together. Canadian Institute of Food Science and Technology Journal, 23(4-5), 239-241. doi:10.1016/S0315-5463(90)70251-9.

Swatland, H. J. (1994). Connective tissues of the carcass. Structure and development of meat animals and poultry (pp. 65-143) CRC Press.

Traore, S., Aubry, L., Gatellier, P., Przybylski, W., Jaworska, D., Kajak-Siemaszko, K., and Santé-Lhoutellier, V. (2012). Higher drip loss is associated with protein oxidation. Meat Science, 90(4), 917-924. doi:10.1016/j.meatsci.2011.11.033.

Van Laack, R. L., and Kauffman, R. G. (1999). Glycolytic potential of red, soft, exudative pork longissimus muscle. Journal of Animal Science, 77(11), 2971. doi:10.2527/1999.77112971x

Voutila, L., Mullen, A. M., Ruusunen, M., Troy, D., and Puolanne, E. (2007). Thermal stability of connective tissue from porcine muscles. Meat Science, 76(3), 474-480. doi:10.1016/j.meatsci.2006.12.012.

Voyle, C. A. (1979). Meat. In J. G. Vaughan (Ed.), Food microscopy (pp. 193-231) Acad. Press.

Wagner, C.T, Owens, R.T, Harper, J.R, and McQuillan, D.J. (2009). Human-derived acellular matrices for dermal replacement. In Orgill, D and Blanco, C (Ed.), Biomaterials for treating skin loss (pp. 150) Woodhead Publishing Series.

Watanabe, G., Motoyama, M., Nakajima, I., and Sasaki, K. (2018). Relationship between water-holding capacity and intramuscular fat content in Japanese commercial pork loin. Asian-Australasian Journal of Animal Sciences, 31(6), 914-918. doi:10.5713/ajas.17.0640.

Weissgerber, T.L., Milic, N.M., Winham, S.J., and Garovic, V. D. (2015). Beyond bar and line graphs: Time for a new data presentation paradigm. PLoS Biology, 13(4), e1002128. doi:10.1371/journal.pbio.1002128.

Wheeler, T.L., Shackelford, S.D., Johnson, L.P., Miller, M.F., Miller, R.K and Koohmaraie, M. (1997). A comparison of warner-bratzler shear force assessment within and among institutions. Journal of Animal Science, 75(9), 2423–2432. doi:https://doi.org/10.2527/1997.7592423x.

Williams, C.S., Williams, J.W., and Chung, R.A. (1986). Comparative microscopy and morphometry of skeletal muscle fibers in poultry.5(2), 207-217. Retrieved from http://digitalcommons.usu.edu/foodmicrostructure/vol5/iss2/4.

Wilson, K.B., Overholt, M.F., Hogan, E.K., Schwab, C., Shull, C.M., Ellis. M and Boler. D.D. (2016). Predicting pork loin chop yield using carcass and loin characteristics. Journal of Animal Science, 94(11), 4903. doi:10.2527/jas2016-0610.

Xiong, Y. L. (2000) Protein oxidation and implications for muscle foods quality. In: Antioxidants in Muscle Foods; Eds: Decker, E. A., Faustman, C., Lopez-Bote, C. J. Wiley: New York. Pp 85-111.

Zemva, M., Ngapo, T.M., Malovrh, S., Levart, A., and Kovac, M. (2015). Effect of sex and slaughter weight on meat and fat quality of the krškopolje pig reared in an enriched environment. Animal Production Science, 55(9), 1200. doi:10.1071/AN14059.

Chapter 4

Summary and general conclusion

4.1 Summary of results

The resemblance between parents and progeny serves as the foundation for selective breeding (Bourdon, 1995). Thus, the use of desirable animals as sire and dams over time, leads to improvements in the mean phenotypic value of subsequent generations for traits of interests. Now, just as some traits tend to exhibit more resemblance than others, so also some are generally more responsive to selection (Falconer and Mackay, 1996). This notion is the fulcrum on which the progress made by humans in animal improvement and breeding rests.

Global pork production has seen a rapid rise over the past half century from 25 million metric tons in the 1960's to 112 million metric tons in 2013 (Ritchie and Roser, 2019). This ability to produce pork at such high throughput has been possible through the adoption of systematic scientific approaches selection and breeding and the fine-tuning of management practices. The ability to produce pork at such a high level has come with some surmountable challenges. For one, unlike the beef industry which has been able to successfully align its grading system with their consumer choices, with quality grades ranging from Canada A to prime in a country like Canada (BCRC, 2019) with similar grading systems in other developed countries, the pork industry still lags behind with its production at the packing and producer level for the most part, being driven by pounds/kilos of lean pork. However, in the wake of the increasing consumer demand for pork of better quality, coupled with the high variability in terms of quality characteristics of pork on retail shelves (Salas and Mingala, 2017; De Vol et at 1988) the pork industry may stand a chance of improving its standing in the food industry by having meat quality standards and updating its grading system. For this to be achieved, various research studies may need to be undertaken to determine phenotypic and genetic relationships of pork quality traits as well as how certain extrinsic and intrinsic characteristics of pork contribute and/or predict quality may need to be examined. This thesis sought to contribute to knowledge in this respect.

In the first study, phenotypic and genetic parameters for loin physical, meat quality and intramuscular collagen characteristics (IMCC) of crossbred Canadian swine populations were examined. Data used were from 500 animals with pedigree information dating back to 8 ancestral generations. The results indicated substantial variation in loin physical attributes, meat quality and IMCC of the populations studied. A similar trend has been reported in other countries (De Vol et al., 1988). Consistency of expectation in the perceptible attributes of the products consumers purchase off-shelf is crucial in their purchasing decisions (Uri, 1995; Ha and Jang, 2012) and thus, this variability may prove to be a disadvantage for the pork industry. In general, moderate to high heritability estimates of loin physical traits were obtained in this study which confirms the potential for these traits to respond to selection. Indeed, other researchers have also found traits related to carcass characteristics to be moderate to highly heritable (Ciobanu et al., 2011; Van Wilk et al., 2005).

The proportions of additive variance obtained for meat color traits and total collagen in the present study indicated that genetic changes in the average population mean can be achieved through traditional breeding approaches. Further, additive genetic variance for intramuscular fat obtained in this study indicates that genetics make a substantial contribution to its total phenotypic variance and this agrees with reports in literature (De Vries 1994; Larzul et al., 1997). The results from the genetic correlations indicated that continuous selection for lean percent will negatively impact correlated fat traits as the correlation between LEW and TFP (0.61±0.16), TFW and LEP (-0.76±0.10), FOF and FOP (-0.93±0.05), FOP and IMF (-0.67±0.18), LEP and FOF (-0.41±0.15) were all moderate to highly negative.

Pale, soft and exudative condition in pork is a muscle defect known to cause considerable financial loss to the pig sector (Grandin, 2000). It is a quality defect caused by variables of both genetic and/or environmental origin. Over the course of studying this condition, a number of indicator traits have been used to predict its presence or absence in carcasses. These include $L*$, pH, moisture content, cooking loss and collagen characteristics. This current study obtained a strong genetic relationship among these traits indicating a likely presence of linkage disequilibrium and/or pleiotropic gene effect existing among the traits related to the PSE defect. Further, the strong genetic correlation of $L*$ with SOLC and ISOLC indicates a potential for using it as an indicator trait for collagen characteristics.

One important specific hypothesis tested in this study was the presence of a genetic relationship between WBSF and collagen characteristics. Indeed, a moderate genetic correlation was found for WBSF with SOLC (-0.38±0.10) and ISOLC (0.42±0.16) indicating that similar gene networks to some degree, influence tenderness and IMCC.

The second study used a number of statistical modelling approaches to assess the contribution of company of origin, sex and certain intrinsic pork characteristics to measures of loin physical, meat and collagen characteristics. Estimation of the differences among group means in the population indicated that there was no significant effect of sex on loin physical, meat and collagen characteristics while company significantly influenced loin physical, collagen characteristics, pH, drip loss and cooking loss but was not significant for total collagen, moisture content, WBSF and Minolta color traits.

Results from regression analysis indicated that pH predicted significant variations in $L*$ and moisture content which agrees with results from other studies (Boler et al., 2010; Dransfield et al., 1995). However, pH was also revealed as an unreliable sole predictor of quality characteristics and that other intrinsic variables will need to be included in order to accurately predict quality. Prediction equation for ISOLC retained IMF indicating that deposition of fat in the perimysium may influence crosslinking ability of collagen fibers.

Research studies (Estevez et al., 2011; Traore et al.,2012; Rowe et al., 2004) have found a relationship among water holding capacity, protein oxidation and tenderness after freeze-thawing. Based on these studies, a hypothesis that drip loss predicts variations in tenderness was formulated. The results indeed showed that drip loss predicted the most variation in tenderness after frozen storage indicating that the samples may have undergone myofibrillar protein oxidation during storage.

Findings from the stratification analysis indicated that roasts with lower IMF content also tend to be tougher with higher lean and cooking loss percent. Further, muscle pH stratification showed that high pH animals tend to also have higher backfat but lower drip loss, cooking loss and $L*$ while stratification based on $L*$ revealed that roast with lower $L*$ values also tend to have lower IMF and total collagen but higher muscling. The findings from this exercise shed light on the potential of these traits for predicting quality.

4.2 Future work and study limitations

In this research, tenderness was shown to be genetically correlated with SOLC and ISOLC. However, as these collagen traits were estimated to be lowly heritable and difficult and expensive to measure, they may be good candidates for prediction using approaches that predicts animals' genetic merit through DNA markers. Further, studies may need to be undertaken to identify candidate functional genes associated with WBSF and SOLC and ISOLC. This research found moderate to high heritability estimates for traits related to fat content and a strong negative genetic relationship between these traits and those related to muscling. However, their fatty acid profiles were not examined. It would have been beneficial to have examined these traits. Also, it would have been revealing to examine the glycolytic potential and the muscle fiber type characteristics of the population and their relationships with muscling and meat quality traits. In addition, an examination of the expression levels of matrix metalloproteinases at different growing phases of pigs and their influence on collagen turn over may be warranted.

In this thesis, textural properties (tenderness) of the samples were examined through WBSF tests only. However, as the evaluation of structural and textural properties of meat is vital in quality assessment (Ávila et al., 2014), an approach which will reveal more information about the samples may be necessary. Thus, texture profile analysis is recommended for use in future studies as data on hardness, fracturability, cohesiveness, adhesiveness, gumminess and chewiness (Novaković and Tomašević, 2017) will also then be available for interpretation.

Another area of interest that could be explored is genetic parameters for collagen characteristics in different pig breeds especially purebreds as well as estimates from comparatively tougher but important primals like the ham. Indeed, collagen characteristics have been shown to vary with carcass part at the phenotypic level (Jeremiah and Martin, 1981) with the least exercised muscles tending to have higher ratio of soluble to insoluble collagen. It will be interesting to assess if this is just a function of environmental factors or genetics play a role. In addition, future studies should also be designed to make it feasible for data on a greater number of samples than used in this thesis to be obtained as this might reduce some of the high standard error estimates associated with a number of genetic correlations in the second study (Chapter 2).

Normally age of an animal is taken into consideration when determining how collagen affects meat quality, as age is known to influence collagen characteristics (Hill 1966). Animal age was not considered in this thesis because the pigs were very similar in age being beteen 5.5 and 6 months of age, but size or muscle fiber type should perhaps be considered in future studies. Muscle fiber composition not only affects muscle color but can affect the content of collagen (Kovanen et al. 1984). Relationships between collagen solubility and $L*$ value in this thesis appeared to indicate that as $L*$ value increased so too did collagen solubility. If this is the case, then glycolytic fibers, which are often associated with increased lightness of muscle color (Listrat et al., 2016), may have more soluble collagen than oxidative fibers. This warrants further investigation to test this hypothesis, as it may have implications for meat quality if pigs are slaughtered at ages greater than 6 months and at slaughter weights greater than 135 kg.

The second study (Chapter 3) found a significant relationship between drip loss and WBSF. Future studies may therefore need to examine the level of protein oxidation pre- and post-freezing and how it affects texture profile in a Canadian context.

4.3 References

Ávila, D.R.M, Cambero, I.M., Ordóñez, J. A., de la Hoz, L., and Herrero, A. M. (2014). Rheological behaviour of commercial cooked meat products evaluated by tensile test and texture profile analysis (TPA). Meat Science, 98(2), 310-315. doi:10.1016/j.meatsci.2014.05.003.

Beef cattle research council BCRC (2019). Carcass Grading. https://www.beefresearch.ca/research-topic.cfm/carcass-grading-41. Accessed on: November 04, 2019.

Boler, D. D., Dilger, A. C., Bidner, B. S., Carr, S. N., Eggert, J. M., Day, J. W. and Killefer, J. (2010). Ultimate ph explains variation in pork quality traits. Journal of Muscle Foods, 21(1), 119-130. doi:10.1111/j.1745-4573.2009.00171.x.

Bourdon, R. M. (1995). Understanding animal breeding. Prentice Hall. Retrieved from http://www.vlebooks.com/vleweb/product/openreader?id=none&isbn=9781292052069&uid=none.

Ciobanu, D.C., Lonergan, S.M and Huff-Lonergan, E.J. (2011). Genetics of meat quality and carcass traits. In Rothschild, M.F and Ruvinsky, A (Ed.), The genetics of the pig (pp. 355-390) CAB International.

De Vries, A. G., van der Wal, P. G., Long, T., Eikelenboom, G., and Merks, J. W. M. (1994). Genetic parameters of pork quality and production traits in yorkshire populations. Livestock Production Science, 40(3), 277-289. doi:10.1016/0301-6226(94)90095-7

DeVol, D. L., McKeith, F. K., Bechtel, P. J., Novakofski, J., Shanks, R. D., & Carr, T. R. (1988). Variation in composition and palatability traits and relationships between muscle characteristics and palatability in a random sample of pork carcasses. Journal of Animal Science, 66(2), 385. doi:10.2527/jas1988.662385x.

Dransfield, E., Nute, G. R., Mottram, D. S., Rowan, T. G., and Lawrence, T. L. J. (1985). Pork quality from pigs fed on low glucosinate rapeseed meal: Influence of level in the diet, sex and ultimate pH. Journal of the Science of Food and Agriculture, 36(7), 546-556. doi:10.1002/jsfa.2740360705.

Falconer, D. S., and Mackay, T. F. C. (1996). Introduction to quantitative genetics (4. ed. ed.). Harlow, Essex [u.a.]: Prentice Hall.

Grandin, T. (2000). Introduction: Management and economic factors of handling and transport. Livestock handling and transport (pp. 1-14). Wallingford, UK: CABI Publishing. doi:10.1079/9780851994093.0001 Retrieved from http://www.cabi.org/cabebooks/ebook/20002212511

Ha, J., and Jang, S. (. (2012). The effects of dining atmospherics on behavioral intentions through quality perception. Journal of Services Marketing, 26(3), 204-215. doi:10.1108/08876041211224004.

Hill, F. (1966). The solubility of intramuscular collagen in meat animals of various ages. Journal of Food Science, 31(2), 161-166. doi:10.1111/j.1365-2621. 1966.tb00472.x.

Jeremiah, L. E., and Martin, A. H. (1981). Intramuscular collagen content and solubility: Their relationship to tenderness and alteration by postmortem aging. Canadian Journal of Animal Science, 61(1), 53-61. doi:10.4141/cjas81-008.

Kovanen, V., Suominen, H., and Heikkinen, E. (1984). Collagen of slow twitch and fast twitch muscle fibres in different types of rat skeletal muscle. European Journal of Applied Physiology and Occupational Physiology, 52(2), 235-42. doi:10.1007/bf00433399

Larzul, C., Lefaucheur, L., Ecolan, P., Gogue, J., Talmant, A., Sellier, P., Roy, P. and Monin, G. (1997). Phenotypic and genetic parameters for longissimus muscle fiber characteristics in relation to growth, carcass, and meat quality traits in large white pigs. Journal of Animal Science, 75(12), 3126. doi:10.2527/1997.75123126x

Listrat, A., Lebret, B., Louveau, I., Astruc, T., Bonnet, M., Lefaucheur, L., Picard, B., and Bugeon, J. 2016. How muscle structure and composition influence meat and flesh quality. The Scientific World Journal 2016, Article ID 3182746, 14 pages. http://dx.doi.org/10.1155/2016/3182746

Merry, U. (1995). Coping with uncertainty: Insights from the new sciences of chaos, self-organization, and complexity. United States: Retrieved from http://catalog.hathitrust.org/Record/002969651

Novaković, S., and Tomašević, I. (2017). A comparison between warner-bratzler shear force measurement and texture profile analysis of meat and meat products: A review. IOP Conference Series: Earth and Environmental Science, 85, 12063. doi:10.1088/1755-1315/85/1/012063.

Ritchie, H. and Roser M. (2019). "Meat and Seafood Production and Consumption". Published online at OurWorldInData.org. Retrieved from: 'https://ourworldindata.org/meat-and-seafood-production-consumption'.

Salas, R. C. D., and Mingala, C. N. (2017). Genetic factors affecting pork quality: Halothane and Rendement napole genes. Animal Biotechnology, 28(2), 148-155. doi:10.1080/10495398.2016.1243550.

Van Wijk, H. J., Arts, D. J. G., Matthews, J. O., Webster, M., Ducro, B. J., & Knol, E. F. (2005). Genetic parameters for carcass composition and pork quality estimated in a commercial production chain. Journal of Animal Science, 83(2), 324-333. Retrieved from http://jas.fass.org/cgi/content/abstract/83/2/324.

Bibliography

Aalhus, J. L., Jones, S. D. M., Robertson, W. M., Tong, A. K. W., and Sather, A. P. (1991). Growth characteristics and carcass composition of pigs with known genotypes for stress susceptibility over a weight range of 70 to 120 kg. Animal Science, 52(2), 347-353. doi:10.1017/S0003356100012873.

Aaslyng, M. D., Bejerholm, C., Ertbjerg, P., Bertram, H. C., and Andersen, H. J. (2003). Cooking loss and juiciness of pork in relation to raw meat quality and cooking procedure. Food Quality and Preference, 14(4), 277-288. doi:10.1016/S0950-3293(02)00086-1.

Aaslyng, M. D., Bejerholm, C., Ertbjerg, P., Bertram, H. C., and Andersen, H. J. (2003). Cooking loss and juiciness of pork in relation to raw meat quality and cooking procedure. Food Quality and Preference, 14(4), 277-288. doi:10.1016/S0950-3293(02)00086-1.

Aass, L. (1996). Variation in carcass and meat quality traits and their relations to growth in dual purpose cattle. Livestock Production Science, 46(1), 1-12. doi:10.1016/0301-6226(96)00005-X.

Abdallah, B.M., Marchello, J. A., and Ahmad, H. A. (1999). Effect of freezing and microbial growth on myoglobin derivatives of beef. Journal of Agricultural and Food Chemistry, 47(10), 4093-4099. doi:10.1021/jf9809434.

Aberle, E. D., Etherton, T. D., and Allen, C. E. (1977). Prediction of pork carcass compositions using subcutaneous adipose tissue moisture or lipid concentration. Journal of Animal Science, 45(3), 449-456. doi:10.2527/jas1977.453449x.

Aitken, A and Learmonth, M. (1996). Quantitation of tryptophan in proteins. in: The protein protocols handbook. In M. J. Walker (Ed.), (pp. 29) Humana Press.

Allen, E., Forrest, J. C., Chapman, A. B., First, N., Bray, R. W., and Briskey, E. J. (1966). Phenotypic and genetic associations between porcine muscle properties. Journal of Animal Science, 25(4), 962-966. doi:10.2527/jas1966.254962x.

Alonso, V., Campo, M. d. M., Español, S., Roncalés, P. and Beltrán, J. A. (2009). Effect of crossbreeding and gender on meat quality and fatty acid composition in pork. Meat Science, 81(1), 209-217. doi:10.1016/j.meatsci.2008.07.021.

American Meat Science Association (AMSA) (1995). Research guidelines for cookery, sensory evaluation, and instrumental tenderness measurements of fresh meat. Chicago: Published by American Meat Science Association in cooperation with National Livestock and Meat Board.

AMSA. (2012). AMSA meat color measurement guidelines. Pp: 1-12.

Ando, M., Nakagishi, Y., Yoshida, K., Nakao, M., Nakagawa, T., Makinodan, Y. and Kawasaki, K. (2006). Pyridinoline concentrations in muscular and skin collagen of fish and relationship between collagen solubility and pyridinoline concentration in fish muscular collagen. Fisheries Science, 72(5), 1104-1108. doi:10.1111/j.1444-2906.2006.01262.x.

Apple J.K. and Yancey. J.W.S. (2013). Water-holding capacity of meat. In C.R. Kerth (Ed.), The science of meat quality. John Wiley and Sons. Pp. 119-139.

Apple, J. K., Maxwell, C. V., Stivarius, M. R., Rakes, L. K., and Johnson, Z. B. (2002). Effects of dietary magnesium and halothane genotype on performance and carcass traits of growing-finishing swine. Livestock Production Science, 76(1), 103-113. doi:10.1016/S0301-6226(02)00004-0.

Archile-Contreras, A. C., Mandell, I. B., and Purslow, P. P. (2010). Disparity of dietary effects on collagen characteristics and toughness between two beef muscles. Meat Science, 86(2), 491-497. doi:10.1016/j.meatsci.2010.05.041.

Arthur R. Gilmour, Robin Thompson, and Brian R. Cullis. (1995). Average information REML: An efficient algorithm for variance parameter estimation in linear mixed models. Biometrics, 51(4), 1440-1450. doi:10.2307/2533274.

Avery, N. C., Sims, T. J., Warkup, C., and Bailey, A. J. (1996). Collagen cross-linking in porcine m. longissimus lumborum: Absence of a relationship with variation in texture at pork weight. Meat Science, 42(3), 355-369. doi:10.1016/0309-1740(95)00021-6.

Ávila, D.R.M, Cambero, I.M., Ordóñez, J. A., de la Hoz, L., and Herrero, A. M. (2014). Rheological behaviour of commercial cooked meat products evaluated by tensile test and texture profile analysis (TPA). Meat Science, 98(2), 310-315. doi:10.1016/j.meatsci.2014.05.003.

Bacon, C. D., Loveday, H. D., Pace, R. D., and Riemann, M. J. (1989). Prediction of pork carcass composition by the pork loin 3-6 rib section. Journal of Animal Science, 67(9), 2328-2332. doi:10.2527/jas1989.6792328x.

Bailey, A. J., and Light, N. D. (1989). Connective tissue in meat and meat products. Elsevier Publishers.

Bailey, A. J., and Shimokomaki, M. S. (1971). Age related changes in the reducible cross-links of collagen. FEBS Letters, 16(2), 86-88. doi:10.1016/0014-5793(71)80338-1.

Baker, L. C., Lampitt, L. H., and Brown, K. P. (1953). Connective tissue of meat. II.—Determination of hydroxyproline. Journal of the Science of Food and Agriculture, 4(4), 165-172. doi:10.1002/jsfa.2740040402.

Bao, Y., and Ertbjerg, P. (2018). Effects of protein oxidation on the texture and water-holding of meat: A review. Critical Reviews in Food Science and Nutrition. 1-15. doi:10.1080/10408398.2018.1498444.

Barbanti, D., and Pasquini, M. (2005). Influence of cooking conditions on cooking loss and tenderness of raw and marinated chicken breast meat. LWT - Food Science and Technology, 38(8), 895-901. doi:10.1016/j.lwt.2004.08.017.

Barton-Gade, P. A., Demeyer, D., Honikel, K. O., Joseph, R. L., Puolanne, E., Severini, M., Smulders, F. and Tornberg, E. (1993). Final version (I) of reference methods for water holding capacity in meat and meat products. Procedures Recommended by an OECD Working Group and Presented at the 39th ICoMST in 1993. in: Proceedings 39th Intern. Congress of Meat Science and Technology, Calgary, Canada, File S4, PO2.WP.

Beattie, V. E., Weatherup, R. N., Moss, B. W. and Walker, N. (1999). The effect of increasing carcass weight of finishing boars and gilts on joint composition and meat quality. Meat Science, 52(2), 205-211. doi:10.1016/S0309-1740(98)00169-7.

Beef cattle research council BCRC (2019). Carcass Grading. https://www.beefresearch.ca/research-topic.cfm/carcass-grading-41. Accessed on: November 04, 2019.

Bekhit, A. E. D., and Faustman, C. (2005). Metmyoglobin reducing activity. Meat Science, 71(3), 407-439. doi:10.1016/j.meatsci.2005.04.032.

Bella, J., Brodsky, B., and Berman, H. M. (1995). Hydration structure of a collagen peptide. Structure, 3(9), 893-906. doi:10.1016/S0969-2126(01)00224-6.

Bendall, J. R. (1967). The elastin content of various muscles of beef animals. Journal of the Science of Food and Agriculture, 18(12), 553-558. doi:10.1002/jsfa.2740181201.

Bendall, J. R., and Swatland, H. J. (1988). A review of the relationships of pH with physical aspects of pork quality. Meat Science, 24(2), 85-126. doi:10.1016/0309-1740(88)90052-6.

Berge, P., Kuypers, R. and Kurth, L. B. (1997). Collagen crosslink profile and meat texture in two beef muscles. In Proceedings 43rd International Congress of Meat Science and Technology (pp. 548-549), 27 July - 1 August, Auckland, New Zealand.

Bertol, T. M., Oliveira, E. A., Coldebella, A., Kawski, V. L., Scandolera, A. J., and Warpechowski, M. B. (2015). Meat quality and cut yield of pigs slaughtered over 100 kg live weight. Arquivo Brasileiro De Medicina Veterinária E Zootecnia, 67(4), 1166-1174. doi:10.1590/1678-4162-8113.

Bidanel, J., Ducos, A., Labroue, F., Guéblez, R., and Gasnier, C. (1994). Genetic parameters of backfat thickness, age at 100 kg and meat quality traits in Pietrain pigs. Annales de zootechnie, 43(2), 141-149. Retrieved from https://hal.archives-ouvertes.fr/hal-00888966.

Biela, E., Galas, J., Lee, B., Johnson, G. L., Darzynkiewicz, Z., and Dobrucki, J. W. (2013). Col-F, a fluorescent probe for ex vivo confocal imaging of collagen and elastin in animal tissues. Cytometry Part A, 83A(6), 533-539. doi:10.1002/cyto.a.22264.

Birk, D. E., Fitch, J. M., and Linsenmayer, T. F. (1986). Organization of collagen types I and V in the embryonic chicken cornea. Investigative Ophthalmology and Visual Science, 27(10), 1470-1477. Retrieved from http://www.iovs.org/cgi/content/abstract/27/10/1470.

Boler, D. D., Dilger, A. C., Bidner, B. S., Carr, S. N., Eggert, J. M., Day, J. W. and Killefer, J. (2010). Ultimate ph explains variation in pork quality traits. Journal of Muscle Foods, 21(1), 119-130. doi:10.1111/j.1745-4573.2009.00171.x.

Boles, J. A. and J. E. Swan. (2002). Heating method and final temperature affect processing characteristics of beef semimembranosus muscle . Meat Science. 62: 107 – 112.

Bonaldo, P., Braghetta, P., Zanetti, M., Piccolo, S., Volpin, D., and Bressan, G.M. (1998). Collagen VI deficiency induces early onset myopathy in the mouse: An animal model for bethlem myopathy. Human Molecular Genetics, 7(13), 2135-2140. doi:10.1093/hmg/7.13.2135.

Bonneau, M. (1998). Use of entire males for pig meat in the European union. Meat Science, 49S1, S257-S272. doi:10.1016/S0309-1740(98)00089-8.

Bornstein, P., and Sage, H. (1980). Structurally distinct collagen types. Annual Review of Biochemistry, 49(1), 957-1003. doi:10.1146/annurev.bi.49.070180.004521.

Bosse, M. (2018). A Genomics Perspective on Pig Domestication, Animal Domestication, Fabrice Teletchea, IntechOpen, DOI: 10.5772/intechopen.82646. Available from:

https://www.intechopen.com/books/animal-domestication/a-genomics-perspective-on-pig-domestication

Bouchard, C., Malina, R. M., and Pérusse, L. (1997). Understanding the methods. In Malina, R.M and Perusse, L. (Ed.), Genetics of fitness and physical performance. Human Kinetics. Pp. 58-78.

Bourdon, R. M. (1995). Understanding animal breeding. Prentice Hall. Retrieved from http://www.vlebooks.com/vleweb/product/openreader?id=none&isbn=9781292052069&uid=none.

Bourdon, R. M. (2013). Understanding animal breeding. Pearson Education. Pp1-111.

Bouton, P. E., Ford, A. L., Harris, P. V. and Ratcliff, D. (1975). Objective-subjective assessment of meat tenderness. Journal of Texture Studies, 6(3), 315-328. doi:10.1111/j.1745-4603.1975.tb01128.x.

Bouton, P. E., Ford, A. L., Harris, P. V., and Ratcliff, D. (1975). Objective-subjective assessment of meat tenderness. Journal of Texture Studies, 6(3), 315-328. doi:10.1111/j.1745-4603.1975.tb01128.x.

Bouton, P. E., Harris, P. V., and Shorthose, W. R. (1976). Factors influencing cooking losses from meat. Journal of Food Science, 41(5), 1092-1095. doi:10.1111/j.1365-2621.1976.tb14394.x.

Bouton, P. E., Harris, P. V., Shorthose, W. R., and Ratcliff, D. (1974). Changes in the mechanical properties of veal muscles produced by myofibrillar contraction state, cooking temperature and cooking time. Journal of Food Science, 39(5), 869-875. doi:10.1111/j.1365-2621. 1974.tb07264. x.

Boutten, B., Brazier, M., Morche, N., Morel, A. and Vendeuvre, J.L (2000). Effects of animal and muscle characteristics on collagen and consequences for ham production. Meat Science, 55(2), 233-238. doi: https://doi.org/10.1016/S0309-1740(99)00148-5.

Bowker, B. C., Grant, A. L., Forrest, J. C., and Gerrard, D. E. (2000). Muscle metabolism and PSE pork. Proceedings of the American Society of Animal Science, 79(E-Suppl_1), 1-8. doi:10.2527/jas.00.079ES1001c.

Braden, K. W. (2013). Converting muscle to meat: The physiology of rigor. In C.R. Kerth (Ed.), The science of meat quality (pp. 79-99) Retrieved from https://library.biblioboard.com/viewer/c2dff0ee-f7e9-48bf-a909-3deb6365a504.

Bratzler, L. J. (1932). Measuring the tenderness of meat by means of a mechanical shear. M.S. Thesis.Pp1-33.

Bray, R. W. (1966). Pork quality-definition, characteristics, and significance. Journal of Animal Science, 25(3), 839-842. doi:10.2527/jas1966.253839x.

Brewer, M. S., Novakofski, J., and Freise, K. (2006). Instrumental evaluation of pH effects on ability of pork chops to bloom. Meat Science, 72(4), 596-602. doi:10.1016/j.meatsci.2005.09.009.

Brewer, M.S. Zhu, L.G. Bidner, B. Meisinger, D.J. and McKeith F.K. (2001). Measuring pork color effects of bloom time, muscle, pH, and relationship to instrumental parameters.

Meat Science, 57(2), 169-176. Retrieved from https://doi.org/10.1016/S0309-1740(00)00089-9.

Brocks, L., Klont, R. E., Buist, W., de Greef, K., Tieman, M., and Engel, B. (2000). The effects of selection of pigs on growth rate vs leanness on histochemical characteristics of different muscles. Journal of Animal Science, 78(5), 1247-1254. doi:10.2527/2000.7851247x

Buck, S. F., Harrington, G., and Johnson, R. F. (1962). The prediction of lean percentage of pigs of bacon weight from carcass measurements. Animal Science, 4(1), 25-36. doi:10.1017/S0003356100034371.

Bulleid, N. J., Dalley, J. A., and Lees, J. F. (1997). The C-propeptide domain of procollagen can be replaced with a transmembrane domain without affecting trimer formation or collagen triple helix folding during biosynthesis. The EMBO Journal, 16(22), 6694-6701. doi:10.1093/emboj/16.22.6694.

Bulliet, R. W., (2005). Post domesticity our lives with animals. Hunters, herders, and hamburgers: The past and future of human-animal relationships (pp. 1-36) Columbia University Press. doi:10.7312/bull13076 Retrieved from https://www.jstor.org/stable/10.7312/bull13076.

Cabling, M. M., Kang, H. S., Lopez, B. M., Jang, M., Kim, H. S., Nam, K. C. and Seo, K. S. (2015). Estimation of genetic associations between production and meat quality traits in duroc pigs. Asian-Australasian Journal of Animal Sciences, 28(8), 1061-1065. doi:10.5713/ajas.14.0783.

Cai, J., Chen, Q., Wan, X., and Zhao, J. (2011). Determination of total volatile basic nitrogen (TVB-N) content and Warner–Bratzler shear force (WBSF) in pork using fourier transform near infrared (FT-NIR) spectroscopy. Food Chemistry, 126(3), 1354-1360. doi:10.1016/j.foodchem.2010.11.098.

Cai, W., Casey, D. S., and Dekkers, J. C. M. (2008). Selection response and genetic parameters for residual feed intake in Yorkshire swine. Journal of Animal Science, 86(2), 287-298. doi:10.2527/jas.2007-0396.

Cambero, M. I., Seuss, I., and Honikel, K. O. (1992). Flavor compounds of beef broth as affected by cooking temperature. Journal of Food Science, 57(6), 1285-1290. doi:10.1111/j.1365-2621. 1992.tb06838. x.

Cameron, N. D. (1990). Genetic and phenotypic parameters for carcass traits, meat and eating quality traits in pigs. Livestock Production Science. 26(2), 119-135. doi:10.1016/0301-6226(90)90061-A.

Cameron, N. D., Warriss, P. D., Porter, S. J., and Enser, M. B. (1990). Comparison of duroc and british landrace pigs for meat a and eating quality. Meat Science, 27(3), 227-247. doi:10.1016/0309-1740(90)90053-9.

Canadian Centre for Swine Improvement Inc. CCSI (2001). Annual report 2001/02. pp 1-31.

Canadian Council on Animal Care. (1993). In Olfert, E.D., Cross, B.M. and McWilliams, A.A, (Ed.), Guide to the care and use of experimental animals Can Counc Anim Care, Ottawa, Ontario, Canada.

Cannata, S., Engle, T. E., Moeller, S. J., Zerby, H. N., Radunz, A. E., Green, M. D. and Belk, K. E. (2010). Effect of visual marbling on sensory properties and quality traits of pork loin. Meat Science, 85(3), 428-434. doi:10.1016/j.meatsci.2010.02.011.

Carlson, K. B., Prusa, K. J., Fedler, C. A., Steadham, E. M., Outhouse, A. C., King, D. A., Huff-Lonergan E., and Lonergan, S. M. (2017). Postmortem protein degradation is a key contributor to fresh pork loin tenderness. Journal of Animal Science, 95(4), 1574-1586. doi:10.2527/jas2016.1032.

Castro, L. M., Rosa, G. J. M., Lopes, F. B., Regitano, L. C. A., Rosa, A. J. M., and Magnabosco, C. U. (2017). Genomewide association mapping and pathway analysis of meat tenderness in polled nellore cattle. Journal of Animal Science, 95(5), 1945. doi:10.2527/jas2016.1348.

Cescon, M., Gattazzo, F., Chen, P., and Bonaldo, P. (2015). Collagen VI at a glance. Journal of Cell Science, 128(19), 3525-3531. doi:10.1242/jcs.169748.

Channon, H. A., D'Souza, D. N., and Dunshea, F. R. (2016). Developing a cuts-based system to improve consumer acceptability of pork: Impact of gender, ageing period, endpoint temperature and cooking method. Meat Science, 121, 216-227. doi: 10.1016/j.meatsci.2016.06.011.

Channon, H. A., Kerr, M. G., and Walker, P. J. (2004). Effect of duroc content, sex and ageing period on meat and eating quality attributes of pork loin. Meat Science, 66(4), 881-888. doi:10.1016/j.meatsci.2003.08.010.

Channon, H. A., Payne, A. M., Kerr, M. G., Weston, P. A., Hofmeyr, C. D., and Baud, S. R. (2000). Variability in eating quality attributes of Australian pork. In: Proceedings 46th

International Congress of Meat Science and Technology, 27 August–1 September, Buenos Aires, Argentina, 596–597.

Cherel, P., Herault, F., Vincent, A., Le Roy, P., and Damon, M. (2012). Genetic variability of transcript abundance in pig skeletal muscle at slaughter: Relationships with meat quality traits. Journal of Animal Science, 90(3), 699-708. doi:10.2527/jas.2011-4198.

Cheung, P. C., Salt, I. P., Davies, S. P., Hardie, D. G., and Carling, D. (2000). Characterization of AMP-activated protein kinase gamma-subunit isoforms and their role in AMP binding. The Biochemical Journal, 346 Pt 3(3), 659-669. doi:3460659.

Chou, M., and Li, H. (2002). Genomic organization and characterization of the human type XXI collagen (COL21A1) gene. Genomics, 79(3), 395-401. doi:10.1006/geno.2002.6712.

Cifuni, G., Amici, A., Contò, M., Viola, P., and Failla, S. (2014). Effects of the hunting method on meat quality from fallow deer and wild boar and preliminary studies for predicting lipid oxidation using visible reflectance spectra. European Journal of Wildlife Research, 60(3), 519-526. doi:10.1007/s10344-014-0814-3.

Ciobanu, D. C., Bastiaansen, J. W. M., Lonergan, S. M., Thomsen, H., Dekkers, J. C. M., Plastow, G. S., and Rothschild, M. F. (2004). New alleles in calpastatin gene are associated with meat quality traits in pigs. Journal of Animal Science, 82(10), 2829. Retrieved from http://jas.fass.org/cgi/content/abstract/82/10/2829

Ciobanu, D.C., Lonergan, S.M and Huff-Lonergan, E.J. (2011). Genetics of meat quality and carcass traits. In Rothschild, M.F and Ruvinsky, A (Ed.), The genetics of the pig (pp. 355-390) CAB International.

Cisneros, F., Ellis, M., McKeith, F. K., McCaw, J., and Fernando, R. L. (1996). Influence of slaughter weight on growth and carcass characteristics, commercial cutting and curing yields, and meat quality of barrows and gilts from two genotypes. Journal of Animal Science, 74(5), 925. doi:10.2527/1996.745925x.

Clark, A. L., Slayden, O. D., Hettrich, K. and Brenner, R. M. (2005). Estrogen increases collagen I and III mRNA expression in the pelvic support tissues of the rhesus macaque. American Journal of Obstetrics and Gynecology, 192(5), 1523-1529. doi:10.1016/j.ajog.2004.11.042.

Cockett, N. E., Jackson, S. P., Shay, T. L., Farnir, F., Berghmans, S., Snowder, G. D., Nielsen, N.D and Georges, M. (1996). Polar overdominance at the ovine callipyge locus. Science, 273(5272), 236-238. doi:10.1126/science.273.5272.236.

Coggins, P. C. (2012). Attributes of muscle foods: Color, texture, flavor. In L. M. L. Nollet (Ed.), Handbook of meat, poultry and seafood quality (pp. 35-44) Blackwell Publishing Ltd. doi:10.1002/9781118352434.ch3.Retrievedfromhttps://onlinelibrary.wiley.com/doi/abs/10.1002/9781118352434.ch3.

Colgrave, M. L., Allingham, P. G., Tyrrell, K. and Jones, A. (2012). Multiple reaction monitoring for the accurate quantification of amino acids: Using hydroxyproline to estimate collagen content. Methods in Molecular Biology (Clifton, N.J.), 828, 291. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/22125153.

Conner, J. K., and Hartl, D. L. (2004). A primer of ecological genetics. Sunderland, Mass: Sinauer. Retrieved from http://www.loc.gov/catdir/toc/ecip0410/2003022664.html.

Correa, J. A., Faucitano, L., Laforest, J. P., Rivest, J., Marcoux, M., and Gariépy, C. (2006). Effects of slaughter weight on carcass composition and meat quality in pigs of two different growth rates. Meat Science, 72(1), 91-99. doi:10.1016/j.meatsci.2005.06.006.

Coulson, C. J. (1994). Molecular mechanisms of drug action (2. ed.) Taylor and Francis.

Cross, H. R., Carpenter, Z. L., and Smith, G. C. (1973). Effects of intramuscular collagen and elastin on bovine muscle tenderness. Journal of Food Science, 38(6), 998-1003. doi:10.1111/j.1365-2621.1973.tb02133.x.

Crownover, R. D., Garmyn, A. J., Polkinghorne, R. J., Rathmann, R. J., Bernhard, B. C., and Miller, M. F. (2017). The effects of hot vs. cold boning on eating quality of new zealand grass fed beef. Meat and Muscle Biology, 1(1), 207-217. doi:10.22175/mmb2017.06.0030.

Cundy, T. Reid R.I. and Grey, A. (2014). Metabolic bone disease. In Marshall, W. J., Lapsley, M., Day, A. and Ayling R. (Ed.), Clinical biochemistry E-book: Metabolic and clinical aspects (pp. 604-636) Elsevier Health Sciences.

David E. Birk, John M. Fitch, Joanne P. Babiarz, and Thomas F. Linsenmayer. (1988). Collagen type I and type V are present in the same fibril in the avian corneal stroma. The Journal of Cell Biology, 106(3), 999-1008. doi:10.1083/jcb.106.3.999.

De Vries, A. G., van der Wal, P. G., Long, T., Eikelenboom, G., and Merks, J. W. M. (1994). Genetic parameters of pork quality and production traits in yorkshire populations. Livestock Production Science, 40(3), 277-289. doi:10.1016/0301-6226(94)90095-7

DeVol, D. L., McKeith, F. K., Bechtel, P. J., Novakofski, J., Shanks, R. D. and Carr, T. R. (1988). Variation in composition and palatability traits and relationships between muscle characteristics and palatability in a random sample of pork carcasses. Journal of Animal Science, 66(2), 385. doi:10.2527/jas1988.662385x.

Di Pasquale, M. G. (1997). Proteins and amino acids. Amino acids and proteins for the athlete (pp. 1-9) CRC Press.

Dikeman, M. E., Reddy, G. B., Arthaud, V. H., Tuma, H. J., Koch, R. M., Mandigo, R. W., and Axe, J. B. (1986). Longissimus muscle quality, palatability and connective tissue histological characteristics of bulls and steers fed different energy levels and slaughtered at four ages. Journal of Animal Science, 63(1), 92-101. doi:10.2527/jas1986.63192x.

Dölz, R., Engel, J., and Kühn, K. (1988). Folding of collagen IV. European Journal of Biochemistry, 178(2), 357-366. doi:10.1111/j.1432-1033. 1988.tb14458. x.

Dransfield, E. (1977). Intramuscular composition and texture of beef muscles. Journal of the Science of Food and Agriculture, 28(9), 833-842. doi:10.1002/jsfa.2740280910.

Dransfield, E., Casey, J. C., Boccard, R., Touraille, C., Buchter, L., Hood, D. E. and Tinbergen, B. J. (1983). Comparison of chemical composition of meat determined at eight laboratories. Meat Science, 8(2), 79-92. doi:10.1016/0309-1740(83)90008-6.

Dransfield, E., Nute, G. R., Mottram, D. S., Rowan, T. G., and Lawrence, T. L. J. (1985). Pork quality from pigs fed on low glucosinate rapeseed meal: Influence of level in the diet, sex and ultimate pH. Journal of the Science of Food and Agriculture, 36(7), 546-556. doi:10.1002/jsfa.2740360705.

Dransfield, E., Nute, G. R., Roberts, T. A., Boccard, R., Touraille, C., Buchter, L., Cosentino, E., Hood, D.E., Joseph, R.L., Schon, I., and Paardekooper, E. J. C. (1984). Beef quality assessed at European research centers. Meat Science, 10(1), 1-20. doi:10.1016/0309-1740(84)90028-7.

Drescher, L.S., Janneke de Jonge, Goddard, E and Thomas Herzfeld. (2012). Consumer's stated trust in the food industry and meat purchases. Agriculture and Human Values, 29(4), 507. doi:10.1007/s10460-012-9375-9.

Dublet, B S Oh, S P Sugrue, M K Gordon, D R Gerecke, B R Olsen, and M van der Rest. (1989). The structure of avian type XII collagen. alpha 1 (XII) chains contain 190-kDa non-triple helical amino-terminal domains and form homotrimeric molecules. Journal of Biological Chemistry, 264(22), 131150-131156. Retrieved from http://www.jbc.org/content/264/22/13150.abstract.

Dunner, S., Sevane, N., García, D., Cortés, O., Valentini, A., Williams, J. L., Mangin, B., Cañón, J. and Levéziel, H. (2013). Association of genes involved in carcass and meat quality traits in 15 european bovine breeds. Livestock Science, 154(1-3), 34-44. doi:10.1016/j.livsci.2013.02.020.

Eikelenboom, G. (1983). Some Dutch developments on the identification of quality. Proc. E.E.C. Symposium on the Long-Term Definition of Meat Quality. Pp. 139-144.

Eikelenboom, G., and Minkema, D. (1974). Prediction of pale, soft, exudative muscle with a non-lethal test for halothane-induced porcine malignant hyperthermia syndrome. Neth. J. Vet. Sci., (99), 421–426.

Eikelenboom, G., Hoving-Bolink, A. H., and Wal, V. D (1996). The eating quality of pork: 1. the influence of ultimate pH. Fleischwirtschaft, 76, 392-393. Retrieved from https://www.narcis.nl/publication/RecordID/oai:library.wur.nl:wurpubs%2F303447.

Enfalt, A. C., Lundstrom, K., Karlsson, A., and Hansson, I. (1997). Estimated frequency of the RN- allele in Swedish Hampshire pigs and comparison of glycolytic potential, carcass composition, and technological meat quality among Swedish Hampshire, landrace, and Yorkshire pigs. Journal of Animal Science, 75(11), 2924-2935. doi:10.2527/1997.75112924x.

Enfält, A., Lundström, K., Hansson, I., Johansen, S., and Nyström, P. (1997). Comparison of non-carriers and heterozygous carriers of the RN − allele for carcass composition, muscle distribution and technological meat quality in Hampshire-sired pigs. Livestock Production Science, 47(3), 221-229. doi:10.1016/S0301-6226(96)01409-1.

Enfield, F. D., and Whatley, J. A., Jr. (1961). Heritability of carcass length, carcass backfat thickness and loin lean area in swine. Journal of Animal Science, 20(3), 631-634. doi:10.2527/jas1961.203631x.

Engel, J., and Prockop, D. J. (1991). The zipper-like folding of collagen triple helices and the effects of mutations that disrupt the zipper. Annual Review of Biophysics and Biophysical Chemistry, 20(1), 137-152. doi:10.1146/annurev.bb.20.060191.001033.

England, E. M., Matarneh, S. K., Scheffler, T. L., and Gerrard, D. E. (2017). Peri-mortal muscle metabolism and its effects on meat quality. In P. P. Purslow (Ed.), New aspects of meat quality (pp. 63-89) Elsevier Ltd. doi:10.1016/B978-0-08-100593-4.00004-7.

Estévez, M., Ventanas, S., Heinonen, M., and Puolanne, E. (2011). Protein carbonylation and water-holding capacity of pork subjected to frozen storage: Effect of muscle type, premincing, and packaging. Journal of Agricultural and Food Chemistry, 59(10), 5435-5443. doi:10.1021/jf104995j

Estrade, M., Vignon, X., and Monin, G. (1993). Effect of the RN − gene on ultrastructure and protein fractions in pig muscle. Meat Science, 35(3), 313-319. doi:10.1016/0309-1740(93)90037-I.

Etherington, D. J., and Sims, T. J. (1981). Detection and estimation of collagen. Journal of the Science of Food and Agriculture, 32(6), 539-546. doi:10.1002/jsfa.2740320603.

Exposito, J., Valcourt, U., Cluzel, C., and Lethias, C. (2010). The fibrillar collagen family. International Journal of Molecular Sciences, 11(2), 407-426. doi:10.3390/ijms11020407.

Falconer, D. S., and Mackay, T. F. C. (1996). Introduction to quantitative genetics (4. ed. ed.). Harlow, Essex [u.a.]: Prentice Hall.

Fan. F.Y. (2016). Fincal: Package for time value of money calculation, time series analysis and computational finance [computer software] Zenodo.

Fang, S. H., Nishimura, T. and Takahashi, K. (1999). Relationship between development of intramuscular connective tissue and toughness of pork during growth of pigs. Journal of Animal Science, 77(1), 120. doi:10.2527/1999.771120x.

Feldhusen, F., and Kühne, M. (1992). Effects of ultra-rapid chilling and ageing on length of sarcomeres, and tenderness of pork. Meat Science, 32(2), 161-171. doi:10.1016/0309-1740(92)90103-B.

Fernandez, X., Monin, G., Talmant, A., Mourot, J., and Lebret, B. (1999). Influence of intramuscular fat content on the quality of pig meat — 1. Composition of the lipid fraction and sensory characteristics of m. longissimus lumborum. Meat Science, 53(1), 59-65. doi:10.1016/S0309-1740(99)00037-6.

Fernandez, X., Neyraud, E., Astruc, T., and Sante, V. (2002). Effects of halothane genotype and pre-slaughter treatment on pig meat quality. part 1. post mortem metabolism, meat quality indicators and sensory traits of m. longissimus lumborum. Meat Science, 62(4), 429-437. doi:10.1016/S0309-1740(02)00034-7.

Fernandez, X., Sante, V., Baeza, E., Lebihan-Duval, E., Berri, C., Remignon, H. and Astruc, T. (2001). Post mortem muscle metabolism and meat quality in three genetic types of turkey. British Poultry Science, 42(4), 462-469. doi:10.1080/00071660120070604.

Feru, J., Delobbe, E., Ramont, L., Brassart, B., Terryn, C., Dupont-Deshorgue, A., Garbar C., Monboisse J.C, Maquart, F.X., and Brassart-Pasco, S. (2016). Aging decreases collagen IV expression in vivo in the dermo-epidermal junction and in vitro in dermal fibroblasts: Possible involvement of TGF-β1. European Journal of Dermatology, 26(4), 350-360. doi:10.1684/ejd.2016.2782.

Fisher, P., Mellett, F. D., and Hoffman, L. C. (2000). Halothane genotype and pork quality. 1. carcass and meat quality characteristics of three halothane genotypes. Meat Science, 54(2), 97-105. doi:10.1016/S0309-1740(99)00077-7.

Fitzgerald, J., and Bateman, J. F. (2001). A new FACIT of the collagen family: COL21A1. FEBS Letters, 505(2), 275-280. doi:10.1016/S0014-5793(01)02754-5.

Fjelkner-Modig, S. (1986). Sensory properties of pork, as influenced by cooking temperature and breed. Journal of Food Quality 9: 89 – 105.

Food and Agriculture Organization of the United Nations (FAO) (2017). Livestock primary: meat, total - production – tonnes. http://www.fao.org/faostat/en/?#data/.

Fox, J., and Weisberg, S. (2011). Anœ R companion to applied regression (2. ed. ed.). Los Angeles, Calif. [u.a.]: Sage. Retrieved from http://bvbr.bib-bvb.de:8991/F?func=service&doc_library=BVB01&local_base=BVB01&doc_number=021186123&sequence=000001&line_number=0001&func_code=DB_RECORDS&service_type=MEDI.

Francisco Penagaricano, Bruno D Valente, Juan P Steibel, Ronald O Bates, Catherine W Ernst, Hasan Khatib, and Guilherme JM Rosa. (2015). Exploring causal networks underlying fat deposition and muscularity in pigs through the integration of phenotypic, genotypic and transcriptomic data. BMC Systems Biology, 9(1), 58. doi:10.1186/s12918-015-0207-6.

Franco, D., Vazquez, J.A. and Lorenzo, J. M. (2014). Growth performance, carcass and meat quality of the Celta pig crossbred with duroc and landrace genotypes.96(1), 195-202. doi:http://dx.doi.org/10.1016/j.meatsci.2013.06.024.

Frantz, C., Stewart, K. M., and Weaver, V. M. (2010). The extracellular matrix at a glance. Journal of Cell Science, 123(Pt 24), 4195-4200. doi:10.1242/jcs.023820.

Fraztl, P. (2008). Collagen: Structure and mechanics, an introduction. Collagen (pp. 1-13) Springer US. doi:10.1007/978-0-387-73906-9_1.

Fredeen, H. T., and Newman, J. A. (1962). Rib and vertebral numbers in swine.: I. variation observed in a large population. Canadian Journal of Animal Science, 42(2), 232-239. doi:10.4141/cjas62-036.

Freise, K., Brewer, S., and Novakofski, J. (2005). Duplication of the pale, soft, and exudative condition starting with normal postmortem pork. Journal of Animal Science, 83(12), 2843-2852. doi:10.2527/2005.83122843x.

Fujii, J, K Otsu, F Zorzato, S de Leon, VK Khanna, JE Weiler, O'Brien PJ., and MacLennan, D.H. (1991). Identification of a mutation in porcine ryanodine receptor associated with malignant hyperthermia. Science, 253(5018), 448-451. doi:10.1126/science.1862346.

Fujii, K., Tanzer, M. L., Nusgens, B. V., and Lapiere, C. M. (1976). Aldehyde content and cross-linking of type III collagen. Biochemical and Biophysical Research Communications, 69(1), 128-134. doi:10.1016/S0006-291X (76)80282-3.

García-Celdrán, M., Ramis, G., Manchado, M., Estévez, A., Navarro, A. and Armero, E. (2015). Estimates of heritabilities and genetic correlations of raw flesh quality traits in a reared gilthead sea bream (sparus aurata L.) population sourced from broodstocks along the spanish coasts. Aquaculture, 446, 181-186. doi:10.1016/j.aquaculture.2015.04.030.

Gelse, K., Pöschl, E., and Aigner, T. (2003). Collagens—structure, function, and biosynthesis. Advanced Drug Delivery Reviews, 55(12), 1531-1546. doi: 10.1016/j.addr.2003.08.002.

Gerbens, F., Jansen, A., van Erp, A. J. M., Harders, F., Meuwissen, T. H. E., Rettenberger, G., Veerkamp, J.H and te Pas, M. F. W. (1998). The adipocyte fatty acid-binding protein locus:

Characterization and association with intramuscular fat content in pigs. Mammalian Genome, 9(12), 1022-1026. doi:10.1007/s003359900918.

Gerbens, F., van Erp, A. J., Harders, F. L., Verburg, F. J., Meuwissen, T. H., Veerkamp, J. H., and te Pas, M. F. (1999). Effect of genetic variants of the heart fatty acid-binding protein gene on intramuscular fat and performance traits in pigs. Journal of Animal Science, 77(4), 846-852. doi:10.2527/1999.774846x.

Gilmour, A. R., Gogel, B. J., Cullis, B. R., Welham, S. J. and Thompson, R. (2015). ASReml user guide release 4.1 structural specification. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK, Retrieved from www.vsni.co.uk.

Gjaltema, R. A. F., and Bank, R. A. (2017). Molecular insights into prolyl and lysyl hydroxylation of fibrillar collagens in health and disease. Critical Reviews in Biochemistry and Molecular Biology, 52(1), 74-95. doi:10.1080/10409238.2016.1269716.

Gjerlaug-Enger, E., Aass, L., Ødegård, J. and Vangen, O. (2010). Genetic parameters of meat quality traits in two pig breeds measured by rapid methods. Animal, 4(11), 1832-1843.doi:10.1017/S175173111000114X.

Goldspink, G., Fernandes, K., Williams, P. E., and Wells, D. J. (1994). Age-related changes in collagen gene expression in the muscles of mdx dystrophic and normal mice. Neuromuscular Disorders, 4(3), 183-191. doi:10.1016/0960-8966(94)90019-1.

Gonzalez, J. M., Johnson, D. D., Elzo, M. A., White, M. C., Stelzleni, A. M., and Johnson, S. E. (2014). Effect of brahman genetic influence on collagen enzymatic crosslinking gene expression and meat tenderness. Animal Biotechnology, 25(3), 165-178. doi:10.1080/10495398.2013.846862.

Goodnight. C.J. (2010). Adaptive landscapes and optimality. In Michael D. Breed, Janice Moore (Ed.), Encyclopedia of animal behavior (pp. 24-29) Academic press. doi: https://doi.org/10.1016/B978-0-08-045337-8.00111-X. Retrieved from https://search.credoreference.com/content/entry/estab/adaptive_landscapes_and_optimality.

Gordon, M. and Hahn., R.A (2010). Collagens. Cell and Tissue Research, 339(1), 247-257. doi:10.1007/s00441-009-0844-4.

Gorjanc, G., Bijma, P., and Hickey, J. M. (2015). Reliability of pedigree-based and genomic evaluations in selected populations. Genetics, Selection, Evolution, 47(1), 65. doi:10.1186/s12711-015-0145-1.

Grandin, T. (2000). Introduction: Management and economic factors of handling and transport. Livestock handling and transport (pp. 1-14). Wallingford, UK: CABI Publishing. doi:10.1079/9780851994093.0001 Retrieved from http://www.cabi.org/cabebooks/ebook/20002212511

Greaser, M. L. and Guo, W. (2015). Proteins. In F. T. L.M.L. Nollet (Ed.), Handbook of food analysis (3rd ed., pp. 357-369) CRC Press.

Greaves, P. (2007). In Greaves P. (Ed.), 7 - cardiovascular system Academic Press. doi://doi.org/10.1016/B978-044452771-4/50008-0.

Gross J and Ligges U. (2015). Nortest: Tests for normality. R Package Version 1.0-4, Retrieved from https://CRAN.R-project.org/package=nortest.

Gudmann, N. S., and Karsdal, M. A. (2016). Chapter 10 - type X collagen. Biochemistry of collagens, laminins and elastin (pp. 73-76) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00010-6.

Gudmann, N. S., and Karsdal, M. A. (2016). Chapter 2 - type II collagen. Biochemistry of collagens, laminins and elastin (pp. 13-20) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00002-7.

Guttmann, R. P., J. S. Elce, P. D. Bell, J. C. Isbell, and G. V. W.Johnson. (1997). Oxidation inhibits substrate proteolysis by calpain I but not autolysis. Journal of Biological Chemistry. 272:2005–2012.

Guzek, D., Głąbska, D., Głąbski, K., and Wierzbicka, A. (2016). Influence of duroc breed inclusion into polish landrace maternal line on pork meat quality traits. Anais Da Academia Brasileira De Ciencias, 88(2), 1079-1088. doi:10.1590/0001-3765201620140679.

Ha, J., and Jang, S. (. (2012). The effects of dining atmospherics on behavioral intentions through quality perception. Journal of Services Marketing, 26(3), 204-215. doi:10.1108/08876041211224004.

Hagg, R., Bruckner, P., and Hedbom, E (1998). Cartilage fibrils of mammals are biochemically heterogeneous: Differential distribution of decorin and collagen IX. The Journal of Cell Biology, 142(1), 285-294. doi:10.1083/jcb.142.1.285.

Hall, L.D. (1910). Market classes and grades of meat Agricultural Experiment Station Bulletin No 147. Retrieved from http://gateway.proquest.com/openurl?url_ver=Z39.88-2004&res_dat=xri:c19index-us&rft_dat=xri:c19index:NSTC:0315704.

Hambrecht, E., Eissen, J. J., and Verstegen, M. W. A. (2003). Effect of processing plant on pork quality. Meat Science, 64(2), 125-131. doi:10.1016/S0309-1740(02)00166-3

Hamm, R. (1961). Biochemistry of meat hydration. Advances in food research (pp. 355-463) Elsevier Science and Technology. doi:10.1016/S0065-2628(08)60141-X Retrieved from https://www.sciencedirect.com/science/article/pii/S006526280860141X.

Hamm, R. (1986). 4 - functional properties of the myofibrillar system and their measurements. In P.J. Bechtel (Ed.), Muscle as food (pp. 135-199) Elsevier Inc. doi:10.1016/B978-0-12-084190-5.50009-6.

Hamzah, A., Nguyen, N. H., Mekkawy, W., Ponzoni, R. W., Khaw, H. L., Yee, H. Y. and Mohd Nor, S. A. (2016). Flesh characteristics: Estimation of genetic parameters and correlated responses to selection for growth rate in the GIFT strain. Aquaculture Research, 47(7), 2139-2149. doi:10.1111/are.12667.

Hayes, E. J. (2010). Sensory descriptors for cooked meat products. Sensory analysis of foods of animal origin (1st ed., pp. 147-173) CRC Press. Retrieved from http://www.crcnetbase.com/isbn/9781439847961.

Health Canada. (2015). General food tips. safe internal cooking temperatures chart. Retrieved from Health Canada Website. Https://Www.Canada.Ca/En/Health-

Canada/Services/General-Food-Safety-Tips/Safe-Internal-Cooking-Temperatures-Chart.Html.

Henriksen, K., and Karsdal, M. A. (2016). Chapter 1 - type I collagen. Biochemistry of collagens, laminins and elastin (pp. 1-11) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00001-5.

Hermesch, S., Luxford, B. G., and Graser, H. -. (2000). Genetic parameters for lean meat yield, meat quality, reproduction and feed efficiency traits for australian pigs: 1. description of traits and heritability estimates. Livestock Production Science, 65(3), 239-248. doi:10.1016/S0301-6226(00)00150-0.

Heymann, H., Hedrick, H. B., Karrasch, M. A., Eggeman, M. K., and Ellersieck, M. R. (1990). Sensory and chemical characteristics of fresh pork roasts cooked to different endpoint temperatures. Journal of Food Science, 55(3), 613-617. doi:10.1111/j.1365-2621.1990.tb05189.x.

Hill, F. (1966). The solubility of intramuscular collagen in meat animals of various ages. Journal of Food Science, 31(2), 161-166. doi:10.1111/j.1365-2621. 1966.tb00472.x.

Hill, F. (1966). The solubility of intramuscular collagen in meat animals of various ages. Journal of Food Science, 31(2), 161-166. doi:10.1111/j.1365-2621.1966.tb00472.x.

Hill, W. G. (2001). Genetic correlation. In Sydney Brenner, Jefferey H. Miller (Ed.), Encyclopedia of genetics (pp. 823-825) Academic press. doi:https://doi.org/10.1006/rwgn.2001.1423. Retrieved from https://search.credoreference.com/content/entry/estbengen/genetic_correlation/0.

Hill, W. G., Visscher, P. M., and Wray, N. R. (2008). Heritability in the genomics era - concepts and misconceptions. Nature Reviews Genetics, 9(4), 255-266. doi:10.1038/nrg2322.

Hocquette, J., Botreau, R., Picard, B., Jacquet, A., Pethick, D. W., and Scollan, N. D. (2012). Opportunities for predicting and manipulating beef quality. Meat Science, 92(3), 197-209. doi:10.1016/j.meatsci.2012.04.007.

Hodgson, R. R., Davis, G. W., Smith, G. C., Savell, J. W., and Cross, H. R. (1991). Relationships between pork loin palatability traits and physical characteristics of cooked chops. Journal of Animal Science, 69(12), 4858-4865. doi:10.2527/1991.69124858x.

Hofmann, K. (1973). Was ist fleischqualitat? Fleischwirtschaft, (53), 485-489.

Hofmann, K. (1974). Notwendigkeit und vorschlageinereinheitlichen definition des begriffes "fleischqualitat". Fleischwirtschaft, 10, 1607-1609.

Honikel, K. O. (1998). Reference methods for the assessment of physical characteristics of meat. Meat Science, 49(4), 447-457. doi:10.1016/S0309-1740(98)00034-5.

Honkavaara M. (1988). Influence of PSE pork on the quality and economics of cooked, cured ham and fermented dry sausage manufacture. Meat Science. 24 (3):201-207.https://doi.org/10.1016/0309-1740(88)90078-2.

Hornstein, I., and Crowe, P. F. (1960). Meat flavor chemistry, flavor studies on beef and pork. Journal of Agricultural and Food Chemistry, 8(6), 494-498. doi:10.1021/jf60112a022.

Hovenier, R., Kanis, E., van Asseldonk, T., and Westerink, N. G. (1992). Genetic parameters of pig meat quality traits in a halothane negative population. Livestock Production Science, 32(4), 309-321. doi:10.1016/0301-6226(92)90002-L.

Hsiang, M. W. and Cole, R. D. (1978). Chapter 12 determination of the primary structures of histones. Methods in cell biology (pp. 189-228) Elsevier Science & Technology. doi:10.1016/S0091679X(08)60140-5. Retrieved from https://www.sciencedirect.com/science/article/pii/S0091679X08601405.

Huff-Lonergan, E., and Lonergan, S. M. (2005). Mechanisms of water-holding capacity of meat: The role of postmortem biochemical and structural changes. Meat Science, 71(1), 194-204. doi:10.1016/j.meatsci.2005.04.022.

Huff-Lonergan, E., Zhang, W., and Lonergan, S. M. (2010). Biochemistry of postmortem muscle — lessons on mechanisms of meat tenderization. Meat Science, 86(1), 184-195. doi: 10.1016/j.meatsci.2010.05.004.

Huffman, K. L., Miller, M. F., Hoover, L. C., Wu, C. K., Brittin, H. C. and Ramsey, C. B. (1996). Effect of beef tenderness on consumer satisfaction with steaks consumed in the home and restaurant. Journal of Animal Science, 74(1), 91-97. doi:10.2527/1996.74191x.

Hugenschmidt, G., Hadorn, R., Guggisberg, D., Silacci, P., Scherrer, D., Haldimann, M., Scheeder, M. and Wenk, C. (2009). Physico-chemical characterization of destructured zones in cooked hams. Fleischwirtschaft, 89(1), 86-91.

Hulmes, D. J. S., Miller, A., Parry, D. A. D., Piez, K. A., and Woodhead-Galloway, J. (1973). Analysis of the primary structure of collagen for the origins of molecular packing. Journal of Molecular Biology, 79(1), 137-148. doi:10.1016/0022-2836(73)90275-1.

Hulmes. D.J.S. (2008). Collagen diversity, synthesis and assembly. In: P. Fratzl (Ed.), Collagen (pp. 15-47) Springer US. doi:10.1007/978-0-387-73906-9_2.

Hynes, R. O. (2002). Integrins: Bidirectional, allosteric signaling machines Elsevier Inc. doi:10.1016/S0092-8674(02)00971-6.

Hynes, R. O. (2009). The extracellular matrix: Not just pretty fibrils. Science, 326(5957), 1216-1219. doi:10.1126/science.1176009.

Ishida, Y., and Nagata, K. (2011). In Whisstock J. C., Bird P. I. (Eds.), Chapter nine - Hsp47 as a collagen-specific molecular chaperone Academic Press. doi://doi.org/10.1016/B978-0-12-386471-0.00009-2.

Jackson, S. R., Eckford, S. D., Abrams, P., Avery, N. C., Tarlton, J. F., and Bailey, A. J. (1996). Changes in metabolism of collagen in genitourinary prolapse. The Lancet, 347(9016), 1658-1661. doi:10.1016/S0140-6736(96)91489-0.

Järveläinen, H, Sainio, A, Koulu, M, Wight, T.N, and Penttinen, R. (2009). Extracellular matrix molecules: Potential targets in pharmacotherapy. Pharmacological Reviews, 61(2), 198-223. doi:10.1124/pr.109.001289.

Jensen, P., Craig, H. B., and Robison, O. W. (1967). Phenotypic and genetic associations among carcass traits of swine. Journal of Animal Science, 26(6), 1252. Retrieved from http://jas.fass.org/cgi/content/abstract/26/6/1252.

Jeremiah, L. E., and Martin, A. H. (1981). Intramuscular collagen content and solubility: Their relationship to tenderness and alteration by postmortem aging. Canadian Journal of Animal Science, 61(1), 53-61. doi:10.4141/cjas81-008.

Jeremiah, L. E., Dugan, M. E. R., Aalhus, J. L., and Gibson, L. L. (2003). Assessment of the relationship between chemical components and palatability of major beef muscles and muscle groups. Meat Science, 65(3), 1013-1019. doi:10.1016/S0309-1740(02)00309-1.

Jeremiah, L. E., Gibson, L. L., Gibson, J. P., Ball, R. O., Aker, C., and Fortin, A. (1999). The influence of breed, gender, and PSS (halothane) genotype on meat quality, cooking loss, and palatability of pork. Food Research International, 32(1), 59-71. doi:10.1016/S0963-9969(99)00077-0.

Johansson, K. (1987). Evaluation of station testing of pigs. Acta Agriculturae Scandinavica, 37(1), 108-119. doi:10.1080/00015128709436548.

Johnson, Z. B., Chewning, J. J., and Nugent, R. A., 3rd. (1999). Genetic parameters for production traits and measures of residual feed intake in large white swine. Journal of Animal Science, 77(7), 1679. doi:10.2527/1999.7771679x.

Jones, H. E., Ramsey, C. B., Hines, R. C., and Hoes, T. L. (1980). Low temperature roasting of thawed or frozen pork loins. Journal of Food Science, 45(2), 178-181. doi:10.1111/j.1365-2621.1980.tb02571.x.

Jonsäll, A., Johansson, L., and Lundström, K. (2001). Sensory quality and cooking loss of ham muscle (M. biceps femoris) from pigs reared indoors and outdoors. Meat Science, 57(3), 245-250. doi:10.1016/S0309-1740(00)00097-8.

Joo, S., Joo, S., and Hwang, Y. (2017). The relationships between muscle fiber characteristics, intramuscular fat content, and fatty acid compositions in M. longissimus lumborum of hanwoo steers. Korean Journal for Food Science of Animal Resources, 37(5), 780-786. doi:10.5851/kosfa.2017.37.5.780

Jung, J., Shim, K., Na, C., and Choe, H. (2015). Studies on intramuscular fat percentage in live swine using real-time ultrasound to determine pork quality. Asian-Australasian Journal of Animal Sciences, 28(3), 318-322. doi:10.5713/ajas.14.0927.

Kassianidou, E., Probst, D., Jäger, J., Lee, S., Roguet, A., Schwarz, U. S., and Kumar, S. (2019). Extracellular matrix geometry and initial adhesive position determine stress fiber network organization during cell spreading. Cell Reports, 27(6), 189-1909.e4. doi:10.1016/j.celrep.2019.04.035.

Kauffman, R.G., and Warner, R.D. (1993). Evaluating pork carcasses for composition and quality. In Hollis.W (Ed.), Growth of the pig (pp. 141-166) CAB Internation.

Kaushal, G.P., Elbein, D.A., and Carver., E.W. (2014). The extracellular matrix. In Baynes, J. W and Dominiczak, M.H (Ed.), Medical biochemistry (4. ed. ed., pp. 380-393) Saunders Elsevier.

Kehlet, S. N., and Karsdal, M. A. (2016). Chapter 21 - type XXI collagen. Biochemistry of collagens, laminins and elastin (pp. 131-133) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00021-0.

Kempster, A. J., Dilworth, A. W., Evans, D. G., and Fisher, K. D. (1986). The effects of fat thickness and sex on pig meat quality with special reference to the problems associated with over leanness 1. butcher and consumer panel results. Animal Science, 43(3), 517-533. doi:10.1017/S0003356100002737.

Khorramizadeh, M. R., Tredget, E. E., Telasky, C., Shen, Q., and Ghahary, A. (1999). Aging differentially modulates the expression of collagen and collagenase in dermal fibroblasts. Molecular and Cellular Biochemistry, 194(1), 99-108. doi:1006909021352.

Khoshnoodi, J., Pedchenko, V., and Hudson, B. G. (2008). Mammalian collagen IV. Microscopy Research and Technique, 71(5), 357-370. doi:10.1002/jemt.20564.

Kim, C. W., Ho, G. P., and Ritchey, S. J. (1967). Collagen content and subjective scores for tenderness of connective tissue in animals of different ages. Journal of Food Science, 32(5), 586-588. doi:10.1111/j.1365-2621. 1967.tb00838. x.

Kim, K., Kim, J., Dekkers, J., and Rothschild, M. (2004b). Polar overdominant inheritance of a DLK1 polymorphism is associated with growth and fatness in pigs. Mammalian Genome, 15(7), 552-559. doi:10.1007/s00335-004-2341-0.

Kim, T. H., Choi, B. H., and Beever, J. E. (2004a). Polymorphism in the porcine agouti signalling protein (ASIP) gene. Animal Genetics, 35(5), 418-420. doi:10.1111/j.1365-2052.2004.01179.x.

Kim, T. W., Kim, C. W., Yang, M. R., No, G. R., Kim, S. W., and Kim, I. (2016). Pork quality traits according to postmortem pH and temperature in berkshire. Korean Journal for Food Science of Animal Resources, 36(1), 29-36. doi:10.5851/kosfa.2016.36.1.29.

Kim, Y. M., Choi, T. J., Ho Cho, K., Cho, E. S., Lee, J. J., Chung, H. J. and Jeong, Y. D. (2018). Effects of sex and breed on meat quality and sensory properties in three-way crossbred pigs sired by duroc or by a synthetic breed based on a Korean native breed. Korean Journal for Food Science of Animal Resources, 38(3), 544-553. doi:10.5851/kosfa.2018.38.3.544.

Kjeld, N. G., and Karsdal, M. A. (2016). Chapter 25 - type XXV collagen. Biochemistry of collagens, laminins and elastin (pp. 147-150) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00025-8.

Knapp, P., Willam, A., and Sölkner, J. (1997). Genetic parameters for lean meat content and meat quality traits in different pig breeds. Livestock Production Science, 52(1), 69-73. doi:10.1016/S0301-6226(97)00120-6.

Knüppel, L., Heinzelmann, K., Lindner, M., Hatz, R., Behr, J., Eickelberg, O., and Staab-Weijnitz, C. A. (2018). FK506-binding protein 10 (FKBP10) regulates lung fibroblast migration via collagen VI synthesis. Respiratory Research, 19(1), 1-14. doi:10.1186/s12931-018-0768-1.

Koch, M., Foley, J. E., Hahn, R., Zhou, P., Burgeson, R. E., Gerecke, D. R., and Gordon, M. K. (2001). Alpha 1(xx) collagen, a new member of the collagen subfamily, fibril-associated collagens with interrupted triple helices. The Journal of Biological Chemistry, 276(25), 23120-23126. doi:10.1074/jbc.M009912200.

Koide, T and Nagata, K. (2005). Collagen biosynthesis. In Jürgen Brinckmann · Holger Notbohm, P. K.Müller (Ed.), Collagen: Primer in structure, processing and assembly (pp. 247: 85–114) Springer. doi:10.1007/b103820.

Kovanen, V. (2002). Intramuscular extracellular matrix: Complex environment of muscle cells. Exercise and Sport Sciences Reviews, 30(1), 20-25. doi:10.1097/00003677-200201000-00005.

Kovanen, V., Suominen, H., and Heikkinen, E. (1984). Collagen of slow twitch and fast twitch muscle fibres in different types of rat skeletal muscle. European Journal of Applied Physiology and Occupational Physiology, 52(2), 235-42. doi:10.1007/bf00433399

Kristensen, L., Therkildsen, M., Riis, B., Sorensen, M. T., Oksbjerg, N., Purslow, P. P., and Ertbjerg, P. (2002). Dietary-induced changes of muscle growth rate in pigs: Effects on in vivo and postmortem muscle proteolysis and meat quality. Journal of Animal Science, 80(11), 2862. Retrieved from http://jas.fass.org/cgi/content/abstract/80/11/2862.

Kular, J. K., Basu, S., and Sharma, R. I. (2014). The extracellular matrix: Structure, composition, age-related differences, tools for analysis and applications for tissue engineering. London, England: SAGE Publications. doi:10.1177/2041731414557112

Lampe, A. K., and Bushby, K. M. D. (2005). Collagen VI related muscle disorders. Journal of Medical Genetics, 42(9), 673-685. doi:10.1136/jmg.2002.002311.

Lanari, M. C., and Cassens, R. G. (1991). Mitochondrial activity and beef muscle color stability. Journal of Food Science, 56(6), 1476-1479. doi:10.1111/j.1365-2621.1991.tb08619.x.

Langrock, T, and Hoffmann, R. (2012). Analysis of hydroxyproline in collagen hydrolysates. In Michail A. Alterman and Peter Hunziker (Ed.), Amino acid analysis: Methods and protocols, methods in molecular biology (pp. 271-280) Springer Science. doi:DOI 10.1007/978-1-61779-445-2_21.

Larzul, C., Lefaucheur, L., Ecolan, P., Gogue, J., Talmant, A., Sellier, P., Roy, P. and Monin, G. (1997). Phenotypic and genetic parameters for longissimus muscle fiber characteristics in relation to growth, carcass, and meat quality traits in large white pigs. Journal of Animal Science, 75(12), 3126. doi:10.2527/1997.75123126x

Latorre, M. A., Lázaro, R., Valencia, D. G., Medel, P., and Mateos, G. G. (2004). The effects of gender and slaughter weight on the growth performance, carcass traits, and meat quality characteristics of heavy pigs1. Journal of Animal Science, 82(2), 526-533. doi:10.1093/ansci/82.2.526.

Le Bihan-Duval, E., Berri, C., Baéza, E., Santé, V., Astruc, T., Rémignon, H. and Fernandez, X. (2003). Genetic parameters of meat technological quality traits in a grand-parental commercial line of turkey. Genetics, Selection, Evolution: GSE, 35(6), 623-635. doi:2003043.

Le Roy, P., Naveau, J., Elsen, J. M., and Sellier, P. (1990). Evidence for a new major gene influencing meat quality in pigs. Genetics Research, 55(1), 33-40. doi:10.1017/S0016672300025179.

Lebret, B. (2008). Effects of feeding and rearing systems on growth, carcass composition and meat quality in pigs. Animal, 2(10), 1548-1558. doi:10.1017/S1751731108002796.

Lebret, B., Le Roy, P., Monin, G., and Lefaucheur. L. (1999). Influence of the three RN genotypes on chemical composition, enzyme activities, and myofiber characteristics of porcine skeletal muscle. Journal of Animal Science, 77(6), 1482. Retrieved from https://search.proquest.com/docview/218108626.

Lebret, B., Listrat, A. and Clochefert, N. (1998). Age-related changes in collagen characteristics of porcine loin and ham muscles. Paper presented at the 718-719.

Lee, F. A. (2012). Basic food chemistry Springer Netherlands. Retrieved from https://ebookcentral.proquest.com/lib/ [SITE_ID]/detail.action?docID=3568176.

Lee, J., Song, K., Lee, H., Cho, K., Park, H., and Park, K. (2015). Genetic parameters of reproductive and meat quality traits in korean berkshire pigs. Asian-Australasian Journal of Animal Sciences, 28(10), 1388-1393. doi:10.5713/ajas.15.0097.

Lee, S. K., Lee, S. H., Choe, J. H., Choi, Y. M., Jung, K. C., Rhee, M. S., Ryu Y.C and Kim, B. C. (2012). The influence of pork quality traits and muscle fiber characteristics on the eating quality of pork from various breeds. Meat Science, 90(2), 284-291. doi:10.1016/j.meatsci.2011.07.012.

Leeming, D. J., and Karsdal, M. A. (2016). Chapter 5 - type V collagen. Biochemistry of collagens, laminins and elastin (pp. 43-48) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00005-2.

Lenth, R. V. (2016). Least-squares means: The R package lsmeans. Journal of Statistical Software, 69(1), 1-33. doi:10.18637/jss.v069.i01.

Li, K Tamai, K Tan, E M and Uitto, J. (1993). Cloning of type XVII collagen. complementary and genomic DNA sequences of mouse 180-kilodalton bullous pemphigoid antigen (BPAG2) predict an interrupted collagenous domain, a transmembrane segment, and unusual features in the 5'-end of the gene and the 3'-untranslated region of the mRNA.

Journal of Biological Chemistry, 268(12), 8825. Retrieved from http://www.jbc.org/content/268/12/8825.abstract.

Li, P., and Wu, G. (2018). Roles of dietary glycine, proline, and hydroxyproline in collagen synthesis and animal growth. Amino Acids, 50(1), 29-38. doi:10.1007/s00726-017-2490-6.

Li, Y. X., Cabling, M. M., Kang, H. S., Kim, T. S., Yeom, S. C., Sohn, Y. G. and Seo, K. S. (2013). Comparison and correlation analysis of different swine breeds meat quality. Asian-Australasian Journal of Animal Sciences, 26(7), 905-910. doi:10.5713/ajas.2012.12622.

Light, N., and Champion, A. E. (1984). Characterization of muscle epimysium, perimysium and endomysium collagens. The Biochemical Journal, 219(3), 1017-1026. doi:10.1042/bj2191017.

Light, N., Champion, A. E., Voyle, C., and Bailey, A. J. (1985). The role of epimysial, perimysial and endomysial collagen in determining texture in six bovine muscles. Meat Science, 13(3), 137-149. doi:10.1016/0309-1740(85)90054-3.

Lilliefors, H. W. (1967). On the kolmogorov-smirnov test for normality with mean and variance unknown. Journal of the American Statistical Association, 62(317), 399. Retrieved from https://search.proquest.com/docview/1311791678.

Lisiak, D., Duziński, K., Janiszewski, P., Borzuta, K., and Knecht, D. (2015). A new simple method for estimating the pork carcass mass of primal cuts and lean meat content of the carcass. Animal Production Science, 55(8), 1044-1050. doi:10.1071/AN13534.

Listrat, A., Lebret, B., Louveau, I., Astruc, T., Bonnet, M., Lefaucheur, L., Brigitte, P, and Bugeon, J. (2016). How muscle structure and composition influence meat and flesh quality. The Scientific World Journal, 2016 doi:10.1155/2016/3182746

Liu, A., Nishimura, T., and Takahashi, K. (1996). Relationship between structural properties of intramuscular connective tissue and toughness of various chicken skeletal muscles. Meat Science, 43(1), 43-49. doi:10.1016/0309-1740(95)00065-8.

Lo, L. L., McLaren, D. G., McKeith, F. K., Fernando, R. L., and Novakofski, J. (1992). Genetic analyses of growth, real-time ultrasound, carcass, and pork quality traits in duroc and landrace pigs: II. heritabilities and correlations. Journal of Animal Science, 70(8), 2387-2396. doi:10.2527/1992.7082387x.

Lonergan, S. M., Huff-Lonergan, E., Rowe, L. J., Kuhlers, D. L., and Jungst, S. B. (2001). Selection for lean growth efficiency in duroc pigs influences pork quality. Journal of Animal Science, 79(8), 2075. doi:10.2527/2001.7982075x.

Lonergan, S.M., Topel, D.G. and Marple, D.N. (2019). The science of animal growth and meat technology. (2nded.).US:AcademicPress.Retrievedfrom https://ebookcentral.proquest.com/lib/[SITE_ID]/detail.action?docID=5568971.

Loyd, E. J., and Hiner, R. L. (1959). Meat tenderness, relation between hydroxyproline of alkali-insoluble protein and tenderness of bovine muscle. Journal of Agricultural and Food Chemistry, 7(12), 860-862. doi:10.1021/jf60106a010.

Lu, H., Wang, H., and Luo, Y. (2017). Changes in protein oxidation, water-holding capacity, and texture of bighead carp (aristichthys nobilis) fillets under chilled and partial frozen storage. Journal of Aquatic Food Product Technology, 26(5), 566-577. doi:10.1080/10498850.2016.1238860.

Mackenzie, K. J. J. (1919). Cattle and the future of beef-production in England University press. Retrieved from http://www.econis.eu/PPNSET?PPN=322064252.

MacLeod, G. and Seyyedain-Ardebili, M. (1981). Natural and simulated meat flavors (with particular reference to beef) doi:10.1080/10408398109527309.

Magowan, E., Moss, B., Fearon, A. and Ball. E. (2011). Effect of breed, finish weight and sex on pork meat and eating quality and fatty acid profile. Agricultural Research Institute of Northern Ireland, 1-22. Retrieved from www.afbini.gov.uk

Mahlapuu, M, Göran,H, Andersson, L., Johansson, C., Krook, A., Barnes, B., Zierath, J., Andersson., L and Marklund, S. (2004). Expression profiling of the gamma-subunit isoforms of AMP-activated protein kinase suggests a major role for gamma 3 in white skeletal muscle. American Journal of Physiology-Endocrinology and Metabolism, 286(2), E194. doi:10.1152/ajpendo.00147.2003.

Malmfors, B., and Nilsson, R. (1978). Meat quality traits in swedish landrace and yorkshire pigs with special emphasis on genetics. Acta Agriculturae Scandinavica, 28(1), 81-90. doi:10.1080/09064702.1978.11884472.

Mammalian Gene Collection (MGC) Program Team. (2002). Generation and initial analysis of more than 15,000 full-length human and mouse cDNA sequences. Proceedings of the National Academy of Sciences of the United States of America, 99(26), 16899-16903. doi:10.1073/pnas.242603899.

Mane, B.G., Mendiratta, S.K., and Dhanze, H. (2014). Tenderization of meat and meat products: A detailed review. In Haghi, A.K., Carvajal-Millan, Elizabeth (Ed.), Food composition and analysis. Pp.95-113. Apple Academic Press. Retrieved from http://www.crcnetbase.com/isbn/9781482231663.

Marchi D.F., Beteto F.M., Santos G.R., Soares A.L., Ida E.I. and Shimokomaki M. (2011). Changes in collagen fractions during PSE meat (pale, soft, exudative) chicken installation. Paper presented at the 1-4.

Marschner, I. C. (2011). Glm2: Fitting generalized linear models with convergence problems. R Journal, 3(2), 12-15.

Mateescu, R. G., Garrick, D. J., Garmyn, A. J., VanOverbeke, D. L., Mafi, G. G., and Reecy, J. M. (2015). Genetic parameters for sensory traits in longissimus muscle and their associations with tenderness, marbling score, and intramuscular fat in angus cattle. Journal of Animal Science, 93(1), 21. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/25412744.

Matsuo, N., Tanaka, S., Yoshioka, H., Koch, M., Gordon, M. K., and Ramirez, F. (2008). Collagen XXIV (Col24a1) gene expression is a specific marker of osteoblast differentiation and bone formation. Connective Tissue Research, 49(2), 68-75. doi:10.1080/03008200801913502.

McClain, P. E., Wiley, E. R. and McCague, K. E. (1971). Species variation in the crosslinking characteristics of collagen from the intramuscular connective tissue of striated muscles (bos taurus, ovis aries, sus scrofa). International Journal of Biochemistry,2,167-172.

McNerny, Erin, M. B., Bo, G., Morris Michael, D., and Kohn David, H. (2015). Bone fracture toughness and strength correlate with collagen cross-link maturity in a dose-controlled lathyrism mouse model. Journal of Bone and Mineral Research, 30(3), 455-464. doi:10.1002/jbmr.2356.

Meek, K.M., Chapman, J.A, and Hardcastle, R.A. (1979). The staining pattern of collagen fibrils. improved correlation with sequence data. Journal of Biological Chemistry, 254(21): 10710-10714. Retrieved from http://www.jbc.org/content/254/21/10710.abstract.

Merry, U. (1995). Coping with uncertainty: Insights from the new sciences of chaos, self-organization, and complexity. United States: Retrieved from http://catalog.hathitrust.org/Record/002969651

Miar, Y., Plastow, G. S., Moore, S. S., Manafiazar, G., Charagu, P., Kemp, R. A. and Wang, Z. (2014). Genetic and phenotypic parameters for carcass and meat quality traits in commercial crossbred pigs. Journal of Animal Science, 92(7), 2869. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/24778330.

Milan, D., Jeon, J., Looft, C., Amarger, V., Robic, A., Thelander., M., Rogel-Gaillard, C., Paul, S., Iannuccelli, N., Rask, L., Ronne, H., Lundström, K., Reinsch, N., Gellin, J., Kalm, E., Roy, P.L., Chardon, P., and Andersson, L. (2000). A mutation in PRKAG3 associated with excess glycogen content in pig skeletal muscle. Science, 288(5469), 1248-1251. doi:10.1126/science.288.5469.1248.

Miles, C. A., Avery, N. C., Rodin, V. V. and Bailey, A. J. (2005). The increase in denaturation temperature following cross-linking of collagen is caused by dehydration of the fibres. Journal of Molecular Biology, 346(2), 551-556.

Miller, K. D., Ellis, M., McKeith, F. K., Bidner, B. S., and Meisinger, D. J. (2000). Frequency of the rendement napole RN- allele in a population of american hampshire pigs. Journal of Animal Science, 78(7), 1811. doi:10.2527/2000.7871811x.

Milz, S., Ockert, B., and Putz, R. (2009). Tenocytes and the extracellular matrix: A reciprocal relationship. Der Orthopade, 38(11), 10711079. doi:10.1007/s00132-009-1490-y.

Mir, N. A., Rafiq, A., Kumar, F., Singh, V., and Shukla, V. (2017). Determinants of broiler chicken meat quality and factors affecting them: A review. Journal of Food Science and Technology, 54(10), 2997-3009. doi:10.1007/s13197-017-2789-z.

Miyada, D. S., and Tappel, A. L. (1956). Colorimetric determination of hydroxyproline. Analytical Chemistry, 28(5), 909-910. doi:10.1021/ac60113a039.

Moeller, S. J., Baas, T. J., Leeds, T. D., Emnett, R. S., and Irvin, K. M. (2003). Rendement napole gene effects and a comparison of glycolytic potentialand DNA genotyping for classification of rendement napole status in hampshire-sired pigs12. Journal of Animal Science, 81(2), 402-410. doi:10.2527/2003.812402x.

Møller, A. J. (1981). Analysis of warner-bratzler shear pattern with regard to myofibrillar and connective tissue components of tenderness. Meat Science, 5(4), 247-260. doi:10.1016/0309-1740(81)90015-2.

Monin, G., and Santé-Lhoutellier, V. (2014). Conversion of muscle to meat color and texture deviations. In C. Devine and M. Dikeman (Ed.), Encyclopedia of meat sciences (pp. 339-345) Elsevier Ltd. doi:10.1016/B978-0-12-384731-7.00097-0.

Monin, G., and Sellier, P. (1985). Pork of low technological quality with a normal rate of muscle pH fall in the immediate post-mortem period: The case of the hampshire breed. Meat Science, 13(1), 49-63. doi:10.1016/S0309-1740(85)80004-8.

Morris, N P and Bachinger, H.P. (1987). Type XI collagen is a heterotrimer with the composition (1 alpha, 2 alpha, 3 alpha) retaining non-triple-helical domains. Journal of Biological Chemistry, 262(23), 11345-11350. Retrieved from http://www.jbc.org/content/262/23/11345.abstract.

Mortimer, S. I., Van der Werf, J. H. J., Jacob, R. H., Hopkins, D. L., Pannier, L., Pearce, K. L. and Pethick, D. W. (2014). Genetic parameters for meat quality traits of Australian lamb meat. Meat Science, 96(2), 1016-1024. doi:10.1016/j.meatsci.2013.09.007.

Morton I.D, Akroyd P., and May C.G. (1960). Flavoring substances and their preparation. Retrievedfromhttps://worldwide.espacenet.com/publicationDetails/biblio?FT=D&date=19600426&DB=EPODOC&locale=&CC=US&NR=2934437A.

Mottram, D. S. (1994). Some aspects of the chemistry of meat flavour. In F. Shahidi (Ed.), Flavor of meat and meat products. (pp. 210-231) Springer, Boston, MA. doi://doi.org/10.1007/978-1-4615-2177-8_12.

Mottram, D. S. (1998). Flavor formation in meat and meat products: A review. Food Chemistry, 62(4), 415-424. doi:10.1016/S0308-8146(98)00076-4.

Murphy, S. K., Nolan, C. M., Huang, Z., Kucera, K. S., Freking, B. A., Smith, T. P., Leymaster, KA., Weidman,J.R and Jirtle, R. L. (2006). Callipyge mutation affects gene expression in cis: a potential role for chromatin structure. Genome research, 16(3), 340–346. doi:10.1101/gr.4389306

Myllyharju, J. (2005). Intracellular post-translational modifications of collagens. Collagen: Primer in structure, processing and assembly (pp. 115-147) Springer Berlin Heidelberg. doi:10.1007/b103821.

Myllyharju, J., and Kivirikko, K. I. (2001). Collagens and collagen-related diseases. Annals of Medicine, 33(1), 7-21. doi:10.3109/07853890109002055.

Myllyharju, J., and Kivirikko, K. I. (2004). Collagens, modifying enzymes and their mutations in humans, flies and worms. Trends in Genetics, 20(1), 33-43. doi: 10.1016/j.tig.2003.11.004.

Nagata, K. and Yamada, K.M. (1986). Phosphorylation and transformation sensitivity of a major collagen-binding protein of fibroblasts. Journal of Biological Chemistry, 261(16), 7531-7536. Retrieved from http://www.jbc.org/content/261/16/7531.abstract.

Nakamura Y.N, Iwamoto H, Tabata S, Ono Y, Shiba N, and Nishimura, S. (2003). Comparison of collagen content, distribution and architecture among the pectoralis, iliotibialis lateralis and puboischiofemoralis muscles with different myofiber composition in silky cocks. Animal Science Journal, 74(2), 119-128. doi:10.1046/j.1344-3941.2003.00096.x.

Nakamura, Y. N., Iwamoto, H., Shiba, N., Miyachi, H., Tabata, S., and Nishimura, S. (2004). Developmental states of the collagen content, distribution and architecture in the pectoralis, iliotibialis lateralis and puboischiofemoralis muscles of male red cornish x new hampshire and normal broilers. British Poultry Science, 45(1), 31. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15115198.

Nakano, T., and Thompson, J. R. (1980). Age- and sex-associated changes in chemical composition of bovine triceps brachii intramuscular and epimysial connective tissue with emphasis on glycosaminoglycans. Canadian Journal of Animal Science, 60(3), 643-662. doi:10.4141/cjas80-075.

Naveena, B. M., Kiran, M., Reddy, K. S., Ramakrishna, C., Vaithiyanathan, S., and Devatkal, S. K. (2011). Effect of ammonium hydroxide on ultrastructure and tenderness of buffalo meat. Meat Science, 88(4), 727-732. doi:10.1016/j.meatsci.2011.03.005.

Neuman, R.E. and Logan, A.M. (1950). The determination of hydroxyproline. J. Biol. Chem, 185, 299-306.

Newcom, D. W., Baas, T. J., Mabry, J. W. and Goodwin, R. N. (2002). Genetic parameters for pork carcass components. Journal of Animal Science, 80(12), 3099. Retrieved fromhttp://jas.fass.org/cgi/content/abstract/80/12/3099.

Nielsen, M. J., and Karsdal, M. A. (2016). Chapter 3 - type III collagen. Biochemistry of collagens, laminins and elastin (pp. 21-30) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00003-9.

Nishimura, T. (2010). The role of intramuscular connective tissue in meat texture. Animal Science Journal, 81(1), 21-27. doi:10.1111/j.1740-0929.2009.00696.x.

Nishimura, T., Hattori, A., and Takahashi, K. (1999). Structural changes in intramuscular connective tissue during the fattening of Japanese black cattle: Effect of marbling on beef tenderization. Journal of Animal Science, 77(1), 93. doi:10.2527/1999.77193x.

Nonneman, D. J., Brown-Brandl, T., Jones, S. A., Wiedmann, R. T., & Rohrer, G. A. (2012). A defect in dystrophin causes a novel porcine stress syndrome. BMC Genomics, 13(1), 233. doi:10.1186/1471-2164-13-233.

Novakofski, J., Park, S., Bechtel, P. J., and Mckeith, F. K. (1989). Composition of cooked pork chops: Effect of removing subcutaneous fat before cooking. Journal of Food Science, 54(1), 15-17. doi:10.1111/j.1365-2621.1989.tb08556.x.

Novaković, S., and Tomašević, I. (2017). A comparison between warner-bratzler shear force measurement and texture profile analysis of meat and meat products: A review. IOP Conference Series: Earth and Environmental Science, 85, 12063. doi:10.1088/1755-1315/85/1/012063.

Oczkowicz, M. (2009). Polar overdominance – a putative molecular mechanism and the new examples in mammals. Journal of Animal and Feed Sciences, 18(1), 17-27. doi:10.22358/jafs/66362/2009.

Odetti, P. R., Borgoglio, A., and Rolandi, R. (1992). Age-related increase of collagen fluorescence in human subcutaneous tissue. Metabolism, 41(6), 655-658. doi:10.1016/0026-0495(92)90059-J.

Official methods of analysis of AOAC international (1995). Official Methods of Analysis of AOAC International. Arlington, Va: AOAC International.

Oksbjerg, N., Petersen, J. S., Sørensen, I. L., Henckel, P., Vestergaard, M., Ertbjerg, P. and Støier, S. (2000). Long-term changes in performance and meat quality of danish landrace pigs: A study on a current compared with an unimproved genotype. Animal Science, 71(1), 81-92.doi:10.1017/S1357729800054916.

Okumura, M., Kadokura, H., and Inaba, K. (2015). Structures and functions of protein disulfide isomerase family members involved in proteostasis in the endoplasmic reticulum. Free Radical Biology and Medicine, 83, 314-322. doi: 10.1016/j.freeradbiomed.2015.02.010.

Olsen, B. R. (1997). Collagen IX. International Journal of Biochemistry and Cell Biology, 29(4), 555-558. doi:10.1016/S1357-2725(96)00100-8.

Papadopoulos, S., Jürgens, K. D., and Gros, G. (2000). Protein diffusion in living skeletal muscle fibers: Dependence on protein size, fiber type, and contraction. Biophysical Journal, 79(4), 2084-2094. doi:10.1016/S0006-3495(00)76456-3.

Parvizi, J. and Kim, G.K. (2010). Chapter 53 - collagen. In: Javad Parvizi, Gregory K. Kim (Ed.), High yield orthopedics (pp. 107-109) W.B. Saunders. doi:10.1016/B978-1-4160-0236-9.00064-X.

Patiyal, S. N., and Katoch, S. S. (2006). Tissue specific and variable collagen proliferation in swiss albino mice treated with clenbuterol. Physiological Research, 55(1), 97. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15857157.

Petitclerc, E., Boutaud, A., Prestayko, A., Xu, J., Sado, Y., Ninomiya, Y., Sarras M.P. Jr, Hudson, B.G., and Brooks, P. C. (2000). New functions for non-collagenous domains of human collagen type IV. novel integrin ligands inhibiting angiogenesis and tumor growth in vivo. The Journal of Biological Chemistry, 275(11), 8051-8061. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/10713126.

Petruska, J.A. and Hodge, A.J. (1964). A subunit model for the tropocollagen macromolecule. Proceedings of the National Academy of Sciences of the United States of America, 51(5), 871-876. doi:10.1073/pnas.51.5.871.

Phillips, C. J. C., (2001). Breeding and reproduction. Principles of cattle production (pp. 108-141) CABI Publishers.

Pinto, N., Beraquet, M., N. J., and Cardoso, S. (2013). Effects of chilling methods and hot boning on quality parameters of M. longissimus lumborum from Bos indicus Nellore steer. Meat Science, 93(2), 201-206. doi: 10.1016/j.meatsci.2012.08.024.

Plumb, D.A, Ferrara, L, Torbica, T, Knowles, L, Mironov Jr, A, Kadler,K.E, Briggs M.D., and Boot-Handford, R.P (2011). Collagen XXVII organises the pericellular matrix in the growth plate. PLoS One, 6(12), e29422. doi: 10.1371/journal.pone.0029422.

Prockop, D. J., Sieron, A. L., and Li, S. (1998). Procollagen N-proteinase and procollagen C-proteinase. two unusual metalloproteinases that are essential for procollagen processing probably have important roles in development and cell signaling Elsevier B.V. doi:10.1016/S0945-053X (98)90013-0.

Provost, J., Kelly, B., Bodwin, J., and Wallert, M. (2016). The science of cooking: Understanding the biology and chemistry behind food and cooking John Wiley and Sons, Incorporated. Retrieved from https://ebookcentral.proquest.com/lib/[SITE_ID]/detail.action?docID=4530809.

Purslow, P. P. (2005). Intramuscular connective tissue and its role in meat quality. Meat Science, 70(3), 435-447. doi:10.1016/j.meatsci.2004.06.028.

Purslow, P. P. (2018). Contribution of collagen and connective tissue to cooked meat toughness; some paradigms reviewed. Meat Science, 144, 127-134. doi: 10.1016/j.meatsci.2018.03.026.

Purslow, P. P., Oiseth, S., Hughes, J., and Warner, R. D. (2016). The structural basis of cooking loss in beef: Variations with temperature and ageing. Food Research International, 89(Pt 1), 739-748. doi:10.1016/j.foodres.2016.09.010.

R Core Team. (2018). R: Language for statistical computing. R foundation for statistical computing. Vienna, Austria: URL https://www.R-project.org/.

Raes, K., Balcaen, A., Dirinck, P., De Winne, A., Claeys, E., Demeyer, D., and De Smet, S. (2003). Meat quality, fatty acid composition and flavour analysis in belgian retail beef. Meat Science, 65(4), 1237-1246. doi:10.1016/S0309-1740(03)00031-7.

Ramírez, R., and Cava, R. (2007). Carcass composition and meat quality of three different iberian × duroc genotype pigs. Meat Science, 75(3), 388-396. doi:10.1016/j.meatsci.2006.08.003.

Reineccius, G. (2016). Flavor chemistry and technology, second edition CRC Press. Retrieved from http://www.crcnetbase.com/isbn/9780203485347.

Ritchie, H. and Roser M. (2019). "Meat and Seafood Production and Consumption". Published online at OurWorldInData.org. Retrieved from: 'https://ourworldindata.org/meat-and-seafood-production-consumption'.

Rowe, L. J., Maddock, K. R., Lonergan, S. M., and Huff-Lonergan, E. (2004). Oxidative environments decrease tenderization of beef steaks through inactivation of mu-calpain. Journal of Animal Science, 82(11), 3254. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15542472.

Roy, B. C., Oshima, I., Miyachi, H., Shiba, N., Nishimura, S., Tabata, S. and Iwamoto, H. (2007). Histochemical properties and collagen architecture of M. iliotibialis lateralis and M. puboischiofemoralis in male broilers with different growth rates induced by feeding at different planes of nutrition. British Poultry Science, 48(3), 312. doi:10.1080/00071660701370491.

Ruoslahti, E. (1988). Structure and biology of proteoglycans. Annual Review of Cell Biology, 4, 229-255

Rusell, S. M. (2000). Functional properties of muscle proteins in processed poultry products. Poultry meat processing (pp. 191-204) CRC Press. doi:10.1201/9781420042177-14 Retrieved from https://doi.org/10.1201/9781420042177-14.

Ryan, M. T., Hamill, R. M., O'Halloran, A. M., Davey, G. C., McBryan, J., Mullen, A. M., McGee, C., Gispert, M., Southwood, O.I., and Sweeney, T. (2012). SNP variation in the promoter of the PRKAG3 gene and association with meat quality traits in pig. BMC Genetics, 13(1), 66. doi:10.1186/1471-2156-13-66.

Sainio, A., and Järveläinen, H. (2014). Extracellular matrix macromolecules: Potential tools and targets in cancer gene therapy. Molecular and Cellular Therapies, 2(1), 14. doi:10.1186/2052-8426-2-14.

Sakakibara, K., Tabata, S., Shiba, N., Gotoh, T., Nishimura, S. and Iwamoto, H. (2000). Myofibre composition and total collagen content in M. iliotibialis lateralis and M. pectoralis of silkie and white leghorn chickens. British Poultry Science, 41(5), 570-574. doi:10.1080/713654983.

Sakuma, H., Saito, K., Kohira, K., Ohhashi, F., Shoji, N., and Uemoto, Y. (2017). Estimates of genetic parameters for chemical traits of meat quality in japanese black cattle. Animal Science Journal, 88(2), 203-212. doi:10.1111/asj.12622.

Salas, R. C. D., and Mingala, C. N. (2017). Genetic factors affecting pork quality: Halothane and Rendement napole genes. Animal Biotechnology, 28(2), 148-155. doi:10.1080/10495398.2016.1243550.

Sand, J. M. B., Genovese, F., and Karsdal, M. A. (2016). Chapter 4 - type IV collagen. Biochemistry of collagens, laminins and elastin (pp. 31-41) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00004-0.

Sato, K., Mera, H., Wakitani, S., and Takagi, M. (2017). Effect of epigallocatechin-3-gallate on the increase in type II collagen accumulation in cartilage-like MSC sheets. Bioscience, Biotechnology, and Biochemistry, 81(6), 1241-1245. doi:10.1080/09168451.2017.1282809.

Scheper, J. (1978). Influence of environmental and genetic factors on meat quality. Acta Agriculturae Scandinavica, 28(1), 20-31. doi:10.1080/09064702.1978.11884465.

Schmelzer, C. E. H., Getie, M., and Neubert, R. H. H. (2005). Mass spectrometric characterization of human skin elastin peptides produced by proteolytic digestion with pepsin and thermitase. Journal of Chromatography. A, 1083(1-2), 120. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/16078697.

Scott, J. E., Hughes, E. W., and Shuttleworth, A. (1981). A collagen-associated ehrlich chromogen: A pyrrolic cross-link? Bioscience Reports, 1(8), 611-618. doi:10.1007/BF01116276

Scott, J. E., Qian, R., Henkel, W. and Glanville, R. W. (1983). An Ehrlich chromogen in collagen cross-links. Biochemical Journal, 209(1), 263-264.

Sellier, P., and Monin, G. (1994). Genetics of pig meat quality: A review. Journal of Muscle Foods, 5(2), 187-219. doi:10.1111/j.1745-4573.1994.tb00530.x.

Serra, X., Gil, F., Pérez-Enciso, M., Oliver, M. A., Vázquez, J. M., Gispert, M., Díaz, I, Moreno, F, Latorre, R and Noguera, J. L. (1998). A comparison of carcass, meat quality and histochemical characteristics of iberian (guadyerbas line) and landrace pigs. Livestock Production Science, 56(3), 215-223. doi:10.1016/S0301-6226(98)00151-1.

Shackelford, S. D., Wheeler, T. L., and Koohmaraie, M. (1999). Evaluation of slice shear force as an objective method of assessing beef longissimus tenderness. Journal of Animal Science, 77(10), 2693. doi:10.2527/1999.77102693x.

Shackelford, S. D., Wheeler, T. L., and Koohmaraie, M. (2004). Technical note: Use of belt grill cookery and slice shear force for assessment of pork longissimus tenderness. Journal of Animal Science, 82(1), 238. Retrieved from http://jas.fass.org/cgi/content/abstract/82/1/238.

Sheard, P. R., Nute, G. R., Richardson, R. I., Perry, A., and Taylor, A. A. (1999). Injection of water and polyphosphate into pork to improve juiciness and tenderness after cooking. Meat Science, 51(4), 371-376. doi:10.1016/S0309-1740(98)00136-3.

Shearer, I. J., and Dunkin, A. C. (1968). Lactose utilisation by the growing pig. New Zealand Journal of Agricultural Research, 11(2), 465-476. doi:10.1080/00288233.1968.10431442.

Shen, L. Y., Luo, J., Lei, H. G., Jiang, Y. Z., Bai, L., Li, M. Z., Tang, G.Q, Li, X W, Zhang, S.H. and Zhu, L. (2015). Effects of muscle fiber type on glycolytic potential and meat quality traits in different tibetan pig muscles and their association with glycolysis-related gene expression. Genetics and Molecular Research: GMR, 14(4), 14366-14378. doi: 10.4238/2015.November.13.22.

Shimokomaki, M., Elsden, D. F., and Bailey, A. J. (1972). Meat tenderness: Age related changes in bovine intramuscular collagen. Journal of Food Science, 37(6), 892-896. doi:10.1111/j.1365-2621. 1972.tb03696. x.

Shin, H. K., Abugroun, H. A., Forrest, J. C., Okos, M. R. and Judge, M. D. (1992). Effect of heating rate on palatability and associated properties of pre - and postrigor muscle. Journal of Animal Science 71: 939 – 945.

Shingfield, K. J., Bonnet, M., and Scollan, N. D. (2013). Recent developments in altering the fatty acid composition of ruminant-derived foods. Animal: An International Journal of Animal Bioscience, 7 Suppl 1(s1), 132-162. doi:10.1017/S1751731112001681.

Shuttleworth, C. A. (1997). Type VIII collagen. International Journal of Biochemistry and Cell Biology, 29(10), 1145-1148. doi:10.1016/S1357-2725(97)00033-2.

Shuttleworth, C. A., and Forrest, L. (1975). Changes in guinea-pig dermal collagen during development. European Journal of Biochemistry, 55(2), 391-395. doi:10.1111/j.1432-1033. 1975.tb02174. x.

Siebuhr, A. S., and Karsdal, M. A. (2016). Chapter 13 - type XIII collagen. Biochemistry of collagens, laminins and elastin (pp. 87-91) Elsevier Inc. doi:10.1016/B978-0-12-809847-9.00013-1.

Sikes, A., Tornberg, E., and Tume, R. (2010). A proposed mechanism of tenderizing post-rigor beef using high pressure–heat treatment. Meat Science, 84(3), 390-399. doi: 10.1016/j.meatsci.2009.09.007.

Sionkowska, A. (2005). Current topics in polymer research. In K. R. Bregg (Ed.), New materials based on the blends of collagen and other polymers (pp. 125-168)

Sionkowska, A. (2011). Current research on the blends of natural and synthetic polymers as new biomaterials: Review. Progress in Polymer Science, 36(9), 1254-1276. doi:10.1016/j.progpolymsci.2011.05.003.

Smith G. C. and Z. L. Carpenter. (1974). National research council (US) board on agriculture and renewable resources. fat content and composition of animal products: Proceedings of a symposium Washington, D.C. December 12-13, 1974. washington (DC): National academies press (US); 1976. eating quality of meat animal products and their fat content. available from: Https://Www.ncbi.nlm.nih.gov/books/NBK216525/., 147-182.

Söderhäll, C., Marenholz, I., Kerscher, T., Rüschendorf, F., Esparza-Gordillo, J., Worm, M., Gruber, C., Mayr, G., Albrecht, M., Rohde, K., Schulz, H., Wahn, U., Hubner, N. and Lee,

Y. A. (2007). Variants in a novel epidermal collagen gene (COL29A1) are associated with atopic dermatitis. PLoS Biology, 5(9), 1952-1961.

Spanier, A. M., Flores, M., Toldrá, F., Aristoy, M. C., Bett, K. L., Bystricky, P., and Bland, J. M. (2004). Meat flavor: Contribution of proteins and peptides to the flavor of beef. Advances in Experimental Medicine and Biology, 542, 33. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/15174571.

Spanier, A. M., Vercellotti, J. R., and James, C. (1992). Correlation of sensory, instrumental and chemical attributes of beef as influenced by meat structure and oxygen exclusion. Journal of Food Science, 57(1), 10-15. doi:10.1111/j.1365-2621. 1992.tb05413. x.

Staab-Weijnitz, C. A., Fernandez, I. E., Knüppel, L., Maul, J., Heinzelmann, K., Juan-Guardela, B. M., Hennen, E., Preissler, G., Winter, H., Neurohr, C., Hatz, R., Lindner, M., Behr, J., Kaminski, N., and Eickelberg, O. (2015). FK506-binding protein 10, a potential novel drug target for idiopathic pulmonary fibrosis. American Journal of Respiratory and Critical Care Medicine, 192(4), 455-467. doi:10.1164/rccm.201412-2233OC.

Stoilov, I., Starcher, B. C., Mecham, R. P., and Broekelmann, T. J. (2018). Measurement of elastin, collagen, and total protein levels in tissues. Methods in Cell Biology, 143, 133-146. doi: 10.1016/bs.mcb.2017.08.008

Strong, C. L. (1951). Standard methods of measuring and grading for pork carcass evaluation American Meat Science Association. Reciprocal Meat Conference Proceedings. pp 123-141.

Suman, S. P. (2012). Application of proteomics to understand meat quality. In Y. H. Hui (Ed.), Handbook of meat and meat processing (2nd ed. ed., pp. 286-303) CRC Press. Retrieved from http://www.crcnetbase.com/isbn/9781439836842.

Sun, S., and Karsdal, M. A. (2016). Chapter 6 - type VI collagen. Biochemistry of collagens, laminins and elastin (pp. 49-55) doi:10.1016/B978-0-12-809847-9.00006-4.

Sun, X., Young, J. M., Liu, J. H. and Newman, D. J. (2017). Comparison of C and D65 illuminants of minolta colorimeter for assessing pork color. Paper presented at the Comparison of C and D65 Illuminants of Minolta Colorimeter for Assessing Pork Color. 68: 25-260.

Sundaramoorthy, M., Meiyappan, M., Todd, P., and Hudson, B. G. (2002). Crystal structure of NC1 domains. structural basis for type IV collagen assembly in basement membranes. The Journal of Biological Chemistry, 277(34), 31142-31153. doi:10.1074/jbc.M201740200.

Sundrum, A., Aragon, A., Schulze-Langenhorst, C., Bütfering, L., Henning, M., and Stalljohann, G. (2011). Effects of feeding strategies, genotypes, sex, and birth weight on carcass and meat quality traits under organic pig production conditions. NJAS - Wageningen Journal of Life Sciences, 58(3), 163-172. doi:10.1016/j.njas.2011.09.006.

Sutmulle, M., Bruijn, J. A., and De Heer, E. (1997). Collagen types vlll and X, two non-fibrillar, short-chain collagens. structure homologies, functions and involvement in pathology. Histol Histopathol. 557-566. Retrieved from http://hdl.handle.net/10201/18946.

Suzuki, K., Irie, M., Kadowaki, H., Shibata, T., Kumagai, M., and Nishida, A. (2005). Genetic parameter estimates of meat quality traits in Duroc pigs selected for average daily gain, longissimus muscle area, backfat thickness, and intramuscular fat content. Journal of Animal Science, 83(9), 2058-2065. doi:10.2527/2005.8392058x.

Swatland, H. J. (1990). A note on the growth of connective tissues binding turkey muscle fibers together. Canadian Institute of Food Science and Technology Journal, 23(4-5), 239-241. doi:10.1016/S0315-5463(90)70251-9.

Swatland, H. J. (1994). Connective tissues of the carcass. Structure and development of meat animals and poultry (pp. 65-143) CRC Press.

Swatland, H. J., and Findlay, C. J. (1997). On-line probe prediction of beef toughness, correlating sensory evaluation with fluorescence detection of connective tissue and dynamic analysis of overall toughness. Food Quality and Preference, 8(3), 233-239. doi:10.1016/S0950-3293(96)00053-5.

Takahara, K., Hoffman, G. G., and Greenspan, D. S. (1995). Complete structural organization of the human alpha 1 (V) collagen gene (COL5A1): Divergence from the conserved organization of other characterized fibrillar collagen genes. Genomics, 29(3), 588. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/8575750.

Tannor, B., Clark, N. G. and Hankins, O. G. (1943). Mechanical determination of the juiciness of meat. illus. Journal of Agricultural Research, 66, 403. Retrieved from https://search.proquest.com/docview/1308248426.

Taye, M., Kim, J., Yoon, S. H., Lee, W., Hanotte, O., Dessie, T., Kemp, S., Mwai O.A., Caetano-Anolles, K., Cho, S., Oh S.J., Lee H.K..and Kim, H. (2017). Whole genome scan reveals the genetic signature of african ankole cattle breed and potential for higher quality beef. BMC Genetics, 18(1), 11. doi:10.1186/s12863-016-0467-1.

Thakur, D. P., Morioka, K., Itoh, Y., and Obatake, A. (2002). Influence of muscle biochemical constituents on the meat texture of cultured yellowtail (seriola quinqueradiata) at different anatomical locations. Journal of the Science of Food and Agriculture, 82(13), 1541-1550. doi:10.1002/jsfa.1227.

Therkildsen, M., Riis, B., Karlsson, A., Kristensen, L., Ertbjerg, P., Purslow, P. P. and Oksbjerg, N. (2002). Compensatory growth response in pigs, muscle protein turn-over and meat texture: Effects of restriction/realimentation period. Animal Science, 75(3), 367-377. doi:10.1017/S1357729800053145.

Thomas, D. P. Scott D. Zimmerman, Thomas R. Hansen, David T. Martin, and Richard J. McCormick. (2000). Collagen gene expression in rat left ventricle: Interactive effect of age and exercise training. Journal of Applied Physiology, 89(4), 1462-1468. doi:10.1152/jappl.2000.89.4.1462.

Thompson, J. M. (2004). The effects of marbling on flavor and juiciness scores of cooked beef, after adjusting to a constant tenderness. Animal Production Science, 44(7), 645-652. doi:10.1071/EA02171.

Tornberg, E. (2005). Effects of heat on meat proteins – implications on structure and quality of meat products. Meat Science, 70(3), 493-508. doi:10.1016/j.meatsci.2004.11.021

Torrescano, G., Sánchez-Escalante, A., Giménez, B., Roncalés, P., and Beltrán, J. A. (2003). Shear values of raw samples of 14 bovine muscles and their relation to muscle collagen characteristics. Meat Science, 64(1), 85-91. doi:10.1016/S0309-1740(02)00165-1.

Traore, S., Aubry, L., Gatellier, P., Przybylski, W., Jaworska, D., Kajak-Siemaszko, K., and Santé-Lhoutellier, V. (2012). Higher drip loss is associated with protein oxidation. Meat Science, 90(4), 917-924. doi:10.1016/j.meatsci.2011.11.033.

Underly, K. (2012). The art of beef cutting (1. Aufl. ed.) Wiley. Retrieved from http://ebooks.ciando.com/book/index.cfm/bok_id/508797.

Van Laack, R. L., and Kauffman, R. G. (1999). Glycolytic potential of red, soft, exudative pork longissimus muscle. Journal of Animal Science, 77(11), 2971. doi:10.2527/1999.77112971x

Van Wijk, H. J., Arts, D. J. G., Matthews, J. O., Webster, M., Ducro, B. J., and Knol, E. F., (2005). Genetic parameters for carcass composition and pork quality estimated in a commercial production chain1. Journal of Animal Science, 83(2), 324-333. doi:10.2527/2005.832324x.

Ventanas, J., Ventanas, S., Ruiz, J., and García, C. (2007). Preference and juiciness of iberian dry-cured loin as affected by intramuscular fat content, crossbreeding and rearing system. Meat Science, 77(3), 324-330. doi: 10.1016/j.meatsci.2007.04.001

Voutila, L., Mullen, A. M., Ruusunen, M., Troy, D., and Puolanne, E. (2007). Thermal stability of connective tissue from porcine muscles. Meat Science, 76(3), 474-480. doi:10.1016/j.meatsci.2006.12.012.

Voyle, C. A. (1979). Meat. In J. G. Vaughan (Ed.), Food microscopy (pp. 193-231) Acad. Press.

Wagner, CT, Owens, RT, Harper, JR, and McQuillan, DJ. (2009). Human-derived acellular matrices for dermal replacement. In Orgill, D and Blanco, C (Ed.), Biomaterials for treating skin loss (pp. 150) Woodhead Publishing Series.

Wang, C., Jackson, G., Jones, T. H., Matsumoto, A. M., Nehra, A., Perelman, M. A., Ronald S Swerdloff, S.R., Traish, A., Zitzmann M and Cunningham, G. (2011). Low testosterone associated with obesity and the metabolic syndrome contributes to sexual dysfunction and cardiovascular disease risk in men with type 2 diabetes. Diabetes Care, 34(7), 1669-1675. doi:10.2337/dc10-2339.

Wang, K., Li, W., Bai, Y., Yang, W., Ling, Y., and Fang, M. (2017). Ssc-miR-7134-3p regulates fat accumulation in castrated male pigs by targeting MARK4 gene. International Journal of Biological Sciences, 13(2), 189-197. doi:10.7150/ijbs.17386.

Warner, K. F. (1952). Adventures in testing meat for tenderness. Proceedings of the Reciprocal Meat Conference, 5(156-160).

Warner, R. D. (2017). Chapter 14 - the eating quality of Meat—IV water-holding capacity and juiciness. In F. Toldra (Ed.), Lawrie's meat science (pp. 419-459) Elsevier Ltd. doi:10.1016/B978-0-08-100694-8.00014-5.

Watanabe, G., Motoyama, M., Nakajima, I., and Sasaki, K. (2018). Relationship between water-holding capacity and intramuscular fat content in Japanese commercial pork loin. Asian-Australasian Journal of Animal Sciences, 31(6), 914-918. doi:10.5713/ajas.17.0640.

Wayne, D. (2019). Rendement napole gene and pork quality. http://www.omafra.gov.on.ca/english/livestock/swine/facts/04-083.htm. Date Retrieved: October 15, 2019.

Weissgerber, T.L., Milic, N.M., Winham, S.J., and Garovic, V. D. (2015). Beyond bar and line graphs: Time for a new data presentation paradigm. PLoS Biology, 13(4), e1002128. doi:10.1371/journal.pbio.1002128.

Werfel, T., Kiess., W., and Spergel. J.M. (2011). Atopic dermatitis in childhood and adolescence (1., neue Ausg. (ed.) Karger. Pp. 41.

Wheeler, T. L., Shackelford, S. D., and Koohmaraie, M. (2000). Variation in proteolysis, sarcomere length, collagen content, and tenderness among major pork muscles. Journal of Animal Science, 78(4), 958. doi:10.2527/2000.784958x.

Wheeler, T.L., Shackelford, S.D., Johnson, L.P., Miller, M.F., Miller, R.K and Koohmaraie, M. (1997). A comparison of warner-bratzler shear force assessment within and among institutions. Journal of Animal Science, 75(9), 2423–2432. doi:https://doi.org/10.2527/1997.7592423x.

Williams, C.S., Williams, J.W., and Chung, R.A. (1986). Comparative microscopy and morphometry of skeletal muscle fibers in poultry.5(2), 207-217. Retrieved from http://digitalcommons.usu.edu/foodmicrostructure/vol5/iss2/4.

Wilson, K.B., Overholt, M.F., Hogan, E.K., Schwab, C., Shull, C.M., Ellis. M and Boler. D.D. (2016). Predicting pork loin chop yield using carcass and loin characteristics. Journal of Animal Science, 94(11), 4903. doi:10.2527/jas2016-0610.

Winder. W. W. (2001). Energy-sensing and signaling by AMP-activated protein kinase in skeletal muscle. Journal of Applied Physiology, 91(3), 1017-1028. doi:10.1152/jappl.2001.91.3.1017.

Winger R.J. and Hagyard C. J. (1994). Juiciness — its importance and some contributing factors. (pp. 94-116) Springer US. doi:10.1007/978-1-4615-2167-9 Retrieved from http://dx.doi.org/10.1007/978-1-4615-2167-9.

Wood, J. D., Brown, S. N., Nute, G. R., Whittington, F. M., Perry, A. M., Johnson, S. P., and Enser, M. (1996). Effects of breed, feed level and conditioning time on the tenderness of pork. Meat Science, 44(1), 105-112. doi:10.1016/S0309-1740(96)00044-7.

Wood, J. D., Nute, G. R., Richardson, R. I., Whittington, F. M., Southwood, O., Plastow, G., Mansbridge R., Da Costa, N., and Chang, K. C. (2004). Effects of breed, diet and muscle on fat deposition and eating quality in pigs. Meat Science, 67(4), 651-667. doi: 10.1016/j.meatsci.2004.01.007.

Woolley, L. D., Spivey, K. S., Martin, J. N., Johnston, J. E., Carmichael, R. N., Gredell, D. A. and Miller, M. F. (2016). A comparison of the foss foodscan and chemical analyses for proximate composition in fresh beef. Meat Science, 112, 151-152. doi:10.1016/j.meatsci.2015.08.113.

Xiong, Y. L. (1997). Structure function relationships of muscle proteins. In S. Damodaran (Ed.), Food proteins and their applications (pp. 341-392) Dekker.

Xiong, Y. L. (2000) Protein oxidation and implications for muscle foods quality. In: Antioxidants in Muscle Foods; Eds: Decker, E. A., Faustman, C., Lopez-Bote, C. J. Wiley: New York. Pp 85-111.

Yancey, J. W. S., and Kropf, D. H. (2008). Instrumental reflectance values of fresh pork are dependant on aperture size. Meat Science, 79(4), 734-739. doi:10.1016/j.meatsci.2007.11.006.

Yang, J., Jeong, D., Na, C., and Hwang, I. (2016). Eating quality traits of Han woo longissimus dorsi muscle as a function of end-point cooking temperature. Korean Journal for Food Science of Animal Resources, 36(3), 291-299. doi:10.5851/kosfa.2016.36.3.291.

Zaher, H. S., and Green, R. (2009). Fidelity at the molecular level: Lessons from protein synthesis. Cell, 136(4), 746-762. doi: 10.1016/j.cell.2009.01.036.

Zayas, J. F. (1997). Solubility of proteins. Functionality of proteins in food (pp. 6-33) Springer.

Zemva, M., Ngapo, T.M., Malovrh, S., Levart, A., and Kovac, M. (2015). Effect of sex and slaughter weight on meat and fat quality of the krškopolje pig reared in an enriched environment. Animal Production Science, 55(9), 1200. doi:10.1071/AN14059.

Zhang, W., Kuhlers, D. L., and Rempel, W. E. (1992). Halothane gene and swine performance. Journal of Animal Science, 70(5), 1307-1313. doi:10.2527/1992.7051307x.

Zheng, Y., Wang, S., and Yan, P. (2018). The meat quality, muscle fiber characteristics and fatty acid profile in Jinjiang and F1 Simmental×Jinjiang yellow cattle. Asian-Australasian Journal of Animal Sciences, 31(2), 301-308. doi:10.5713/ajas.17.0319.