

Genetics and adiposity in pigs: state of the art and new challenges for meat product quality

Sandrine SCHWOB¹, Bénédicte LEBRET², Isabelle LOUVEAU²

¹IFIP - Institut du Porc, BP 35104, 35651, Le Rheu, Cedex, France

²PEGASE, INRAE, Institut Agro, 35590, Saint-Gilles, France

*E-mail: sandrine.schwob@ifip.asso.fr

■ **Pork fatty tissues have many advantages, both for processing into processed products and for the sensory and nutritional qualities of fresh meat and pork products. A review of the situation of the genetic variability of adiposity in pigs in France in relation to product quality is necessary to define future breeding strategies and thus better meet the various expectations of industry and consumers¹.**

Introduction

Pork is the second most consumed meat worldwide just behind poultry, and the most consumed meat in Asia and Europe, as well as in France, with 33.3 kg carcass/inhabitant equivalent in 2018, corresponding to 38.3% of meat consumption (IFIP, 2019). In France, pork is consumed mainly in the form of processed products, with fresh meat accounting for a quarter of consumption (IFIP, 2019). The main categories of products are sausages (32%, of which 1/3 are dry sausages), ham and cooked meats (28%), salted, cured, dried and smoked meats (15%), "pâtés" and "rillettes" (10%) and delicatessen products (16%) (IFIP, 2019). These products are associated with a diversity of recipes, brands, collective or private "signatures", and products with official quality and geographical origin labels ("Label

Rouge", PDO, PGI, organic production) (Dourmad *et al.*, 2018).

Even though the total volume remains stable given the change in population, per capita meat consumption, including pork, has been declining in France since 2000. The decrease in pork consumption affects fresh meat more than processed products (FranceAgriMer, 2018). However, it is important to note that the production of pork and products with official quality labels is increasing, even though it represents only a small percentage of national production (Label Rouge: 4.1%, organic pigs: 0.7%; IFIP, 2019). For these products, quality expectations vary among pig industry actors: farmers, slaughterers, meat processors, distributors, consumers.

Pig genetic selection is concerned with meeting these multiple expectations. Thus, since the beginning of

the 1980s, meat technological quality parameters (pH, colour, water holding capacity) have been included in the breeding objectives of French pig populations to avoid decreasing meat quality due to the reduction of animal adiposity (Bidanel *et al.*, 2018). In addition, two genes identified as responsible for major pork technological quality defects (Halothane and RN genes), which also influence sensory quality, are included in breeding programmes.

In this review, we have chosen to focus on the advantages of fatty tissues and to assess the progression of genetic improvement of pigs in France in relation to adiposity and product quality. After a reminder of the characteristics of fatty tissues and their contribution to the quality of pork and processed pork products, the factors of variation in adiposity and the traits related to fat quantity included in breeding programmes

¹ This article was presented at the 51st Journées de la Recherche Porcine (Schwob *et al.*, 2019).

(measurement methods, genetic parameters) are presented. An inventory of the genetic variability that remains within French pig populations (selected breeds and local breeds) in terms of quantity, distribution and composition of adipose tissue is developed. This assessment is necessary to define future breeding strategies, so as to better respond to the changing expectations of pig industry actors and consumers.

1. Location, characteristics, roles and development of adipose tissues in pigs

■ 1.1. Anatomical location, cellular and molecular characteristics

Within the body, there are several sites of fat deposit with a wide range of sizes. In pigs, the most quantitatively important depots are subcutaneous, with backfat as the main depot, and intermuscular, with the other fat depots (perirenal or leaf fat, intramuscular fat) representing only a small fraction of body fat (Henry, 1977). In an animal with 115 kg of body weight (commercial slaughter stage), subcutaneous and intermuscular fat depots represent 74% and 26% of total carcass fat, respectively (Monziols *et al.*, 2005).

Structurally, adipose tissue is composed essentially of adipocytes, which are cells specialised in the storage of lipids (Louveau *et al.*, 2016). These spherical cells, which can be more than 100 µm in diameter, are characterised by the presence of a single lipid vacuole that occupies up to 95% of the total cell volume. They are enclosed in a mesh of connective fibres that also support blood and lymphatic vessels and nerve endings. In addition to adipocytes, adipose tissue contains adult stem cells,

pre-adipocytes, endothelial cells, fibroblasts and immune cells. Unlike many mammals, in which two types of adipocytes, white and brown, coexist or replace each other during growth, pigs have only white adipocytes in their adipose tissues (Trayhurn *et al.*, 1989).

Chemically, subcutaneous adipose tissue in pigs contains on average 69-77% lipids and 14-22% water, with internal adipose tissues (perirenal fat) containing more lipids (Wood *et al.*, 2003; Gondret *et al.*, 2014). Muscle lipids are essentially triglycerides, which are reserve lipids (0.5-5%), phospholipids, which are structural lipids present in cell membranes (0.5-1%) and cholesterol (0.05-0.1%) (Lebret and Picard, 2015). Triglycerides are stored mainly in the lipid vacuole of adipocytes that develop along fibre bundles and, to a lesser extent (5-20%), in the cytoplasm of muscle fibres in the form of lipid droplets. The phospholipid content varies relatively little, while the triglyceride content varies greatly and depends strongly on the size and number of intramuscular adipocytes (Listrat *et al.*, 2015).

Tissue lipids are made up of Fatty Acids (FAs), which are divided into three classes: saturated (SFA), which represent an average of 38% (muscle) to 40% (backfat) of FAs and are mainly C16: 0 (palmitic) and C18: 0 (stearic); mono-unsaturated (MUFA), which represent ca. 45% of the FAs (muscle and backfat) and are essentially C18: 1 (oleic); and polyunsaturated (PUFA), which represent 15-20% of the FAs (Mourot, 2010). Within PUFAs, distinction is made between n-6 or omega-6 PUFAs, which are the most common, essentially C18: 2 (linoleic or LA), and n-3 or omega-3 PUFAs, which include C18: 3 (linolenic or ALA), C20: 5 (eicosapentaenoic or EPA) and C22: 6 (docosahexaenoic or DHA). Among these FAs, C18: 2 and C18: 3 are

indispensable because they are not synthesised by the pigs. Their levels, as well as those of their derivatives, EPA and DHA, therefore depend directly on dietary intake.

■ 1.2 Roles of adipose tissue in the body

The first roles attributed to adipose tissue were those of organ support and thermal insulation. Adipose tissue is also recognised for its essential role in energy storage. It has the capacity to store large amounts of FAs in the form of triglycerides in the adipocytes, thus ensuring the maintenance of energy homeostasis. This storage capacity is the result of a balance between the uptake of exogenous FAs, *de novo* synthesis of FAs or lipogenesis, their esterification into triglycerides, the hydrolysis of triglycerides and the re-esterification of the products of lipolysis. In pigs, adipose tissue is the major site of lipogenesis (Henry, 1977).

In addition to its various roles, adipose tissue has a secretory function. Since the discovery of leptin in 1994, many products secreted by fat cells have been identified (Komolka *et al.*, 2014). Products of a peptidic nature are grouped under the term adipokines. These products, whose list continues to grow, are involved in various biological functions such as food intake, growth, inflammation and immunity. Through this secretory capacity, adipose tissue can interact with its close environment but also with the entire body.

■ 1.3 Establishment and development of adipose tissues during growth phases of the pig

The chronology of appearance of fat depots varies depending on their anatomical location. The first groups of adipocytes appear in pigs during the foetal period. They are observed

subcutaneously from 50-75 days of gestation (which lasts ca. 115 days) and develop in the pericardial, epididymal and perirenal regions at ca. 70 days of gestation, whereas the first intramuscular adipocytes do not develop until the first month of post-natal life (Bonnet *et al.*, 2015). The development of adipose tissues during embryogenesis results from the engagement of embryonic stem cells in adipocyte differentiation pathways, followed by an increase in the number (hyperplasia) and volume (hypertrophy) of the constituent cells of these tissues during the post-embryonic growth phases (Bonnet *et al.*, 2015).

Fat accretion occurs almost exclusively after birth in pigs and may continue throughout life. It increases from 1-2% at birth (Canario *et al.*, 2007) to ca. 15% at 20 kg and 25% at 90 kg body weight in Large White male pigs (Karège, 1991). The growth of adipose tissue results primarily from adipocyte hypertrophy, with hyperplasia considered to contribute little to adipose accretion (Gardan *et al.*, 2006; Bonnet *et al.*, 2015).

2. Adiposity and its contribution to quality of pork and products

The concept of pork quality (lean and fat) is complex. In addition to the intrinsic dimensions of the meat as a food product (food safety, sensory, nutritional and technological qualities), it includes extrinsic dimensions related to the production conditions of the animals and their perception by citizens (Lebret and Picard, 2015; Lebret *et al.*, 2015), which will not be addressed in this review. We will limit ourselves here to meat quality components directly influenced by animal adiposity: sensory, nutritional and technological qualities.

■ 2.1. The uses of fatty tissues in pork products

In pigs, the vast majority of the fatty tissues that make up the carcass is used as raw material for meat processing technologies, and the surplus is used for lard production (IFIP, 2016). They contribute to the taste and texture of meat and pork products and to the technological processing of products. However, depending on their anatomical origin, not all fatty tissues are as useful for product quality.

The subcutaneous tissues, which have the largest mass, are visible on the carcass or cuts. They can therefore be isolated easily and removed totally or partly before sale or processing. They are used to produce bacon, pork bard for roasts or galantines, dry or cooked pork products (sausages, pâtés, rillettes, etc.). In comparison, except for cooked ham, which is usually made from defatted ham pieces or muscles, intermuscular adipose tissues remain in the meat pieces marketed and are an integral part of the products offered to consumers (dry-cured ham, pork belly, etc.), as is intramuscular fat. They therefore play a major role in the visual acceptability of products (roasts, chops, dry-cured hams, smoked bacon, coppa, etc.) and their nutritional characteristics. Perirenal fat is, for its part, used mainly for the production of lard, marketed as is or used as an ingredient in processed products (IFIP, 2016).

■ 2.2. Sensory quality: the challenge of invisible fat

The sensory properties of food products are the characteristics that consumers perceive through their senses. For meat, these are appearance (colour; presence of drip loss; amount of external, intermuscular, and intramuscular or marbled fat), texture (tenderness, juiciness) and flavour (odour, taste). It is well established that these parameters determine the appreciation of pork and influence

the act of purchase or re-purchase by consumers, although marketing factors (packaging, price, availability) or psychological factors (values, socio-cultural aspects) also influence purchasing behaviour (Dransfield *et al.*, 2005; Font-i-Furnols and Guerrero, 2014).

The sensory qualities of meat depend on complex interactions among (i) tissue characteristics at slaughter: diameter and types of muscle fibres, glycogen content, content and nature of IntraMuscular Fat (IMF), amount and distribution of the extracellular matrix; (ii) *peri and post-mortem* muscle metabolism: rate and amplitude of pH drop; temperature, duration and conditions of meat ageing (proteolysis and lipolysis, lipid oxidation); and (iii) meat preparation and cooking conditions or processing techniques and conditions (Ngapo and Gariépy, 2008; Lebret *et al.*, 2015; Listrat *et al.*, 2015; Warner and Dunshea, 2018).

The sensory characteristics of meat can be assessed by trained panels that evaluate, under defined conditions, the intensity of multiple descriptive traits of appearance, texture and flavour, or by consumers in taste tests to measure the pleasure experienced when tasting a product (appearance, texture, flavour). Analysis of about twenty publications based on a trained panel shows that the association between IMF content and the sensory quality of pork (loin) is positive in most studies (Lebret, 2009) but varies depending on the IMF content considered (a minimum content of 2.5% is considered favourable for sensory quality), the level of other major meat quality indicators (pH), the method and temperature of meat cooking, etc (Listrat *et al.*, 2015; Warner and Dunshea, 2018).

What about the influence of IMF content on consumers' appreciation of meat? Before consumption, consumer

preferences (overall appreciation, consumption or purchase intention) are directed mostly towards meats (loins) with the lowest amount of IMF, whereas preferences are often reversed after consumption, with the most-marbled meats judged to be juicier, more tender and tastier (Fernandez *et al.*, 1999; Fonti-Furnols and Guerrero, 2014). These studies confirm the optimum of 2.5-3.5% IMF to enhance overall acceptability of meat by consumers. However, this association depends on their food habits and cultures (Dransfield *et al.*, 2005) but also their age. Thus, increasing the IMF content improves overall acceptability of dry-cured ham among consumers over 25 years of age, but has the opposite effect among younger consumers (Ventanas *et al.*, 2007). The influence of IMF content on the perceived quality also depends on the product: while the hedonic appreciation of dry-cured ham increases with IMF content (Ventanas *et al.*, 2007), the opposite is observed for cooked ham (Fernandez *et al.*, 2000). Finally, unlike IMF, the amount of subcutaneous fat almost always has a negative effect on the appreciation of meat or dry-cured hams (Dransfield *et al.*, 2005; Ventanas *et al.*, 2007).

■ 2.3. Nutritional quality: the search for healthy fat

The nutritional quality of meat corresponds to its capacity to satisfy human nutritional needs: protein (including essential amino acids), lipids, vitamins (including A, E, B1) and minerals (iron, zinc, selenium) (Lebret and Picard, 2015). It is now recommended to increase energy intake in the form of lipids, which ideally should constitute 35-40% of the energy ingested (ANSES, 2016), as well as omega-3 (n-3) PUFAs, with the recommendation of 1% of energy intake in the form of ALA (C18: 3), 250 mg/day of EPA (C20: 5) and DHA (C22: 6), and a LA (C18: 2): ALA ratio less than 5 (ANSES, 2011).

Concerning total fat content, pork is lean when the visible fat is removed: 3-4% lipids in a cooked roast, and ca. 15% in a grilled rib. In comparison, the fat content of processed products varies greatly: less than 4% in premium cooked ham, 12% in dry-cured ham, 20% in raw sausages, ca. 30% in dry sausage and 35-40% in pure pork rillettes (Ciquel, 2017).

In terms of FA composition, oleic acid (C18: 1) predominates in pig muscles and adipose tissues (35-40%). The percentage of n-3 PUFAs is generally lower than that of n-6 (0.8-1.5% vs. 12-18% of total FAs, respectively), leading to a n-6: n-3 ratio of ca. 15 (Mourot, 2010).

Another important phenomenon that influences these qualities is lipid peroxidation, to which PUFAs are particularly sensitive. These are radical reactions that lead to the formation of several end products, including volatile compounds. When peroxidation is low, the compounds formed have a beneficial effect on the flavour of meat and processed products. However, high peroxidation leads to the production of toxic compounds that alter the nutritional quality, but also the colour and sometimes the flavour (Gandemer, 1999; IFIP, 2018). It is therefore essential to control oxidation phenomena in meat and products to control their sensory and nutritional qualities. The nature and proportions of the compounds formed depend on several factors: nature of the FAs, iron content, presence of oxygen, pH, etc. In processed products, mechanical (mincing, grinding) or thermal treatments, addition of salt, and storage duration promote peroxidation (IFIP, 2018). Lipid peroxidation of meat and products can be limited by the presence, in fat and lean tissues, of antioxidants provided through animal feed: vitamin E, plant extracts high in polyphenols, selenium, etc., some of which interact (Falowo *et al.*, 2014).

■ 2.4. Technological quality: for each product its fat

The technological quality of adipose tissues corresponds to their aptitude for processing and conservation, i.e. their consistency and cohesion (anatomically separable adipose tissues: subcutaneous, internal and intermuscular) and sensitivity to oxidation (all adipose tissues, including intramuscular).

Firmness depends on chemical composition: lipid and water content, extent of the supporting collagen framework and FA composition. A low lipid content and subsequently high water content leads to a lack of consistency of the adipose tissues, whereas a high protein content ensures a certain firmness at room temperature (Lebret and Mourot, 1998). The nature of the FAs plays a major role in the consistency of adipose tissues: the more unsaturated the FAs, the lower their melting point (< 0°C for PUFAs). Several studies have shown the predominant role of the proportion of SFAs (especially C16: 0 and C18: 0) compared to MFAs or PUFAs on the firmness of adipose tissues (Lebret and Mourot, 1998; Wood *et al.*, 2003; Hugo and Roodt, 2007). The shelf life of adipose tissues is limited by the development of lipid peroxidation reactions, which are favoured by high water and PUFA contents associated with the absence of antioxidant agents (see above), and can also occur in the frozen state.

The physical (firmness, colour) and biochemical (sensitivity to peroxidation) characteristics of adipose tissues are essential to be able to process products (Hugo and Roodt, 2007). In cooked (with rind) and dry-cured hams, fat tissue that is poorly oxidisable and white is required; for dry ham, minimum subcutaneous fat thickness helps to avoid too rapid and excessive drying that would worsen the texture of the

product (IFIP, 2014). For dry sausage processing, white fat with a high melting point, low melting and rancidity risk is required to optimise the processing, as well as the flavour and texture of the product. Similarly, firm fats, i.e. high in SFAs, are required to produce emulsified sausages and rillettes, while fats high in low-melting-point PUFAs hinder the binding of the fat to the lean and the homogenisation of the mixture (IFIP, 2014).

Thus, the technological qualities of pig adipose tissues involve having a high proportion of SFAs and a high lipid content (low water content). Requirements for pig feed (< 1.9% linoleic acid in the diet of animals more than 12 weeks old) and the quality of the fat ("white and firm fat") are set out in the specifications for Label Rouge pork production (Official Bulletin No. 31, 2017) as well as for other products under official quality labels. These properties are also favourable for organoleptic qualities (limiting oxidation) but go against the nutritional quality. It therefore seems that management of these antagonisms would consist of directing fat tissues to different uses: fresh products (lard for roasts, chops, etc.) or processing of raw or cooked sausages that contain whole or minced fat tissues, depending on their physical and biochemical characteristics.

3. Factors of variation in subcutaneous and intramuscular fat depots

Quantitative and qualitative characteristics of subcutaneous and intramuscular fat depots and the nature of the FAs in triglycerides are influenced by genetic type, sex type and slaughter weight, but also by farming conditions, with a major effect of feeding (Lebret

et al., 2015). Thus, pig feeding is a major strategy to increase the FA content in meat considered to be good for human health (Wood *et al.*, 2003; Mourot, 2010; Lebret *et al.*, 2015).

In this section, emphasis will be placed on the variation in fat depots according to genetic type, sex type and anatomical location. Two main quantitative traits of fat depots are considered: BackFat Thickness (BFT), an indicator of the amount of subcutaneous fat, which plays an important role in processing, and the IMF content of the *Longissimus* muscle, which plays a major role in the sensory quality of products.

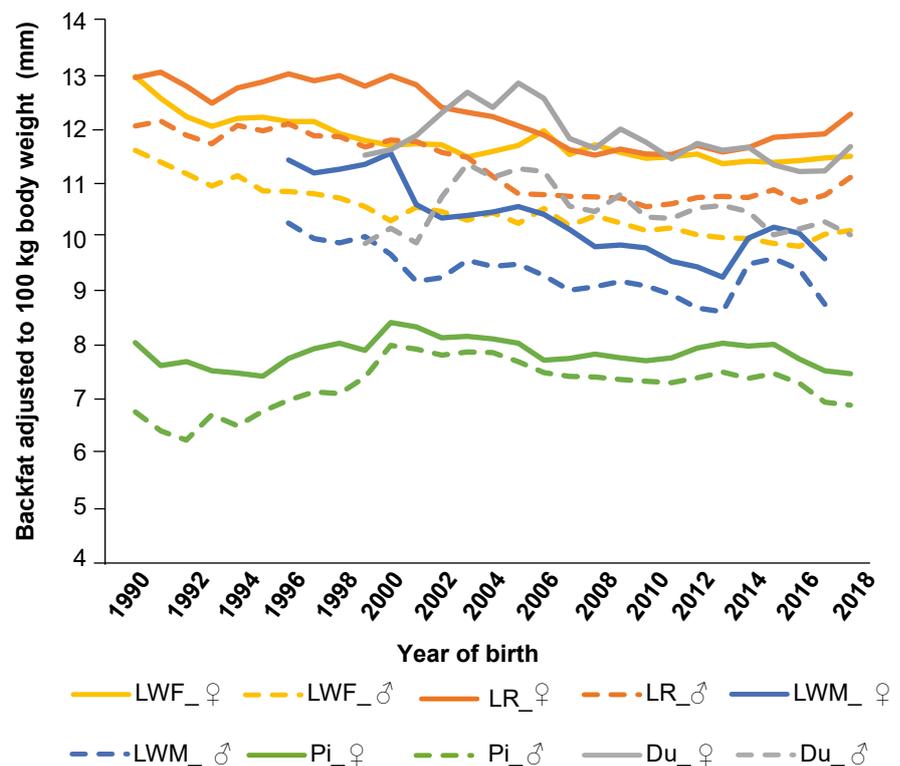
■ 3.1. Variation according to genetic type

The genetic selection performed since the early 1970s in French pig populations, oriented towards producing increasingly leaner animals, has led to the reduction

of BFT by nearly 3 Phenotypic Standard Deviations (PSD), i.e. -6.3% PSD per year on average in purebred populations (Bidanel *et al.*, 2018). This is also observed at the production stage in commercial pigs, as shown by performance test results of crossbred pigs: -10 mm BFT from 1977-1997, i.e. -40% in 20 years (Monin *et al.*, 1998).

Since the end of the 1990s, the reduction in BFT has slowed in all selected French pig populations compared to that during the two previous decades, due to lower selective pressure on this trait, which had already reached very low levels. Unsurprisingly, the Piétrain (Pi) breed has the thinnest subcutaneous fat cover: depending on sex, 7-7.5 mm BFT adjusted to 100 kg body weight in 2017 (Figure 1). Duroc is more like a dam line, such as Large White Female and French Landrace, with 10.5-11.5 mm BFT adjusted to 100 kg body weight

Figure 1. Evolution of backfat thickness adjusted to 100 kg body weight, measured by ultrasound on female (♀) and entire male (♂) selection candidates during the on-farm testing (French National Swine Genetic Database, 2020).



LWF: Large White Female line; LR: French Landrace; LWM: Large White Male line; Pi: Piétrain; Du: Duroc.

on average. The Large White Male line has an intermediate BFT of 9.5-10.5 mm, depending on sex. Although purebred animals have achieved very low BFT levels due to genetic selection, there is still high variability between genetic types for this trait.

The relation between BFT and IMF content has been the subject of multiple studies, both on purebred and crossbred animals, but their results are not easy to summarise, as their experimental conditions are not always similar (differences in feeding management; sex, age and weight at measurement; site and method of measurement; etc.). Ten studies that measured both mean BFT and IMF content of *Longissimus* muscle in animals of different pure breeds with contrasting adiposity were selected (Figure 2). The four main breeds selected in France (Large White, Landrace, Piétrain and Duroc) are

represented, as is the Meishan breed, used in Sino-European crossbreeds, and two local French breeds: Gascon and Basque. For the selected breeds, recent references were favoured to limit bias due to phenotypic evolution of the traits under the effect of selection.

Among the indicators of adiposity, BFT appears to be a better indicator than IMF content for distinguishing local breeds, which are not subject to a breeding programme, from selected breeds. This observation reflects the fact that the European conventional breeds (Large White, Landrace and Piétrain) have been selected against BFT for many years, whereas the interest in selecting for IMF content is more recent.

European conventional breeds have low overall adiposity, both in terms of subcutaneous fat and IMF. While Duroc pigs have a moderate BFT and an IMF

content that varies among studies (i.e. depending on the line considered), Meishan pigs have a high BFT and moderate IMF content. The French local breeds have high overall adiposity (BFT and IMF content), although IMF content varies between local breeds (Figure 2).

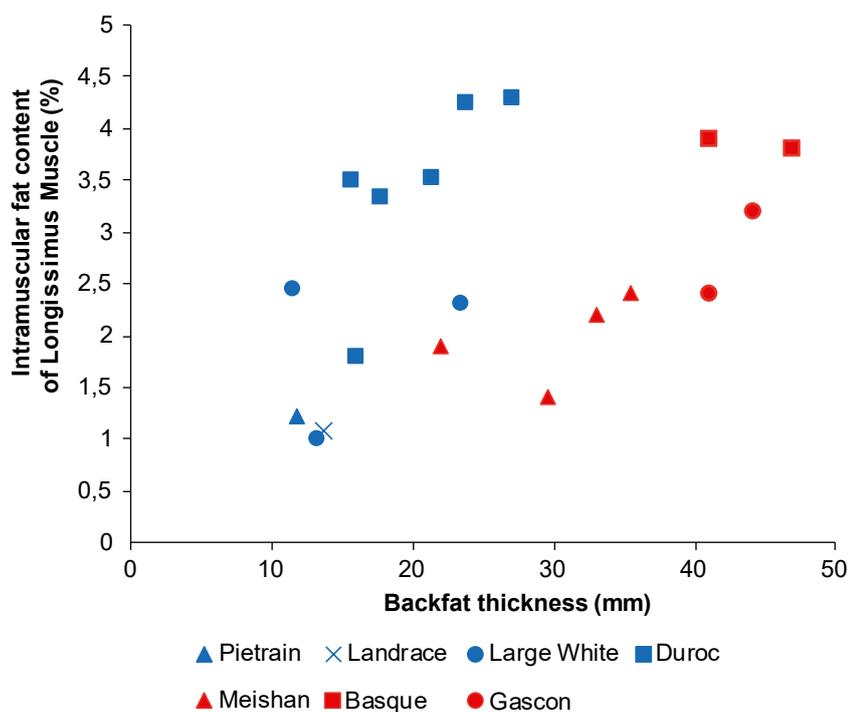
These studies illustrate the high variability in IMF content, which varies from 1% to over 4%, depending on the breed. Average IMF content in Iberian pigs can reach up to 10% (Pugliese and Sirtori, 2012). These results confirm that the Duroc breed has a higher IMF content than the other selected breeds. In the latter, the IMF contents are adapted to the fresh meat market and the production of cooked ham. However, the threshold of 2.5% IMF, considered the minimum necessary to produce meat with satisfactory sensory quality, is not reached.

In commercial crossbred pigs, which are intended for meat production, adiposity depends on the parental lines. In Sino-European lines, the more Meishan genes in the crossbreed scheme, the higher the IMF content and BFT (Jiang *et al.*, 2012). In addition, comparisons between crossbred pigs from Duroc vs. Large White or Piétrain sires indicate that the IMF content of *Longissimus* muscle is 0.55-0.64 percentage points higher in Duroc crossbred animals (Alonso *et al.*, 2009).

3.2. Variation according to sex type

In French collective populations, intra-genetic type variability due to sex type is observed in subcutaneous fat deposition (Figure 1): regardless of genetic type, females are fatter than entire males. This difference, well established in the literature, is also associated with a difference in the composition of adipose tissue, which contains more

Figure 2. Average values for seven pure breeds of backfat thickness and intramuscular fat content of *Longissimus* muscle.



Data from White *et al.* (1995); Čandek-Potokar *et al.* (1998); Labroue *et al.* (2000); Lebret *et al.* (2005); Newcom *et al.* (2005); Plastow *et al.* (2005); Renaudeau *et al.* (2005); Suzuki *et al.* (2009); Lebret *et al.* (2014); Ros-Freixedes *et al.* (2014); Lebret *et al.* (2019).

water and protein and less lipids in entire males than in females (Lebret and Mourot, 1998). Conversely, the adipose tissues of castrated males contain more lipids and less water than those of entire males and females, due to the increased adiposity after castration. Immunocastrated pigs, as an alternative to surgical castration of male piglets, have an intermediate adiposity between those of entire and castrated males (Batorek *et al.*, 2012). Sex type influences the lipogenic activity of adipose tissues, which varies in the same way as the adiposity of the animals: consequently, for a given live weight, the degree of lipid unsaturation is higher in entire males than in females or castrated males (Lebret and Mourot, 1998).

Differences in IMF contents among sex types are sometimes smaller than those observed in carcass fat. However, several studies or meta-analyses show that castrated males have a higher IMF content than entire males, whereas females have an intermediate content (Trefan *et al.*, 2013; Font-i-Furnols *et al.*, 2019).

■ 3.3. Variation according to anatomical location

Characteristics of fat depots, in particular their lipid content and FA composition, vary depending on their anatomical location (backfat, perirenal fat). In general, PUFAs are located preferentially in subcutaneous adipose tissue, and SFAs of endogenous origin in internal adipose tissues (Lebret and Mourot, 1998). Differences in BFT are observed along the carcass, depending on the anatomical zone: BFT profiles obtained by X-ray tomography (X-ray) show that BFT decreases from shoulder to ham, with the anatomical transition zones from shoulder to loin and then from loin to ham marked by greater decreases in BFT (Mercat *et al.*, 2016).

Carcass muscles also show differences in IMF content: it is lower in loin than in ham, whose muscles have different IMF contents (Maignel *et al.*, 2013; Font-i-Furnols *et al.*, 2019). Furthermore, IMF content can vary within the same muscle depending on the anatomical site, as in the *Longissimus* muscle (Faucitano *et al.*, 2004; Schwob *et al.*, 2018). Magnetic Resonance Imaging (MRI) analysis of the entire loin shows clear rib/inter-rib variation in IMF content with, in extreme cases, up to 1 percentage point difference depending on whether the cut is centred on the rib (minimum value) or between two ribs (Figure 3). However, IMF content is relatively constant along the *Longissimus* muscle, except at the ends, which are fatter (Faucitano *et al.*, 2004; Schwob *et al.*, 2018).

The correlation between the average IMF content of the *Longissimus* muscle and that predicted by MRI at each position of the loin is high (R^2 of 0.76-0.88), with the highest correlations near the 13th rib. A sample taken at this level thus represents the average IMF content of

the loin. However, this study shows that it is possible to choose a sampling site closer to the cranial end of the *Longissimus* muscle to limit devaluation of the loin while maintaining good representativeness of its average lipid content (Schwob *et al.*, 2018).

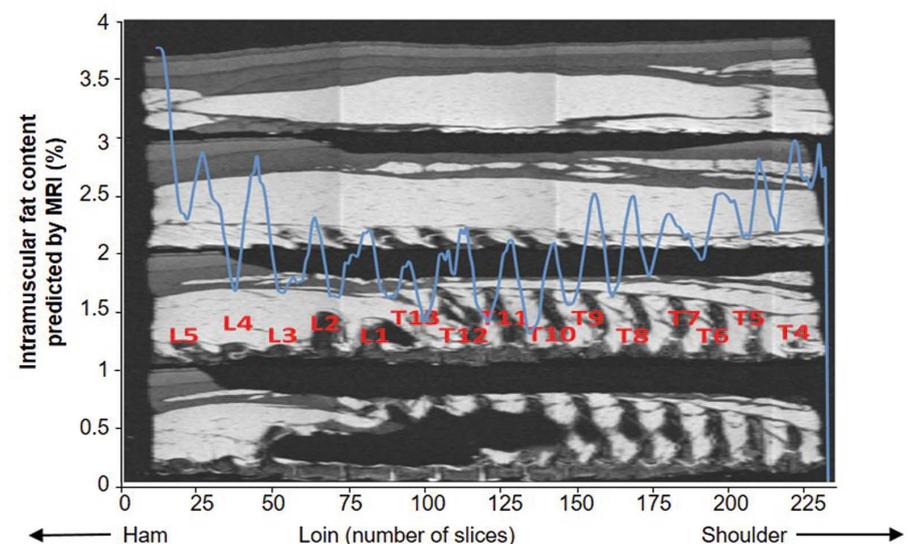
4. From phenotyping to adiposity trait selection in pigs

Optimizing adiposity through breeding requires the ability to objectively assess traits related to fat deposition on live animals or carcasses based on reliable, inexpensive, early, non-invasive and large-scale measurements. This requires rapid, standardised and automated methods for predictive indicators or adiposity traits (see box 1).

■ 4.1. New technologies for phenotyping fat depots

The imaging technologies now available allow *in vivo* study of body composition and anatomical tissue distribution in pigs. Advantages and disadvantages

Figure 3. Variation in the intramuscular fat content along the loin measured by magnetic resonance imaging (average over 5 joined slices, thickness 12.5 mm) on a bone-in loin (see background images).



T4 to T13: thoracic vertebrae (cranial end), L1 to L5: lumbar vertebrae (caudal end).

Box 1. Presentation of the main imaging technologies available to quantify two traits of fat depots on live animals or carcasses: BackFat Thickness (BFT) and IntraMuscular Fat (IMF) content.

	<i>In vivo</i>				Carcasses
	Ultrasound (US)	Magnetic Resonance Imaging (MRI)	Dual-energy X-ray Absorptiometry (DXA)	TX-ray tomography (X-ray)	Carcass classification devices
					
BFT	X	X	X	X	X
IMF	X	X	-	-	-

Photo sources: Nucléus, IRSTEA, Agroscope, IFIP, Uniporc Ouest, Frontmatec.

Ultrasound (US): The use of US is based on propagating high-frequency sound waves (ultrasound), which are reflected by tissues and return to their starting point by producing an echo. The resulting image is a section in which the tissues are identified in greyscale images. The thicknesses of backfat and muscle of the selection candidates are measured by US at three or six anatomical sites (the kidney, back and shoulder) 4 cm on either side of the spine. The IMF content in the loin is also measured using US between the 10th and 11th ribs. The choice of the probe, which emits and receives the US, depends on the type of measurement (depth and degree of accuracy).

Magnetic Resonance Imaging (MRI): MRI is based on the physical phenomenon of magnetic resonance of atomic nuclei, which requires a strong magnetic field produced by a magnet and radio waves to excite the atoms. MRI provides highly accurate 2D and then 3D images of the inside of the body (organs and soft tissues). This technology can be performed *in vivo* or *post-mortem*, on the entire animal or a targeted region of interest.

Dual-energy X-ray absorptiometry (DXA): DXA is based on the phenomenon of absorption of X-rays by matter. The higher the density of a tissue, the more it will absorb the X-rays emitted (at two energy levels). Thus, DXA provides 2D images of the entire body or a targeted region of interest, depending on the density of the tissue. DXA technology can be used *in vivo* or *post-mortem* to perform accurate and comprehensive analyses of body composition, including bone density and fat/lean distribution.

X-ray tomography (X-ray): Like DXA, X-ray technology is based on differential absorption of X-rays depending on the density of the matter. The tomograph emits X-rays over 360° of the animal's body, which makes it possible to recreate 2D or 3D images of the anatomical structures of the entire animal or a targeted region of interest. X-ray technology can be used *in vivo* or *post-mortem*.

Carcass classification devices: Pig carcasses are classified using equipment that uses, among others, imaging technologies: US and computer vision. US technology has been used in France since the 1990s to predict the lean meat content of carcasses. Some semi-automatic devices are equipped with a US probe that measures the thickness of fat and of muscle at a specific site on the carcass, such as the UltraFom 300 (Danish company Frontmatec) and the Ultra-Meater (German company CSB). AutoFom (Frontmatec), the first automatic classification machine authorised in France (2007), uses US technology to recreate the carcass in 3D to predict the weight, muscle and fat thicknesses and Lean Meat Content (LMC) of cuts at the rate of the slaughter line. Furthermore, in 2013, Uniporc Ouest equipped the large slaughterhouses of its zone with a vision device, the Image-Meater (CSB). It consists of a video camera connected to an image analyser that determines the fat and muscle thicknesses of the half-carcass at the split (loin-ham junction) and converts it into an estimate of the LMC for carcass classification.

of the main non-invasive technologies have been compared (Carabus *et al.*, 2016): ultrasound (US), dual-energy X-ray absorptiometry (DXA), X-ray and MRI. All of these methods are used to analyse the internal composition of the animal. They provide 2D (US, DXA) or 3D (X-ray, MRI) images taken of different anatomical sites or tissues (see inset). X-ray and MRI technologies have the highest image resolution, followed by DXA and US. However, the accuracy

of the images and the predictions obtained depend on several parameters: calibration of the device, data source used for prediction (thickness, surface area, volume, density, etc.), prediction equations (which may depend on genetic type, sex, weight, etc.), predicted parameter (carcass or cut weight, tissue weight, tissue volume, fat or lean content, IMF content, etc.). X-ray technology is suitable for predicting changes in carcass and cut composition

during growth (Carabus *et al.*, 2016) but is not suitable for predicting IMF content *in vivo* because the image quality is too low and the prediction error is too high (Font-i-Furnols *et al.*, 2019).

Imaging technologies are also being tested in pigs to predict *post-mortem* the IMF content of *Longissimus* muscle samples at high analysis rates. For example, MRI provides the opportunity to predict the IMF content of ca.

400-500 loin samples per day with high accuracy (Davenel *et al.*, 2012). Near InfraRed Spectroscopy (NIRS) is also a promising method for the meat industry. Using it to predict IMF content is now well established and applicable in industrial conditions (Andueza *et al.*, 2015). Other studies have also shown the utility of NIRS measurements on the slaughter line for predicting the FA content, particularly omega-3, in pig adipose tissues (Andueza *et al.*, 2015; Kucha *et al.*, 2018).

■ 4.2. Genetic determinism of adiposity traits in pigs

Additive genetic variance, i.e. the part of phenotypic variation in a trait that depends on genes and thus on which selection can act, is high for adiposity traits. For example, BFT has high heritability (≥ 0.44) when measured *in vivo* by US (Table 1), which explains why it is relatively easy to change through selection. While meat quality traits are moderately heritable (0.10-0.30), IMF content is an exception, with mean heritability close to 0.50. Thus, both BFT and IMF content are highly heritable, making them suitable traits for classic breeding methods.

The genetic correlation between BFT and IMF content, which induces the indirect selection response, is moderate, ranging from 0.13-0.40 (Table 1). Consequently, selection to increase IMF content, which is often the goal sought for the loin, will cause BFT to increase slightly. Thus, there is moderate antagonism between carcass quality (lean content) and meat quality indicators, including IMF content (Ciobanu *et al.*, 2011). However, from a phenotypic viewpoint, it is possible to decrease the fat content of the carcass while limiting the decrease in IMF content through constrained selection (Ros-Freixedes *et al.*, 2013).

Some of the genetic variability in BFT and IMF content is explained by certain genes that have variable effects on these traits. For example, several genes whose polymorphism is associated with variation in adiposity are known to influence BFT, such as HAL, IGF2 and MC4R (Ciobanu *et al.*, 2011; Mercat *et al.*, 2012), or on IMF content, such as H-FABP (Gerbens *et al.*, 1999). In addition, since the early 2000s, many studies have identified Quantitative Trait Loci (QTLs) that explain some of the genetic

variability in traits. Indeed, more than 3,000 QTLs related to criteria of adiposity (BFT ($n = 408$), fat content of carcass or cuts, IMF content ($n = 652$), marbling, etc.) have been identified, and almost twice as many QTLs that influence FA composition (content of SFAs ($n = 800$), MUFAs ($n = 729$), stearic acid ($n = 796$) or oleic acid ($n = 762$)) are referenced in the PigQTLdb database (Hu *et al.*, 2005; <https://www.animalgenome.org/cgi-bin/QTLdb/SS/index>). QTLs related to adiposity traits with a high significance level have been identified on all pig chromosomes. Several examples are detailed in the literature (Ciobanu *et al.*, 2011).

■ 4.3. Use for selection purposes

Objectives of genetic improvement are defined by breeding companies to produce animals adapted to market needs, which differ among countries. In France, the carcass payment scale is based on carcass weight and the muscle content of the cuts; nearly 75% (by volume) of pork is processed by the pig industry into a multitude of products, among which cooked ham and cooked meats account for 27% of pork processed products (IFIP, 2019). This specificity of the French market pushes breeders to reduce carcass adiposity as much as possible, both in terms of subcutaneous and intramuscular fat, to produce commercial pigs with a low fat: lean ratio and a low degree of marbling. However, there are many and sometimes contradictory expectations in the pork industry, including about the quantity and quality of fat (e.g. the need for higher or lower IMF content depending on whether fresh-meat, cooked or cured-ham processing is considered).

Genetic relationships among the traits of interest should be considered when defining breeding objectives.

Table 1. Heritabilities (h^2) and genetic correlations (rg) estimated for BackFat Thickness (BFT) and IntraMuscular Fat (IMF) content in different studies.

References	Genetic type	h^2 BFT	h^2 IMF	rg BFT-IMF
Hermesch <i>et al.</i> (2000a) Hermesch <i>et al.</i> (2000b)	Large White and Landrace	0.62 ± 0.05	0.35 ± 0.06	0.27 ± 0.16
Newcom <i>et al.</i> (2005)	Duroc	0.44 ± 0.11	0.69 ± 0.12	0.27 ± 0.18
Suzuki <i>et al.</i> (2009)	Duroc	0.72 ± 0.03	0.51 ± 0.03	0.19 ± 0.05
Maignel <i>et al.</i> (2009)	Duroc	0.49 ± 0.04	0.69 ± 0.07	0.13 ± 0.11
Ros-Freixedes <i>et al.</i> (2014)	Duroc	0.48	0.64	0.40
Miar <i>et al.</i> (2014)	Duroc x (Large White x Landrace)	0.45 ± 0.07	0.26 ± 0.06	0.34 ± 0.04

Table 2. Review of adiposity indicators measured in sire lines of the pig breeding programmes on the French market.

Breed societies and breeding (Genetic type)	Backfat thickness	Intramuscular fat content	Other adiposity indicators
LGPC (Pietrain NN halothane-negative, Pietrain nn halothane-positive)	Ultrasound*		
LGPC (Duroc)		Ultrasound*	
Hypor (Pietrain NN halothane-negative, Duroc)		Ultrasound*, NIRS, marbling (NPPC** marbling standards – visual), chemical analysis	Carcass fat content
Topigs Norsvin (Duroc)		NIRS	Fatty acid composition (NIRS)
DanBred (Duroc)			Carcass fat content
PIC (Duroc)		Ultrasound*, marbling	Fatty acid profile, tenderness
Genesis (Duroc)		Ultrasound*, marbling (NPPC** marbling standards – visual), chemical analysis	Carcass backfat thickness, Loin fat colour
Choice (Pietrain NN halothane-negative, Duroc)			Carcass fat content* (X-ray tomography)

*Measurements recorded *in vivo*. Data taken from the websites www.axiom-genetics.com, www.nucleus-sa.com, www.hypor.com, www.danbred.com, www.topignorsvin.com, gb.pic.com, www.genesus.com, and choice-genetics.com and supplemented by the genetic managers of the Axiom, Nucléus, Hypor, DanBred, PIC, Genesis and Choice breeding programmes.

** NPPC : National Pork Producers Council

Breeding programmes give preference to traits that are measurable *in vivo* because they can be recorded for all selection candidates (not just slaughtered siblings) using non-invasive methods. In addition, collecting data is simpler than taking measurements in slaughterhouses, which requires individual traceability of each carcass or cut.

Thus, in the pig breeding programmes on the French market, genetic improvement in adipose tissue is based mainly on measuring of two major traits (Table 2): BFT, measured exclusively *in vivo* by US, and the IMF content of the *Longissimus* muscle, estimated by different methods on either live animals or carcasses, as described above. Although some indicators of adiposity are also recorded in dam lines to estimate the genetic value of reproducers, the selection effort on BFT and IMF content is greater in sire lines.

As early as the 1950s, selection for BFT was greatly facilitated by the development of non-invasive, US-based methods to measure BFT accurately in live animals (Monin *et al.*, 1998). More recently, tools based on the same technology have been developed to estimate IMF content in live pigs (Newcom *et al.*, 2002; Maignel *et al.*, 2009). It is an interesting alternative to estimating IMF content in meat using an expensive chemical method, which devalues the carcass and is not feasible at a large scale, as well as to assessing marbling visually, which has many constraints (subjective evaluation, little discriminating when the average content is lower than 2%, traceability at the slaughterhouse, etc.). Other imaging technologies, described above, allow analysis of the internal composition of the animal (X-ray, DXA, MRI) but have some constraints in using them for breeding purposes: need to fast pigs and administer anaesthetics or

sedatives before taking measurements, non-portable and expensive equipment, and need for an experienced operator to acquire images.

In addition, BFT is measured at the slaughterhouse on carcasses to classify them, at the dorsal level with the fat/lean evaluation system or, more recently, at the split (loin-ham junction) with the Image-Meater (Daumas, 2008; see inset). Tools for tracing individual carcasses in slaughterhouses (RFID chips), currently being implemented, should soon facilitate collection of routine measurements from a larger number of animals. These developments will offer new perspectives on carcass composition for breeding programmes.

Finally, genomic tools are currently available to identify new regions of the genome that have significant effects on traits of interest, *via* genome-wide

association analyses, in order to include this information in breeding programmes and thus increase the accuracy of estimated breeding values of reproducers and selection candidates. Genomic selection is particularly useful for polygenic traits that are costly to measure and require slaughtering animals, such as indicators of meat or carcass quality and adipose tissue composition (Samorè and Fontanesi, 2016).

Conclusion

Pig breeding programmes have long had as the main objective the reduction of carcass adiposity. Spectacular genetic gains have indeed been observed for this trait, which has the advantage of being highly heritable, expressed in both sexes and measurable *in vivo* with very high accuracy. However, the utility of fat for

the industry is obvious if one considers the sensory, nutritional and technological qualities of meat and pork products. In conventional production, the carcass payment scale, based on weight and lean content, does not value these quality dimensions. On the contrary, the positive, albeit moderate, genetic correlation between BFT and IMF content would tend to have the opposite effect on the sensory quality of pork. Similarly, the technological quality of fats decreases as animal adiposity does. The streamlining of pig production since the end of the 1960s through combined progress in genetic selection, animal nutrition and animal husbandry has made it possible to meet the growing demand for meat of satisfactory health-related quality that is lean and inexpensive. However, this has led to standardisation of production and a decrease in the quality of fat (higher in lipids and unsaturated FAs) and lean

tissues (lower pHu, increased drip losses, the often-mentioned decrease in IMF content being less clear) (Lebret, 2004). Recent changes in the meat-product market, including pork, which is marked by an overall decrease in per capita consumption but an increase in products under official quality labels or brands that claim an improvement in intrinsic qualities compared to those of standard products, show consumer expectations of this type of diversification and illustrate the potential to create value in the pig industry. "Fat" has its place!

Acknowledgments

This article was translated with www.DeepL.com/Translator and the authors thank warmly Michelle and Michael Corson from "Editor du Jour" for English language editing.

References

- Alonso V., del Mar Campo M., Espagnol S., Roncales P., Beltran J.A., 2009. Effect of crossbreeding and gender on meat quality and fatty acid composition in pork. *Meat Sci.*, 81, 209-217.
- Andueza D., Mourou B.P., Ait-Kaddour A., Prache S., Mourou J., 2015. Utilisation de la spectroscopie dans le proche infrarouge et de la spectroscopie de fluorescence pour estimer la qualité et la traçabilité de la viande. In : Numéro spécial, Le muscle et la viande. Picard B., Lebret B. (Éds). INRA Prod. Anim., 28, 197-208.
- ANSES, 2011. Actualisation des apports nutritionnels conseillés pour les acides gras. 327p.
- ANSES, 2016. Actualisation des repères du PNNS : élaboration des références nutritionnelles. 196p.
- Batorek N., Čandek-Potokar M., Bonneau M., van Milgen J., 2012. Meta-analysis of the effect of immunocastration on production performance, reproductive organs and boar taint compounds in pigs. *Animal*, 6, 1330-1338.
- Bidanel J.P., Silalahi P., Tribout T., Canario L., Ducos A., Garreau H., Gilbert H., Larzul C., Milan D., Riquet J., Schwob S., Mercat M.J., Hassenfratz C., Bouquet A., Bazin C., Bidanel J., 2018. Cinquante années d'amélioration génétique du porc en France : bilan et perspectives. *Journ. Rech. Porcine*, 50, 61-74.
- Bonnet M., Louveau I., Cassar Malek I., Lefaucheur L., Rescan P.Y., 2015. Comprendre le développement des muscles et des tissus adipeux : un préalable pour maîtriser les qualités des carcasses et des produits des animaux d'élevage. In : Numéro spécial, Le muscle et la viande. Picard B., Lebret B. (Éds). INRA Prod. Anim., 28, 137-149.
- Canario L., Père M.C., Tribout T., Thomas F., David C., Gogué J., Herpin P., Bidanel J.P., Le Dividich J., 2007. Estimation of genetic trends from 1977 to 1998 of body composition and physiological state of Large White pigs at birth. *Animal*, 1, 1409-1413.
- Čandek-Potokar M., Žlender B., Bonneau M., 1998. Effects of breed and slaughter weight on longissimus muscle biochemical traits and sensory quality in pigs. *Ann. Zootech.*, 47, 3-16.
- Carabus A., Gispert M., Font-i-Furnols M., 2016. Imaging technologies to study the composition of live pigs: A review. *Spanish J. Agric. Res.*, 14, e06R01.
- Ciobanu D.C., Lonergan S.M., Huff-Lonergan E.J., 2011. Genetics of meat quality and carcass traits. In: *The Genetics of the Pigs*, 2nd Edition. Rothschild M.F., Ruvinsky A. (Eds CAB Int.), 355-389
- Ciqual, 2017. Table de composition nutritionnelle des aliments. <https://ciqual.anses.fr/> accédé le 20/05/2019.
- Daumas G., 2008. La visionneuse désormais autorisée en France pour le classement des carcasses : avec le CSB Image-Meater. *TechniPorc*, 31, 29-30.
- Davenel A., Bazin C., Quellec S., Challos S., Gispert M., Mercat M.J., Muller N., 2012. Dosage haut débit des lipides intramusculaires de la viande de porc par imagerie par résonance magnétique. *Journ. Rech. Porcine*, 44, 53-54.
- Dourmad J.Y., Salaün Y., Lebret B., Riquet J., 2018. Diversité des productions porcines en France. *Innov. Agron.*, 68, 151-170.
- Dransfield E., Ngapo T.M., Nielsen N.A., Bredahl L., Sjöden P.O., Magnusson M., Campo M.M., Nute G.R., 2005. Consumer choice and suggested price for pork as influenced by its appearance, taste and information concerning country of origin and organic pig production. *Meat Sci.*, 69, 61-70.
- Falowo A.B., Fayemi P.O., Muchenje V., 2014. Natural antioxidants against lipid-protein oxidative deterioration in meat and meat products: A review. *Food Res. Int.*, 64, 171-181.
- Faucitano L., Rivest J., Daigle J.P., Lévesque J., Gariépy C., 2004. Distribution of intramuscular fat content and marbling within the longissimus muscle of pigs. *Can. J. Anim. Sci.*, 84, 57-61.
- Fernandez X., Monin G., Talmant A., Mourou J., Lebret B., 1999. Influence of intramuscular fat content on the quality of pig meat -2. Consumer acceptability of m. longissimus lumborum. *Meat Sci.*, 53, 67-72.
- Fernandez X., Mourou J., Lebret B., Gilbert S., Monin G., 2000. Influence of intramuscular fat content on lipid composition sensory qualities and consumer acceptability of cured cooked ham. *J. Sci. Food Agric.*, 80, 705-710.

- Font-i-Furnols M., Guerrero L., 2014. Consumer preference, behavior and perception about meat and meat products: An overview. *Meat Sci.*, 98, 361-371.
- Font-i-Furnols M., Brun A., Gispert M., 2019. Intramuscular fat content in different muscles, locations, weights and genotype-sexes and its prediction in live pigs with computed. *Animal*, 13, 666-674.
- FranceAgriMer, 2018. Fiche Élevage Filière Porc. www.franceagrimer.fr
- Gandemer G., 1999. Lipids and meat quality: lipolysis, oxidation, Maillard reaction and flavor. *Sci. Aliments*, 19, 439-458.
- Gardan D., Gondret F., Louveau I., 2006. Lipid metabolism and secretory function of porcine intramuscular adipocytes compared with subcutaneous and perirenal adipocytes. *Am. J. Physiol. Endocrinol Metab.*, 291, E372-E380.
- Gerbens F., Van Erp A.J.M., Harders F.L., Verburg F.J., Meuwissen T.H.E., Veerkamp J.H., Te Pas M.F.W., 1999. Effect of genetic variants of the heart fatty acid-binding protein gene on intramuscular fat and performance traits in pigs. *J. Anim. Sci.*, 77, 846-852.
- Gondret F., Louveau I., Mourot J., Duclos M.J., Lagarrigue S., Gilbert H., van Milgen J., 2014. Dietary energy sources affect the partition of body lipids and the hierarchy of energy metabolic pathways in growing pigs differing in feed efficiency. *J. Anim. Sci.*, 92, 4865-4877.
- Henry Y., 1977. Développement morphologique et métabolique du tissu adipeux chez le porc : influence de la sélection, de l'alimentation et du mode d'élevage. *Ann. Biol. Anim. Bioch. Biophys.*, 17, 923-952.
- Hermesch S., Luxford B.G., Graser H.U., 2000a. Genetic parameters for lean meat yield, meat quality, reproduction and feed efficiency traits for Australian pigs: 1. Description of traits and heritability estimates. *Livest. Prod. Sci.*, 65, 239-248.
- Hermesch S., Luxford B.G., Graser H.U., 2000b. Genetic parameters for lean meat yield, meat quality, reproduction and feed efficiency traits for Australian pigs: 2. Genetic relationships between production, carcass and meat quality traits. *Livest. Prod. Sci.*, 65, 249-259.
- Hu Z.L., Dracheva S., Jang W., Maglott D., Bastiaansen J., Rothschild M.F., Reacy J.M., 2005. A QTL resource and comparison tool for pigs: PigQTLDB. *Mamm. Genome*, 15, 792-800.
- Hugo A., Roodt E., 2007. Significance of porcine fat quality in meat technology: a review. *Food Rev. Int.*, 23, 175-198.
- IFIP, 2014. Mémento viandes et charcuteries. 1^{re} Édition. IFIP-Institut du porc, Paris, France. <https://ifip.asso.fr/fr/content/vient-de-paraitre-m%C3%A9m%C3%A9nto-viandes-et-charcuteries-1%C3%A8re-%C3%A9dition-2014>
- IFIP, 2016. Code des Usages de la Charcuterie, de la Salaison et des Conserves de Viandes, Ed. IFIP-Institut du Porc, Paris, France, 512p. <https://www.ifip.asso.fr/fr/documentation/Code-des-usages-de-la-charcuterie-de-la-salaison-et-des-conserves-de-viandes>
- IFIP, 2018. Mémento viandes et charcuteries, Cahier Oxydation et qualité des viandes et produits carnés. Ed. IFIP-Institut du porc, Paris, France, <https://www.ifip.asso.fr/fr/memento-viandes-et-charcuteries>
- IFIP, 2019. Le porc par les chiffres, édition 2019-2020. La filière porcine en France, dans l'UE et le monde. Ed IFIP-Institut du Porc, Paris, France, 39p. <https://www.ifip.asso.fr/fr/content/le-porc-par-les-chiffres>
- Jiang Y.Z., Zhu L., Tang G.Q., Li M.Z., Jiang A.A., Cen W.M., Xing S.H., Chen J.N., Wen A.X., He T., Wang Q., Zhu G.X., Xie M., Li X.W., 2012. Carcass and meat quality traits of four commercial pig crossbreeds in China. *Genet. Mol. Res.*, 11, 4447-4455.
- Karège C., 1991. Influence of age and sex on energy utilization and body composition of growing pig. PhD Thesis, University of Montpellier II, France.
- Komolka K., Albrecht E., Wimmers K., Michal J.J., Maak S., 2014. Molecular heterogeneities of adipose depots – potential effects on adipose-muscle cross-talk in humans, mice and farm animals. *J. Genom.*, 2, 31-44.
- Kucha C.T., Liu K., Ngadi M.O., 2018. Non-Destructive spectroscopic techniques and multivariate analysis for assessment of fat quality in pork and pork products: A Review. *Sensors*, 18, 377. 23p. <https://doi.org/10.3390/s18020377>
- Labroue F., Goumy S., Gruand J., Mourot J., Neelz V., Legault C., 2000. Comparaison au Large White de quatre races locales porcines françaises pour les performances de croissance, de carcasse et de qualité de la viande. *Journ. Rech. Porcine*, 32, 403-411.
- Lebret B., 2004. Conséquences de la rationalisation de la production porcine sur les qualités des viandes. *INRA Prod. Anim.*, 17, 79-91.
- Lebret B., 2009. Stratégies nutritionnelles visant à moduler la croissance et la composition des dépôts tissulaires chez le porc : conséquences sur la qualité de la viande. Thèse de Doctorat, Agrocampus Ouest, Rennes, France, 115p.
- Lebret B., Mourot J., 1998. Caractéristiques et qualité des tissus adipeux chez le porc. Facteurs de variation non génétiques. *INRA Prod. Anim.*, 11, 131-143.
- Lebret B., Picard B., 2015. Les principales composantes de la qualité des carcasses et des viandes dans les différentes espèces animales. In : Numéro spécial, Le muscle et la viande. Picard B., Lebret B. (Éds). *INRA Prod. Anim.*, 28, 93-98.
- Lebret B., Dourmad J.Y., Mourot J., Pollet P.Y., Gondret F., 2014. Production performance, carcass composition, and adipose tissue traits of heavy pigs: Influence of breed and production system. *J. Anim. Sci.*, 92, 3543-3556.
- Lebret B., Prache S., Berri C., Lefèvre F., Bauchart D., Picard B., Corraze G., Médale F., Faure J., Alami-Durante H., 2015. Qualités des viandes : influences des caractéristiques des animaux et de leurs conditions d'élevage. In : Numéro spécial, Le muscle et la viande. Picard B., Lebret B. (Éds). *INRA Prod. Anim.*, 28, 151-168.
- Lebret B., Lenoir H., Daré S., Fonseca A., Mercat M.J., 2019. Qualité des produits de porcs gascons élevés en système d'élevage extensif de la filière Noir de Bigorre : effets de la saison et des ressources alimentaires. *Journ. Rech. Porcine*, 51, 217-222.
- Listrat A., Lebret B., Louveau I., Astruc T., Bonnet M., Lefaucheur L., Bugeon J., 2015. Comment la structure et la composition du muscle déterminent la qualité des viandes ou chairs. In : Numéro spécial, Le muscle et la viande. Picard B., Lebret B. (Éds). *INRA Prod. Anim.*, 28, 125-136.
- Louveau I., Perruchot M.-H., Bonnet M., Gondret F., 2016. Pre- and postnatal adipose tissue development in farm animals: from stem cells to adipocyte physiology. *Animal*, 10, 1839-1847.
- Maignel L., Daigle J.P., Sullivan B., 2009. Utilisation de la technologie ultrasons pour la prédiction in vivo du pourcentage de gras intramusculaire de la longe et perspectives d'utilisation en amélioration génétique porcine. *Journ. Rech. Porcine*, 41, 13-18.
- Maignel L., Daigle J.P., Fortier M.P., Wyss S., Sullivan B., 2013. Prédiction de la teneur en gras intramusculaire dans le jambon de porcs vivants par la technologie aux ultrasons et relation avec le gras intramusculaire dans la longe. *Journ. Rech. Porcine*, 45, 247-248.
- Mercat M.J., Fève K., Muller N., Schwob S., Le Roy P., Bidanel J.P., Larzul C., Riquet J., 2012. Estimation, dans un dispositif familial issu des populations porcines françaises en sélection, de l'effet quantitatif de mutations dans des gènes majeurs et des gènes candidats. *Journ. Rech. Porcine*, 44, 1-6.
- Mercat M.J., Monziols M., Cordonnier S., Gault E., Le Roy P., Larzul C., 2016. Effet du type génétique et du génotype halothane sur l'épaisseur de lard mesurée par tomographie RX tout au long de la carcasse. *Journ. Rech. Porcine*, 48, 273-278.
- Miar Y., Plastow G., Bruce H., Moore S., Manafiazar G., Kemp R., Charagu P., Huisman A., Van Haandel B., Zhang C., McKay R., Wang Z., 2014. Genetic and phenotypic correlations between performance traits with meat quality and carcass characteristics in commercial crossbred pigs. *Plos One*, 9, 12p.
- Monin G., Sellier P., Bonneau M., 1998. Trente ans d'évolution de la notion de qualité de la carcasse et de la viande de porc. *Journ. Rech. Porcine*, 30, 13-27.
- Monziols M., Bonneau M., Davenel A., Kouba M., 2005. Tissue distribution in pig carcasses exhibiting large differences in their degree of leanness, with special emphasis on intermuscular fat. *Livest. Prod. Sci.*, 97, 267-274.
- Mourot J., 2010. Que peut-on attendre des pratiques d'élevage pour la viande de porcs et autres monogastriques ? *OCL*, 17, 37-42.
- Newcom D.W., Bass T.J., Lampe J.F., 2002. Prediction of intramuscular fat percentage in live swine using real-time ultrasound. *J. Anim. Sci.*, 80, 3046-3052.
- Newcom D.W., Bass T.J., Schwab C.R., Stalder K.J., 2005. Genetic and phenotypic relationships between individual subcutaneous backfat layers and percentage of longissimus intramuscular fat in Duroc swine. *J. Anim. Sci.*, 83, 316-323.
- Ngapo T.M., Gariépy C., 2008. Factors affecting the eating quality of pork. *Crit. Rev. Food Sci. Nutr.*, 48, 599-633.

- Plastow G.S., Carrión D., Gil M., García-Regueiro J.A., Font-i-Furnols M., Gispert M., Oliver M.A., Velarde A., Guàrdia M.D., Hortós M., Rius M.A., Sárraga C., Díaz I., Valero A., Sosnicki A., Klont R., Dornan S., Wilkinson J.M., Evans G., Sargent C., Davey G., Connolly D., Houeix B., Maltin C.M., Hayes H.E., Anandavijayan V., Foury A., Geverink N., Cairns M., Tilley R.E., Mormède P., Blott S.C., 2005. Quality pork genes and meat production. *Meat Sci.*, 70, 409-421.
- Pugliese C., Sirtori F., 2012. Quality of meat and meat products produced from southern European pig breeds. *Meat Sci.*, 90, 511-518.
- Renaudeau D., Hilaire M., Mourot J., 2005. A comparison of carcass and meat quality characteristics of Creole and Large White pigs slaughtered at 150 days of age. *Anim. Res.*, 54, 43-54.
- Ros-Freixedes R., Reixach J., Bosch L., Tor M., Estany J., 2013. Response to selection for decreased backfat thickness at restrained intramuscular fat content in Duroc pigs. *J. Anim. Sci.*, 91, 3514-3521.
- Ros-Freixedes R., Reixach J., Bosch L., Tor M., Estany J., 2014. Genetic correlations of intramuscular fat content and fatty acid composition among muscles and with subcutaneous fat in Duroc pigs. *J. Anim. Sci.*, 92, 5417-5425.
- Samorè A.B., Fontanesi L., 2016. Genomic selection in pigs: state of the art and perspectives. *Ital. J. Anim. Sci.*, 15, 211-232. <https://doi.org/10.1080/1828051X.2016.1172034>
- Schwob S., Vautier A., Leuret B., Blanchet B., Mercat M.J., Faure J., Castellano R., Quéllec S., Challos S., Davenel A., 2018. Développement de nouveaux outils haut débit pour l'évaluation précoce de la qualité de la viande de porc (QualiPorc). *Innov. Agron.*, 63, 407-419.
- Schwob S., Leuret B., Louveau I., 2019. Adiposité et amélioration génétique chez le porc : état des lieux et nouveaux enjeux pour la qualité des produits. *Journ. Rech. Porcine*, 51, 327-338.
- Suzuki K., Inomata K., Katoh K., Kadowaki H., Shibata T., 2009. Genetic correlations among carcass cross-sectional fat area ratios, production traits, intramuscular fat, and serum leptin concentration in Duroc pigs. *J. Anim. Sci.*, 87, 2209-2215.
- Trayhurn P., Temple N.J., Van Aerde J., 1989. Evidence from immunoblotting studies on uncoupling protein that brown adipose tissue is not present in the domestic pig. *Can. J. Physiol. Pharmacol.*, 67, 1480-1485.
- Trefan L., Doeschl-Wilson A., Rooke J.A., Terlouw C., Bünger L., 2013. Meta-analysis of effects of gender in combination with carcass weight and breed on pork quality. *J. Anim. Sci.*, 91, 1480-1492.
- Ventanas S., Ruiz J., Garcia C., Ventanas J., 2007. Preference and juiciness of Iberian dry-cured loin as affected by intramuscular fat content, crossbreeding and rearing system. *Meat Sci.*, 77, 324-330.
- Warner R.D., Dunshea F.R., 2018. Producing consistent quality meat from the modern pig. Mathew A. (Ed). *Achieving sustainable production of pig meat volume 1: Safety, quality and sustainability*, Burleigh Dodds Science Publishing, Cambridge, UK. 38p.
- White B.R., Lan Y.H., McKeith F.K., Novakofski J., Wheeler M.B., McLaren D.G., 1995. Growth and body composition of Meishan and Yorkshire barrows and gilts. *J. Anim. Sci.*, 73, 738-749.
- Wood J.D., Richardson R.I., Nute G.R., Fisher A.V., Campo M.M., Kasapidou E., Sheard P.R., Enser M., 2003. Effects of fatty acids on meat quality: a review. *Meat Sci.*, 66, 21-32.

Abstract

Carcass adiposity of pigs slaughtered in France has decreased by 45% on average between 1977 and 2016. The production of increasingly lean animals was initiated in the 1950-1960s by setting up commercial grading scales for carcasses and differentiated payment according to their lean content, to the detriment of adipose tissues. This evolution led to a standardization of production, leading to difficulties in meeting the quality demand of certain market segments. However, a renewed interest in fat has occurred recently within the French pork industry. Indeed, fatty tissues have many advantages, both for the ability for processing into cured and processed products, as for sensory and nutritional qualities of products. This review provides an update on pig genetics improvement in France in relation to adiposity and product quality. After recalling the characteristics of adipose tissues and their importance for the quality of meat and pork products, the factors influencing adiposity and the traits related to fat quantity taken into account in breeding programs are presented. An inventory of the genetic variability of adiposity that remains within French pig populations (selected and local breeds) is drawn up. This will allow defining future selection strategies to better meet the various expectations of the pork industry and consumers.

Resume

Adiposité et génétique chez le porc : état des lieux et nouveaux enjeux pour la qualité des produits

L'adiposité des carcasses des porcs abattus en France s'est réduite en moyenne de 45 % entre 1977 et 2016. La production d'animaux de plus en plus maigres a été initiée dans les années 1950-1960 avec la mise en place des grilles de classement commercial des carcasses et de paiement différencié en fonction de leur teneur en tissus maigres, au détriment des tissus gras. Cette évolution a conduit à une standardisation de la production, entraînant des difficultés pour répondre à la demande qualitative de certains segments de marché. Toutefois, le gras connaît actuellement un regain d'intérêt au sein de la filière porcine française. Les tissus gras présentent en effet de nombreux atouts, tant pour l'aptitude à la transformation en produits de charcuterie et salaison que pour les qualités sensorielles et nutritionnelles des produits. Cette synthèse fait le point sur les évolutions de l'amélioration génétique du porc en France en lien avec l'adiposité et la qualité des produits. Après un rappel des caractéristiques des tissus gras et leur intérêt pour les qualités des viandes et produits du porc, les facteurs de variation de l'adiposité et les caractères de quantité de gras pris en compte dans les programmes d'amélioration génétique sont présentés. Un état des lieux de la variabilité génétique de l'adiposité qui demeure au sein des populations porcines françaises (races sélectionnées et races locales) est dressé. Ce bilan permettra de définir les futures stratégies de sélection, afin de mieux répondre aux diverses attentes des industriels et des consommateurs.

SCHWOB S., LEBRET B., LOUVEAU I., 2020. Genetics and adiposity in pigs: state of the art and new challenges for meat product quality. *INRAE Prod. Anim.*, 33, 17e-30e

<https://doi.org/10.20870/productions-animales.2020.33.1.3112>



This article is published under the Creative Commons license (CC BY 4.0).

<https://creativecommons.org/licenses/by/4.0/deed.en>

The citation and use of all or part of the contents of this article must mention the authors, the year of publication, the title, the name of the journal, the volume, the pages and the DOI in accordance with the information given above.

