# Genetics of Omega-3 Long-Chain Polyunsaturated Fatty Acid Metabolism and Meat Eating Quality in Tattykeel Australian White Lambs

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**Abstract:** Meat eating quality with a healthy composition hinges on intramuscular fat (IMF), fat melting point (FMP), tenderness, juiciness, flavour and omega-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA) content. These health-beneficial n-3 LC-PUFA play significant roles in optimal cardiovascular, retinal, maternal and childhood brain functions, and include alpha linolenic (ALA), eicosapentaenoic (EPA), docosahexaenoic (DHA) and docosapentaenoic (DPA) acids. The primary objective of this review was to access, retrieve, synthesise and critically appraise the published literature on the synthesis, metabolism and genetics of n-3 LC-PUFA and meat eating quality. Studies on IMF content, FMP and fatty acid composition were reviewed to identify knowledge gaps that can inform future research with Tattykeel Australian White (TAW) lambs. The TAW is a new sheep breed exclusive to MARGRA brand of lamb with an outstanding low fat melting point (28–39°C), high n-3 LC-PUFA EPA+DHA content (33–69mg/100g), marbling (3.4–8.2%), tenderness (20.0–38.5N) and overall consumer liking (7.9–8.5). However, correlations between n-3 LC-PUFA profile, stearoyl-CoA desaturase (SCD), fatty acid binding protein 4 (FABP4), fatty acid synthase (FASN), other lipogenic genes and meat quality traits present major knowledge gaps. The review also identified research opportunities in nutrition–genetics interactions aimed at a greater understanding of the genetics of n-3 LC-PUFA, feedlot finishing performance, carcass traits and eating quality in the TAW sheep. It was concluded that studies on IMF, FMP and n-3 LC-PUFA profiles in parental and progeny generations of TAW sheep will be foundational for the genetic selection of healthy lamb eating qualities and provide useful insights into their correlations with SCD, FASN and FABP4 genes.

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## 1. Introduction

Sheep production is an important economic activity in many countries because lamb is one of the world's four major meat classes along with pork, chicken and beef [1]. Sheep are produced mainly for their meat (lamb or mutton) and wool [2]. In 2017–2018, Australia exported 532,000 tonnes carcass weight of lamb representing 61% of total lamb production from 72.1 million head of sheep and was the largest sheep meat exporter in the world worth A\$3.28 billion [3]. Apart from sheep meat exports, Australians were also the world's highest consumers of lamb estimated at 7.3 kg/capita in 2018 [1]. Thus, lamb is a very significant contributor to the Australian economy and a major part of the Australian diet.

Lamb is a very nutritious, easily digestible and highly valued food with a healthy fatty acid composition [4]. Lamb consumers demand meat that is safe, of consistent eating quality, healthy composition and conveniently easy to prepare [5]. Meat quality is the constitutional standard of lean-to-fat ratio and palatability indices that include visual appearance, aroma, drip loss, colour, texture, pH, intramuscular fat profile, tenderness, flavour and juiciness [6]. The entire processes of feeding culminating in the finishing of animals including their genetic constitution, husbandry practices and handling, all affect the overall quality of meat [7]. There are genuine concerns about high fat consumption, especially fats of animal origin, as their profile has a significant influence on human health because excessive consumption of saturated fatty acids (SFA) is associated with high levels of low density-lipoproteins and cholesterol [8,9]. Both low density-lipoproteins and hypercholesterolemia are predisposing risk factors for cardiovascular disease [10], prostate, mammary and colorectal cancer [11,12], dry eye disease, [13], depression [14], obesity, diabetes [15,16] and neuro-degenerative conditions including Schizophrenia, Alzheimer's, Parkinson's disease [17]. In spite of animal lipids being criticised as health-risk factors, it is evident that they actively support many physiological functions and provide health-beneficial omega-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA) [5]. This is the basis for various animal production strategies aimed at enhancing health-beneficial fatty acids in meat and meat products [18,19]. This is because intramuscular fat, fatty acid content, water holding capacity and consistency largely influence meat organoleptic traits and retail potential namely, juiciness, tenderness, flavour, colour, shelf life and firmness [20,21].

In the quest for a meat sheep breed with good body conformation, superior eating qualities, low fat melting point (FMP), high intramuscular fat (IMF) and healthy n-3 LC-PUFA composition, the Gilmore Family in Black Springs, Oberon, New South Wales, pioneered the development of the Tattykeel Australian White (TAW) breed. This breed was developed over a 15-year period of rigorous breeding, culling and selection of Poll Dorset, Dorper, Texel and Van Rooy rams and ewes with an extensive utilisation of embryo transfer, artificial insemination and natural mating. Although preliminary evidence from our data in Table 1 suggests that the TAW sheep breed exclusive to the MARGRA brand of lamb has an outstanding low FMP, high n-3 LC-PUFA content and IMF, comprehensive peer-reviewed publications on its eating quality attributes and n-3 LC-PUFA profile are currently lacking. This necessitates further research into genetic factors that may determine IMF, FMP, n-3 LC-PUFA in this breed. Many genes and enzymes are responsible for fatty acid metabolism and their correlations with meat quality traits. However, the roles of stearoyl-CoA desaturase (SCD), fatty acid binding protein 4 (FABP4), and fatty acid synthase (FASN) are the most critical [22,23] and need further elucidation herein. Therefore, the primary objective of this review was to critically appraise the published literature regarding fatty acid synthesis and metabolism, IMF, FMP, and carcass quality to identify knowledge gaps and highlight research opportunities associated with nutrition–genetics

interactions influencing n-3 LC-PUFA that can inform future meat-eating quality investigations in TAW lambs.

**Table 1.** Tattykeel Australian White carcass and meat quality characteristics (*n* = 217).

| Trait | Mean ± SE | Range |
|---|---|---|
| Fat melting point (°C) | 34.08 ± 1.4 | 28.0–39.0 |
| Intramuscular fat (%) | 4.4 ± 0.2 | 3.4–8.2 |
| Hot standard carcass weight (kg) | 24.6 ± 2.7 | 19.5–30.7 |
| Dressing percentage | 50.2 ± 2.2 | 47.0–54.4 |
| Fat score | 4.7 ± 0.6 | 4–5 |
| GR fat depth (mm) | 16.4 ± 3.5 | 10–24 |
| Tenderness (N) | 32.3 ± 5.1 | 20.0–38.5 |
| pH | 5.63 ± 0.11 | 5.53–6.83 |
| Overall consumer liking (9-point scale) | 8.2 ± 0.9 | 7.9–8.5 |
| Omega-3 long chain PUFA (mg/100g) | | |
| EPA (20:5n-3) | 24.3 ± 5.2 | 17.8–44.8 |
| DHA (22:6n-3) | 8.3 ± 2.7 | 3.4–12.1 |
| DPA (22:5n-3) | 25.2 ± 8.0 | 14.0–80.3 |
| EPA + DHA | 32.6 ± 7.0 | 33.6–69.9 |
| EPA + DHA + DPA | 57.9 ± 13.6 | 49.1–132.5 |

EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; DPA, docosapentaenoic acid.

## 2. Fatty Acids, Classifications and Functions

Lipids are preferentially utilised as the major energy source in enteral diets owing to their high caloric value [24]. Fats are triglycerides comprising glycerol and fatty acids. Apart from their main biological function of energy storage, lipids are essential components of cellular membranes and signalling molecules [25]. Thus, Patterson et al. [26] stated that fatty acids as the "building units" of lipids, are hydrocarbon chains having a carboxyl (-COOH) group at one end and a methyl (-CH3) group at the other. When three fatty acids are attached to a glycerol molecule, energy-storing triacylglycerols are formed [27]. The amphiphilic structure of fatty acids arising from their hydrophilic carboxyl group attachment to a hydrophobic hydrocarbon chain or tail provides the ideal energy storage powerhouse that is characteristic of triacylglycerols [21]. The bonds between the carbon atoms in a hydrocarbon chain differentiate between saturated (SFA) and unsaturated (UFA) fatty acids. However, SFA consist of less reactive single bonds only, while UFA have one (monounsaturated, MUFA) or at least two (polyunsaturated, PUFA) reactive double bonds. Fats containing significant levels of MUFA like oleic acid (C18:1), contribute to high quality meat due to low melting point which leads to favourable meat flavour, tenderness and juiciness [28]. C18:1 as the most abundant MUFA in the adipose and muscle tissues of ruminants, and it is not easily susceptible to oxidation [29]. PUFA are further divided into four families: omega-3 (n-3), omega-6 (n-6), omega-7 (n-7) and omega-9 (n-9), based on the position of the initial double bond on the methyl terminal [30] or the location of the last double bond relative to the terminal methyl end of the molecule [31].

Fatty acids can also be subdivided into essential and non-essential fatty acids. The latter can be synthesised de novo (mainly in the liver), without the need for dietary supplementation [32] while the former on the other hand, cannot be synthesised by mammals and need to be included in the diet [21]. Essential fatty acids play significant roles in enzymatic regulation, eicosanoid synthesis, cell signalling, control of neuronal migration, neuromodulatory and neurotransmitter activities [33,34]. Some deficiency symptoms of essential fatty acids have been identified in a number of nutrition-related complications in the liver and kidneys, especially in children, to include dry and flaky skin, diarrhoea, anaemia, stunted growth and poor wound healing as well as compromised immunity leading to secondary infections [35]. Therefore, it is important to supply this group of fatty acids in correct proportions right from conception, throughout pregnancy and infancy.

*2.1. Omega-3 Long-Chain Polyunsaturated Fatty Acids*

The word "omega" (ω) in relation to fatty acids denotes the terminal carbon atom furthest from the functional carboxylic acid group (-COOH). These structural differences confer unique individual functions. Omega-3 (n-3) long-chain polyunsaturated fatty acids are a family of PUFA made up of α-linolenic acid (ALA, C18:3n-3), a precursor for the more functionally potent longer chain Eicosapentaenioc acid, 20:5n-3 (EPA) and Docosahexaenoic acid, 22:6n-3 (DHA) members of the family [36–38]. Omega-3 PUFA increase the stability of cell membranes, regulate immune function, block excessive inflammatory reaction [39], reduce systemic inflammatory response syndrome, various organ dysfunction syndromes, infectious complications and depress tumour growth [28,40]. The most important functional n-3 LC-PUFA related to human well-being are EPA and DHA [41]. Furthermore, the hitherto neglected roles of docosapentaenoic acid (DPA; 22:5n-3) are currently evolving [42,43]. A number of research findings have established that n-3 LC-PUFA are potent therapeutic agents for the suppression of inflammation, thus playing critical roles in a number of inflammatory conditions including diabetes, artherosclerosis, asthma and arthritis [34,44].

Cardiovascular ailments and cancer are the main causes of human death globally [45–47]. Thus, consumption of n-3 LC-PUFA decreases the danger of cardiovascular diseases by depressing systolic resting heart rate, diastolic blood pressure [48], blood viscosity [49], plasma fibrinogen [50] and platelet aggregation [51]. They also improve blood vessel function [52]. In adults, increased intake of n-3 LC-PUFA has remarkable brain health benefits, reduced risk of dementia and late cognitive malfunction [53], overall health at pregnancy [54], insulin resistance [16], depression and retarding the progression of certain cancers [55,56]. Gould et al. [57] reported that n-3 LC-PUFA play significant roles in neural development in embryos and at infancy. High consumption of EPA and DHA has also proved useful in improving foetal brain, retinal development, and reducing the risks associated with cardiovascular and Alzheimer's diseases [53]. Welch et al. [57] proposed DHA, EPA, n-3, ALA and LA dietary intakes of 0.16, 0.11, 1.50, 1.23 and 12.35g/d for men and 0.13, 0.09, 1.22, 0.99 and 9.42 for women, respectively. It has been recommended that patients susceptible to coronary heart disease should consume at least 1g of DPA and DHA daily; and good sources of these nutrients include seafood, particularly fatty fish (for example, mackerel, herring, sardines, salmon, trout, kippers, pilchards, eels and tuna), whales, seals and oil supplements from fish, cod liver, krill and algae [58,59]. However, the use of marine fish oil has some drawbacks including typical fishy smell, unpleasant taste, expensive cleansing procedure and adulteration by environmental contaminants including radioisotopes, dioxins and heavy metals [60,61]. Western diets contain 1.5–10.0 g of n-6 fatty acids which are derived from plant oils rich in linoleic acid. ALA is also found in canola (rapeseed) oil, flaxseed (linseed) oil, rapeseed oil, soybean oil, pumpkin seeds and walnut oil [62–64]. However, humans lack the enzymes required to transform n-3 from n-6 fatty acids, they also have a limited capacity to elongate and change ALA to EPA and DHA [63].

Figure 1 depicts the pathway where EPA is produced from simpler, plant-sourced n-3 fatty acids like ALA (18:3n-3) [59]. The enzymes involved in n-3 fatty acid interconversion are identical with the analogous n-6 fatty acid pathway for the transformation of linoleic acid (18:2n-6) to arachidonic acid (20:4n-6). Majority of these processes involve the addition of a double bond between two carbon atoms (desaturation) and addition of two carbon atoms (elongation reactions) [59,64]. While the enzymes involved in elongation and desaturation pathways are fairly understood in monogastrics, their roles in the interconversion of n-6 to n-3 fatty acids in ruminants is less understood, especially in Tattykeel Australian White lambs, due to biohydrogenation. This represents a major knowledge gap.
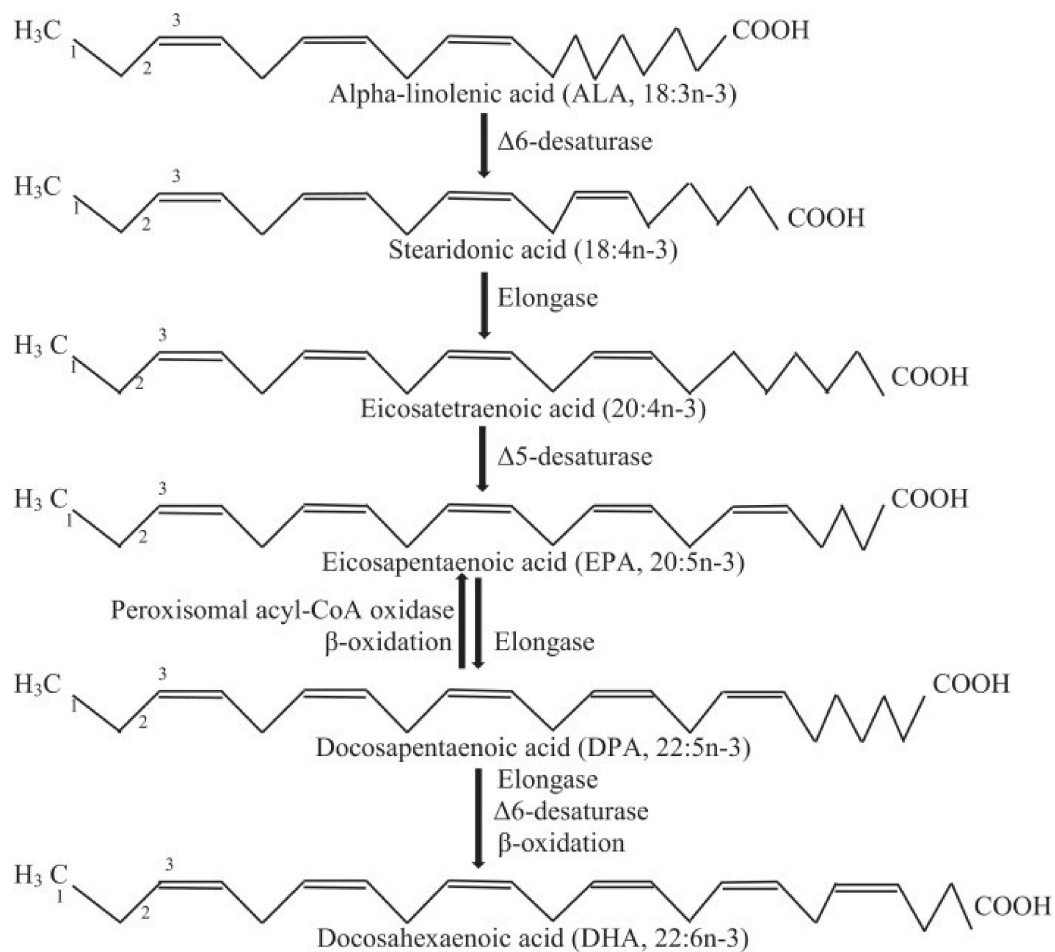
**Figure 1.** Pathway for the biosynthesis of omega-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA) from α-linolenic acid (ALA) [59].

Kris-Etherton et al. [65] reported that even though fish oil remains an excellent source of EPA and DHA, Lum et al. [66] recommended that attention is increasingly shifting towards cheaper but equally good substitute sources of n-3 fatty acids, including microalgae known to have high elongase and desaturase enzyme activities necessary for the biosynthesis of EPA and DHA [67]. DPA (C22:5) is similar to EPA with the same number of double bonds but has two more carbon chain units [68]. Its functions were in the past, poorly understood, but currently unravelled [43]. Epidemiological trials in humans have demonstrated high levels of DPA to be favourably correlated with lesser blood triglycerides, cholesterol, inflammation and a reduced total risk of cardiovascular diseases and acute myocardial infarction [46,69–71]. DPA is an active and potent stimulator of endothelial cell migration, an important part of the embryonic vascular system [72]. It also acts as a precursor for the synthesis of resolvins which are neuroprotective in function [43]. In other studies, Phang et al. [73] demonstrated that when applied to platelets or PC-21 human epithelial cell lines, purified DPA reduces platelet accumulation and aggregation more efficiently than EPA and DHA [74] and leads to endothelial cell migration [75] and inhibition of chronic inflammation [76].

Fatty Acid Profile and Nutritional Value

The fatty acid profile of meat is related to meat quality sensory attributes, nutritional value and health benefits [18,77]. For instance, a direct relationship between the content of stearic acid in the fat and fat hardness exists, because as the content of stearic acid increases, so does the fat hardness. This in turn, influences marbling fat melting point and meat juiciness. The quantity and type of intramuscular fat and fatty acids in both muscle and adipose tissues influence eating quality, juiciness, tenderness,

flavour, colour, shelf life and firmness of meat [20,21,78]. Fat content and amount of fatty acids are quantified in mg/100g of meat [79], whereas human nutritionists assess nutrient value of food per 100 g of serve. For food to be categorised or claimed as a source of n-3 LC-PUFA in Australia and New Zealand, its EPA and DHA contents should be greater than 30mg per serve, and declared a good source if it has at least 60mg of EPA and DHA for each standard serve [79–81]. In Europe, it is 40mg per 100g [82]. The World Health Organization [83] recommended that daily fat intake should be 30% of total energy, and of this, SFA should be reduced to 300mg per day. They also advocated that a reasonable balance of fatty acids in food should be established where intakes of cholesterol and SFA are decreased. The ratios between SFA and PUFA and n-6 and n-3 fatty acids determine the nutritional value of meat [78]. However, Simopoulos et al. [84] documented that in developed and industrialised countries, there is growth in the consumption of SFA, n-6 PUFA and trans fatty acids and a marked reduction in n-3 PUFA intake. The diets in these parts of the world have an n-6:n-3 PUFA ratio of about 15:1, compared to an ideal recommended ratio of 4:1 [51,85]. This unbalanced consumption leads to low tissue levels of DHA and EPA [86], resulting in higher incidences of inflammatory processes, cardiovascular diseases, obesity, inflammatory bowel disease, rheumatoid arthritis and cancer [87].

## 2.2. Factors Affecting Fat Profile in Ruminant Muscle and Adipose Tissues

Fatty acid profile is influenced by biohydrogenation in the rumen, dietary concentrate supplementation versus pasture finishing and genetics [17,88].

### 2.2.1. Biohydrogenation

Sheep, like all other ruminants, harbour a diverse microbial population in their rumen that enables the digestion of complex plant materials into more absorbable nutrients [89]. The rumen ecosystem is composed of anaerobic bacteria, protozoa, fungi, methanogenic archaea and phages [90]. Microbes play different, yet complimentary, roles in the rumen. Bacteria enzymatically convert sugars to volatile fatty acids (acetic 60–70%, propionic 15–20% and butyric acids 10–15%), which are the main energy substrates for ruminants [91,92]. Protozoa on the other hand, degrade complex carbohydrates and nitrogen into nutrients that are made available to the host, while anaerobic fungi engage in cellulolytic degradation activities [93]. The type and amount of fat delivered to the rumen [94], temperature of 38–39 °C [95] and pH range between 6.0 and 6.7 [96] dictate optimal rumen microbial function.

Ruminant diets are commonly made up of forages and concentrates with fats sometimes included, to raise the energy level in rations for lactating females or to enlarge the amount of human-health beneficial n-3 LC-PUFA, and bioactive conjugated linoleic acid in meat and milk [97]. Upon entry into the rumen, ingested lipids are degraded by microbial lipases via lipolysis [93,95,98]. Lipolysis breaks down lipids and releases free fatty acids from esters, thus facilitating biohydrogenation where the number of double bonds is reduced on the carbon chain [95], or under ideal conditions, 85% of esterified dietary lipids in the form of galactolipids, phospholipids and triacylglycerols are hydrolysed [95,99]. UFA get converted into SFA in the rumen due to microbial biohydrogenation activities involving series of consecutive conversion pathways leading to an abundance of fatty acid isomers [97], and remain a major human public health issue [100]. The bulk of the dietary fatty acids are 18-carbon UFA (linolenic acid, 18:3n-3; linoleic acid, 18:2n-6 and oleic acid, cis-9 18:1) [101]. However, the major biohydrogenation intermediate product in a ruminant fed forage diet is trans-vaccenic acid (trans-11 C18:1, t-VA) [102]. t-VA acts as a precursor required for the production of SFA in the rumen to yield stearic acid (C18:0). Conversely, it is desaturated by Δ9-desaturase enzyme in the mammary gland to yield cis-9, trans-11 C18:2 and its CLA isomer that can be easily detected in milk and meat [103]. Other end products of rumen metabolism are carbon dioxide, methane and traces of hydrogen [104] used as energy sources for the reduction of carbon dioxide to methane [105]. Short chain fatty acids (acetic acid (C2), propionic acid (C3), and butyric acid (C4)) produced are absorbed, transported and metabolised by different organs in the body of the host animal while carbon dioxide and methane are expelled from the body through different cycles of eructation or belching [106].

2.2.2. Influence of Concentrate or Forage Finishing on Lamb Performance and Meat Quality

Lamb finishing on pasture is cheaper than grain feeding [107], but the viability of pasture-finishing depends on a consistent supply of good quality forage [108]. This is achieved by growing a mixture of grasses and legumes. Legumes increase the nutritional quality through higher digestibility and protein content [109,110], healthier fatty acid composition and increased oxidative stability [111]. Meat derived from pasture-finished animals has higher CLA and PUFA content especially of the n-3 series in the *longissimus thoracis et lumborum* muscle than meat from feedlot or grain-fed ruminants and at the same time, the proportion of fat and cholesterol in meat from grass-fed ruminants is lower [19,112,113]. Mixed pasture finishing improves growth performance and carcass traits of grazing ruminants [114]. Apart from contributing to landscape maintenance, nature preservation, pasture feeding system is generally desired by health-conscious organic meat consumers [5]. However, pasture-finished meat has some limitations that include lower carcass weight [115] and extended periods of feeding to attain market weight specifications compared to their contemporaries finished on grains [114,116,117]. Furthermore, grain finishing gives higher attainment of desired weights, better meat quality with regard to tenderness, marbling, ribeye area (REA) and backfat thickness (BFT), higher stocking rate per land unit than their counterparts finished on pasture [116,118]. In a grain finishing system, the net energy and glucose available for fat synthesis as muscles grow, reduce in older animals, and this leads to a higher fat content than obtained in a grass finishing system.

The biochemical processes outlined above are influenced by genetic differences and particularly enzymes and genes involved in fat metabolism. There are no reference materials in peer-reviewed sources on how all these biochemical processes relate to the TAW.

## 3. Lipogenic Genes and Associations with Genetic Selection for Meat Quality

Routine phenotypic data collection may be an arduous task given that live-animal proxies hardly exist for meat quality traits and the related costs of such data collection are high [119], ranging from Au$50 to 100 per animal. Genomic data therefore is significant in the design and implementation of animal breeding and improvement programmes to rapidly increase the frequency and potency of desirable genes in the population [120,121]. The utilisation of genomic data can raise the accuracy level of estimated breeding values (EBV), thus increasing the rate of genetic progress [122–124]. Progressive advancements in molecular genetics have resulted in an increased identification and documentation of genes or markers influencing meat quality traits [125]. Casas et al. [125] reported that DNA polymorphisms in some identified candidate genes were associated with meat tenderness. Genomic selection involves decisions that are focused on breeding values utilising genome wide markers such as SNP [124]. In sheep production, genomic prediction offers reliable alternatives because many traits influence fatty acid inheritance. Accurate genomic estimated breeding values (GEBV) for these traits would lead to greater genetic gains [122]. GEBV calculation is dependent upon the reference population that has been determined for the trait and genotyped for the markers [122]. Hayes et al. [126] established the fact that the degree of accuracy of GEBV on selection candidates rests on the proportion of this reference population and the level of the linkage disequilibrium between SNPs and quantitative trait loci (QTL). Traits that are difficult or expensive to measure are quite challenging to get large reference populations for accurate GEBV prediction [122].

SNPs in a number of genes can influence the fatty acid profile of ruminants [127], however, SNPs in FASN, SCD and FABP4 would be considered in this review because of their critical roles in fatty acid metabolism. Furthermore, Bhuiyan et al. [128] reported five SNPs in the FASN gene in cattle, and one of the SNPs was correlated with the composition of lipids, and may be utilised as a marker in breeding programs. However, in sheep, there is paucity of information on these genes. From the literature, there are research attempts aimed at linking the lipid profile of lambs with SNP [129], but to our current knowledge, there is no published information on any identified SNP in TAW sheep. This represents a major knowledge gap.

### 3.1. Stearoyl-CoA Desaturase (SCD)

The SCD gene encodes for delta-9 desaturase enzyme. It is an iron-containing endoplasmic reticulum enzyme [130,131], that catalyses a rate-limiting step in the conversion of SFA into MUFA in mammalian adipose cells [131,132]. The principal product of the desaturase enzyme is oleic acid, which is formed by the desaturation of stearic acid [133]. In cattle, the SCD gene comprises two isoforms; SCD1 and SCD5 [134]. The SCD1 gene, mapped on bovine chromosome 26, codes for stearoyl-CoA desaturase [130]. The fatty acid profile of stored fat reflects the earlier action of SCD on substrates such as palmitic or stearic acids [135]. Similarly, Smith et al. [136] reported that there are three fatty acid desaturases in animal tissues: Δ5, Δ6, and Δ9 desaturases, and that of these, only Δ9 desaturase acts upon SFA to convert them to their respective MUFA. It serves as a catalyst in the synthesis of UFA by incorporating a *cis*-bond between the 9th and 10th carbon atoms of FA with chain lengths of 10-18 carbons in adipose tissues and mammary glands [137]. Other researchers agree that the SCD enzyme is essential in the biosynthesis of MUFA such as oleic (C18: 1n-9) and palmitoleic (C16: 1n-9) acids, formed after the addition of a double bond in the Δ9 position of their precursors, C18: 0 and C16: 0 fatty acids [138]. It has been documented that SCD converts C18:1 trans-11 to C18:2 cis-9, trans-11, said to be correlated with anticarcinogenic and antiatherogenic effects [139,140]. It also increases the ratio of MUFA to SFA [141]. In sheep milk, this gene encodes the SCD enzyme found in a locus where a positional QTL has been identified for the CLA:VA ratio [142].

In sheep, an SCD SNP (SCD5, rs423661926) was found to be significantly associated with rib eye area and genotypic effects ranged from 0.035 to 0.923 [143]. The SCD gene has also been reported to harbour polymorphisms that affect milk fat content, specifically, palmitoleic acid, LA, VA, SFA and MUFA and ratios of n-6:n-3 and palmitoleic acid:palmitic acid [144]. The expression of this gene is controlled by the diet (particularly its content of n-6 and n-3 PUFA), environmental and hormonal factors [145]. In sheep, as reported by Dervishi et al. [146], grazing raises the quantities of CLA, total PUFA and n-3 PUFA in lamb, which is a favourable and desirable option in line with health-beneficial human dietary guidelines [141].

### 3.2. Fatty Acid Synthase (FASN)

FASN is the gene encoding for fatty acid synthase enzyme and is a versatile and valuable protein complex that controls the de novo biosynthesis of long chain fatty acids [147]. According to Chirala et al. [148], this gene plays essential roles during embryogenesis and adulthood fatty acid synthesis. Zhang et al. [149] demonstrated associations arising from meat fatty acid profile and FASN candidate gene polymorphisms. In bovine species, the FASN gene has been mapped on BTA19 where many QTL influencing beef fatty acid profile, adipose and milk fat contents were found [150,151]. The four exons (39–42) in the FASN complex which encode for the thioesterase (TE) domain are accountable for the synthesis of fatty acids, especially C16:0, by hydrolysing the acyl-S-phosphopantetheine thioester. Consequently, Zhang et al. [149] observed that the TE domain dictates the product chain length of FASN and variability in the TE domain amongst individuals is said to be a heritability candidate for variability in fatty acid profiles. Roy et al. [151] found higher bovine FASN expressed in a number of tissues and organs especially the brain, testis and adipose tissue and less in liver and heart and FASN assists in catalysing the reaction steps involved in the transformation of acetyl-CoA and malonyl-CoA to palmitic acid. Similarly, FASN gene uses Malonyl CoA and Acetyl CoA as substrates, while NADPH acts as a co-factor [152]. The FASN action in mammals largely yields C16:0 with negligibly minute levels of C14:0.

In humans, Chakravarty et al. [153] reported that the TE domain possesses a hydrophobic groove which contributes the fatty acyl substrate binding site with high specificity regarding C16-acyl ACP, but not C14-acyl ACP. Oh et al. [154] demonstrated a favourable impact of FASN gene on fatty acid profile. FASN is a versatile and important protein complex which catalyses the synthesis of long-chain SFA. However, the differences in TE domain (that is exons 39–42, that account for fatty acid synthesis termination of the FASN gene), would be a candidate for heritable differences in fatty acid profile [154].

To our current knowledge, apart from the short communication of Sanz et al. [155] that identified novel polymorphisms in the 5′UTR of FASN, PROP1, GPAM, MC4R, FADS and PLIN1 ovine candidate genes and their relationships with gene expression and diet in a study with Spanish sheep (Rasa Aragonesa, Roja Mallorquina and Assaf), Chinese Sunit sheep [156], and New Zealand sheep [157], there is no literature published on FASN-FADS-PROP1 genes and their correlations with growth and meat quality traits in TAW or any other sheep breed, thus presenting a significant knowledge gap.

### 3.3. Fatty Acid Binding Protein4 (FABP4)

To date, nine sub-types of fatty acid binding proteins (FABP) can be identified *(FABP1–FABP9)* and are named based on the tissues they are found in highest concentration [158]. FABP4 is also known as adipocyte fatty acid binding proteins (A-FABP or aP2). The location of FABP4 gene varies with livestock species; for instance, in sheep and cattle, it is located on chromosomes 9 and 14, respectively [158]. FABP4 encodes for a group of fatty acid binding proteins and is abundantly expressed in the adipose tissue where these binding proteins are important in glucose homeostasis, FA metabolism, transport and absorption, by their association with peroxisome proliferator-activated receptors (PPAR) [159,160]. Apart from differences in two regions of ovine FABP4 in lean and fat selection lines of Coopworth [161], Romney [162], and Rasa Aragonesa [163], breeds, published reports on the FABP4 gene in sheep are few and scanty.

Most of the reported studies on FABP4 gene have been in beef cattle. Barendse et al. [164] reported that a splice site SNP of the FAPB4 gene appeared to be connected with the deposition of IMF in the *Longissimus thoracis et lumborum* muscle. In terms of variation in the FABP4 gene, Yan et al. [162] found that it is linked with growth, deposition of fat and carcass traits. In Japanese black cattle, Hoashi et al. [165] documented a relationship existing between FABP4 and fatty acid profile, while Ardicli et al. [166] associated SNPs in bovine FABP4 with escalation in live weight, chilled carcass weight, marbling score and back-fat thickness, but without any colour differences or carcass dimension measurements. In Aberdeen Angus and Blonde d'Aquitaine cattle, the FABP4 SNP 7516G>C was analysed for association with IMF composition of the *Longissimus thoracis et lumborum* muscle between the 12th and 13th ribs. In Angus cattle, the CC genotype was reported to be 52% and 64% lower in myristoleic acid, and 33% and 35% lower in LA than CG and GG genotypes, respectively. On the other hand, in Blonde d'Aquitaine cattle, the CC genotype had elevated levels of arachidonic acid and EPA, and comparatively less oleic acid and total SFA than CG genotype. The GG genotype was only detected in one cow [167]. In Wagyu × Limousin crosses, the g.7516G>C SNPs were investigated for any existing relationship between marbling score and depth of subcutaneous fat. An association was established between CC genotype with lower marbling and fat depth. While GC genotype recorded the highest scores, GG genotype was intermediate [160]. Furthermore, in Korean Native cattle, FABP4 SNPs had a correlation with backfat thickness [168].

In sheep, FABP4 plays an important part in glucose and lipid metabolism in adipocytes [169,170]. Therefore, FABP4 polymorphisms are believed to have a significant influence on live performance and carcass characteristics [162,171], meat tenderness, marbling score and IMF content in sheep. For instance, in Romney sheep, [156,157] reported five variants (A1 − E1) in region-1 (exon 2 − intron 2) and three variants (A2 − C2) in region-2 (exon 3 − intron 3) wherein A1 was associated with a decrease in leg, loin and total meat yield, while A2 was associated with a decrease in weaning weight and pre-weaning growth rate. Haplotype A1-A2 was found to be associated with a decrease in birth weight, pre-weaning growth-rate, hot carcass weight, loin meat yield, shoulder meat yield and total meat yield, while haplotype A1-B2 was associated with increased fat depth at the 12th rib (V-GR). Taken together, their finding supports the contention that variation in FABP4 affects growth and meat production. To our current knowledge, nothing is known about the FABP4 gene in TAW breed and this major knowledge gap needs to be filled by researchers.

### 3.4. Other Fat Related Genes

Several other genes reported to be associated with fat are cocaine- and amphetamine-regulated transcript (CART) with *Longissimus thoracis et lumborum* muscle IMF content [172]. The genes encoding leptin are associated with backfat thickness and marbling score [173], while the gene encoding diacylglycerol O-acyltransferase (DGAT1) is associated with liveweight, fat thickness, rib-eye area and shoulder weight in Texel lambs [143] and IMF [174]. The growth hormone 1 (GH1) gene is weakly correlated with rump fat [175] and sterol regulatory element-binding protein 1 (SREBP1) has been reported to be correlated with FA profile [128]. However, all these studies were in cattle. Similar investigations in TAW have not been published and represent major research knowledge gaps. An updated summary of candidate genes associated with meat quality in livestock [176] is shown in Table 2:

**Table 2.** Candidate genes associated with meat quality traits in livestock.

| Animal | Candidate Genes | Traits | References |
|--------|-----------------|--------|------------|
| Sheep | CAST | Carcass | [177] |
| | MSTN | Carcass, meat quality | [178] |
| | FADS2, ELOVL2, SCD, CPT1$\alpha$, SREBF-1 | Fatty acids | [179] |
| | FABP4 | Carcass yield | [161,162] |
| | MYF5 | Leg and loin yield | [180] |
| | Callipyge | Muscular hypertrophy | [181] |
| | GDF8 | Muscular hypertrophy | [182] |
| | FAD | Omega-3 long-chain PUFA | [183] |
| | CAST | Tenderness | [184] |
| | FASN, FABP4, DGAT1, SCD | Fat metabolism | [146,163] |
| Cattle | FABP4, SCD, PPAG, ACACA, LPL | Fatty acid profile | [185] |
| Pig | CAST | Meat tenderness | [184] |
| | Leptin/Thyroglobulin | Marbling | [186] |
| | Myostatin | Growth and profile | [187] |
| | DGAT$_1$ | IMF/marbling | [174] |
| | HAL | Meat quality/stress | [188] |
| | MC$_4$R | Growth and fatness | [189] |
| | RN, PRKAG$_3$ | Meat quality | [190] |
| | AFABP/FABP$_4$ | IMF | [191] |
| | HFABP/FABP$_3$ | IMF | [192] |
| | CAST | Tenderness | [193] |
| | IGF$_2$ | Growth and fatness | [194] |
| Chicken | EX-FABP | Fatness | [195] |
| | L-FABP | Fatness | [196] |

## 4. Meat Eating Quality

Meat eating quality is influenced mainly by marbling, juiciness, tenderness and flavour [197]. Studies with lamb have shown that carcass intramuscular fat deposition and FA composition account for eating quality variation [198,199]. Consumption of lamb IMF is important to humans since it helps with the delivery and absorption of fat-soluble vitamins, and exerts positive effects on immune response [200] as exemplified by Calder's work [58] demonstrating the relationship between fatty acid composition of immune cells and their function. Marbling score to date remains one of the most important traits and reason why carcass evaluation is carried out in the abattoir [201]. In the United States of America for instance, it is the major index considered in assigning beef quality grades [202] because the quantity and distribution of IMF in the longissimus muscle area have marked effects on tenderness, flavour, juiciness and colour [203]. The amount of IMF is greatly influenced by a number of factors. These include animal age and breed, weight at slaughter [204], diet [205] and growth rate [206]. Adipogenesis in the animal's life commences with deposition of visceral fat, subcutaneous, intermuscular and intramuscular fat occurs last [207].

Deposition of IMF is a highly heritable trait and is positively correlated with overall body fatness [203]. Nutritional value is an essential determinant of meat quality. Hocquette et al. [208] reported that awareness amongst consumers has greatly increased over the years regarding the relationships that exists between diet, health and well-being which has resulted in selection of foods which are healthier and nourishing. Level of marbling, fatty acid composition, biological value of protein, minerals and vitamins are essential elements of nutritive value of any food [209].

### 4.1. Influence of IMF on Lamb Eating Quality

### 4.1.1. Tenderness

Meat tenderness has been identified as the most important sensory trait consumers consider when making decisions to purchase meat [210] as it probably affects consumers' understanding of acceptability. They are prepared to pay a premium for consistently tender meat and other traits they value [211]. Meat tenderness affects the profitability of the lamb meat industry. It depends on a number of factors including muscle sarcomere length, integrity, connective tissue content and composition [212]. Meat tenderness differs within and between animals and the different muscles [213] and is influenced by age of the animal, its sex, breed, genotype, nutrition, ante-mortem stress and post-mortem handling [214]. Refrigerating carcasses just after slaughter leads to intense contraction of the fibre muscles known as "cold shortening" which is an undesirable trait [215]. Cold shortening is the result of the rapid chilling of carcasses immediately after slaughter, before the glycogen in the muscle is converted to lactic acid. With glycogen still present as an energy source, the cold temperature induces an irreversible contraction of the muscle, thus impacting negatively on tenderness. Perlo et al. [216] reported that meat from lambs finished on forage-based diets was less tender than meat from their counterparts fed concentrates. In contrast, Sanudo et al. [217] reported that meat from grazing animals was more tender than from concentrate-fed lambs. This difference could be due to variation in carcass fatness resulting in differential cooling rates during rigor development. Furthermore, the use of fatness measures as covariates during statistical analysis can provide an unbiased basis for treatment comparison to judge if the observed differences are solely due to intrinsic dietary influences [218]. Meat from young lambs is more tender, has lower fat content and preferred by most consumers compared to mutton from older sheep [219]. The metabolic processes of lipogenesis, lipolysis and fatty acid transport culminate in IMF deposition [220]. Therefore, a diet with high-energy content leads to more lipogenesis [221]. Furthermore, the level of intramuscular fatty acids is mainly regulated by either inducing or inhibiting genes encoding for specific metabolic enzymes normally linked with lipid metabolism or transcription factors [222].

Tenderness is a proclamation of meat texture and is regarded as a major sensory quality attribute that is related with consumer satisfaction and positively correlated with juiciness and flavour, with consumers willing to pay more for tender meat [223]. It is closely related to meat structure, biochemical activity as well as time that elapses between slaughter and consumption [224]. Ali et al. [225] reported that meat tenderness is influenced by the rate and level of glycolysis and the onset of rigor post-slaughter. According to Starkey et al. [226], meat tenderness is dependent on intrinsic physiological traits of the live muscle and processing elements developed after rigor, while Rhee et al. [227] attributed it to sarcomere length. Sarcomere length governs the overall length of muscle fibres and plays a significant role in the mechanical structure of muscles [228].

### 4.1.2. Flavour

Flavour is mainly as a result of volatile substances that impact strongly on the sensory characteristics of red meat [229]. Meat flavour is affected by animal breed, nutrition, genotype, temperament, aging after slaughter, cooking method and their interactions [229,230]. Meat flavour is derived through cooking, as raw meat possesses slight or no aroma. During cooking, a number of complex reactions are observed between a number of non-volatile compounds of lean and fatty tissues making the meat

flavoursome [231,232]. The major reactions seen in aromatic volatile production are the Maillard reactions between amino acids and carbohydrates and heat degradation of fats [233]. Gylcosylamine which is a product of condensation of amino compounds with carbonyl group of reducing sugar precipitated by heat, becomes dehydrated to yield furfural, furanone, hydroxyketones and dicarbonyl compounds [231]. However, these results of Maillard reactions arising from interaction linking carbohydrates and proteins contribute significantly to meat flavour [234]. In sheep, lamb and mutton have a distinct strong species-related flavour that is influenced by various antemortem and postmortem factors such as pH, age, sex, diet, type of cooking, and curing. Post-cooking storage and modulation of lipid oxidation in mutton also has effects on flavour characteristics and various chemical compounds have been implicated as responsible for or contributing to ovine flavour [232,234]. Of those compounds, medium-length branched-chain fatty acids are the most important. Although processing methods that reduce or modify species flavour such as washing and extrusion with non-meat ingredients have been evaluated, definitive generalisations regarding sheep production management practices yielding meat with the most desirable flavour attributes have not yet been made [232].

### 4.1.3. Juiciness

Juiciness is an organoleptic index of the quantity of moisture released from meat and the degree of salivation during the process of mastication [235]. Meat juiciness is dependent on water and fat contents [236]. de Lima et al. [237] reviewed the intrinsic factors affecting sheep meat quality and reported that the level of marbling affects different sensory attributes, especially juiciness. Cloete et al. [238] evaluated sheep breeds and reported that the lower proportion of IMF in meat from Merino breed was responsible for lower sensory score for initial juiciness and lasting succulence compared to other sheep breeds. This therefore explains why juiciness has a positive correlation with water holding capacity as well as level of intramuscular fat in meat as demonstrated by the work of Hocquette et al. [239] showing that IMF has a profound effect on juiciness and flavour. Human perception of juiciness is elevated as the IMF level in meat increases [240]. In general terms, juiciness is more of a sensory trait for pork than flavour and tenderness [241] while beef consumers rate tenderness higher [242].

### 4.2. Fat Melting Point

The hardness or softness of fat is determined by its melting point. Flakemore et al. [199] stated that soft fat has a comparatively lower melting point than hard fat and this has implications for meat processors in abattoirs. MUFA are characterised by lower melting points than SFA, an attribute that favours meat flavour, tenderness and juiciness [28]. Fat melting point is affected by the physical and chemical structures of fatty acids, which in turn, drive carcass evaluation, classification and sensory characteristics of meat [243]. Furthermore, fat melting point is influenced by the molecular weight, the number and configuration of double or triple bonds in the fatty acid structure [244]. Red meat consumers prefer fats with low melting point [199,245] because of their association with reduced risks of cardiovascular diseases [246]. Hard fats pose meat processing and safety challenges in the boning room [247]. In sheep, Holman et al. [205] reported FMP in Merino, Dorset, Black and White Suffolk breeds ranging from 41.5 to 44.8 °C. FMP ranging from 40.6 to 48.0 °C have also been reported in Dorset, White Suffolk and Merino breeds [199]. However, published data on FMP in the TAW sheep breed are currently not available.

## 5. Conclusions and Future Research

The TAW is a new breed. Mechanisms explaining the impacts and expression patterns of genes associated with intramuscular fat, fat melting points and n-3 LC PUFA on meat sensory attributes are neither currently published nor fully understood. Future work should attempt to unravel single nucleotide polymorphisms, expression patterns and molecular mechanisms of various fat related genes

and growth responses of TAW lambs to diverse feedlot finishing diets with and without omega-3 oil inclusion.

Specific knowledge gaps include:

- Early selection decision tools for meat quality traits in TAW lambs are currently non-existent. Most reported selection programmes on fatty acid profile and meat quality traits in other sheep breeds are based on carcass data after the animals have been slaughtered and long gone. Pioneering studies using biopsy sampling of the *Longissimus* muscle in rams, ewes and lambs to directly determine n-3 LC-PUFA, IMF and FMP contents while the animals are young and alive for early selection and breeding purposes are needed.
- Published data on how parents selected for their high n-3 LC-PUFA, IMF and low FMP pass these genes to their offspring are currently non-existent in the TAW breed. Pioneer studies to estimate heritability values based on actual performance data and not estimated breeding values are recommended.
- SCD, FASN and FABP4 genes have been documented to exert some influence on carcass fat traits in other bovine and ovine breeds. No such data exist for the TAW breed. There is the need to sequence the FABP4, FASN and SCD genes to provide foundational data underpinning their roles in fatty acid metabolism unique to the TAW breed.
- In-depth feedlot growth studies are required for better understanding of the interactions between n-3 LC-PUFA oil diets, finishing performance, and carcass traits of TAW lambs to afford industry players the opportunity to utilise them for greater economic gains.
- A cost–benefit analysis of the implication of including n-3 LC-PUFA rich oil in feedlot finishing diets will be of immense industry significance to lamb producers, feed millers and meat processors.

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