

Identification of Genes for Carcass Merit and Meat Quality in the Pig

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Summary

Advances in the fields of molecular genetics and genomics have been considerable over the past several years. Recent discoveries in human genetics and in molecular biology have led to the development of a very useful genetic map of the pig. Several recent quantitative trait loci (QTL) scans and candidate gene analyses have identified important chromosomal regions and individual genes associated with carcass and meat quality traits. The causative mutations for porcine stress syndrome (*HAL* or *RYRI*) and the acid meat (*RN*) disorder, both with effects on meat quality are now known. Candidate genes for carcass merit (*MC4R*) and meat quality (*PRKAG3*, *CAST*) have also been identified. The commercial pig industry is actively using this information and traditional performance information to improve meat quality by marker assisted selection (MAS). Research to study the co-expression of thousands of genes is now advancing and methods to combine these approaches to aid in candidate gene discovery are underway. This research will aid in our understanding of genetic systems and how to manipulate their relationships to simultaneously improve pig production along with meat quality.

Introduction

Modern molecular biology and the science of genomics have opened up new and exciting possibilities to dissect complex phenotypic traits. These advances in molecular biology have made it possible to develop comprehensive genetic linkage maps in the pig (e.g. Ellegren *et al.*, 1994; Archibald *et al.*, 1995; Rohrer *et al.*, 1994; 1996). To date over 4,000 genes and markers have been added to the gene map of the pig. In addition to identifying and mapping genes and markers, animal geneticists have begun to search for the individual genes that affect carcass and meat quality in the pig. Carcass and meat quality traits are complex traits that are affected by many genes. Measurement of these traits includes objective methods for carcass composition (backfat, loin muscle area or depth) and quality (pH, lipid content, texture, water holding capacity). Many of these traits can also be classified with subjective methods by trained individuals (marbling, tenderness, texture, flavor). For many of these traits, heritabilities are moderate to high (Sellier, 1998). While it is clear that these traits are likely to be controlled by many genes some individual genes may have large effects. To find these genes three approaches have been employed. The first has been to find or observe that alleles in “major” genes are segregating in a population. This has been true for the *HAL* gene that has been known for well over 25 years. The second approach is the “genomic scan” method which uses

specialized crossbred resource families and random genetic markers to scan regions of the genome which are associated with meat quality traits. The final approach is called the candidate gene approach (Rothschild and Soller, 1997). The purpose of this paper is to review the progress made in identifying genes and genomic regions affecting carcass merit and meat quality traits in the pig.

Major Genes Identified in Populations

The best-known and well-described gene affecting meat quality in the pig is the *HAL* gene (Christian, 1972). Pigs that are homozygous for the recessive *HAL* n allele have PSS or Porcine Stress Syndrome and they are subject to sudden death from stress. In addition, those surviving and those heterozygous for the condition have many meat quality problems including pale, soft, and exudative (PSE) meat caused by the rate and/or the extent of post mortem pH decline. The mutation causing PSS is now known and located in the porcine ryanodine receptor (*RYR1*) that maps to chromosome 6. A DNA test for the defective allele (*HAL 1843*TM) is patented and used widely throughout the world (Fujii *et al.*, 1991). The recessive deleterious meat quality allele is associated with more lean meat. It is this association that has allowed the gene frequency to be increased initially through selection for increased muscularity. Worldwide the frequency of this defective allele has decreased to nearly zero, though some lines maintain the mutation in order to capture the increased lean produced from heterozygous pigs. What has not been confirmed is whether this association is a direct effect of the *HAL* locus or a closely linked gene. Recent attempts to dissect the varied effects that *HAL* has on meat quality and composition to determine if they are direct effects and not due to linkage have failed to produce alternate genes responsible for the effects seen.

The second meat quality major gene found segregating in populations is the *RN* gene. It was first noticed in France that meat from Hampshire pigs often had extremely low pH and had a much lower yield of a cured-cooked ham product called the “Paris Ham.” Once termed the “Hampshire Effect,” the effect was found to be dominant and it has now been named *RN* which is an abbreviation for “Rendement Napole”, referring to a method of estimating ham yield. Further analysis has shown that the *RN* allele increases the amount of glycogen by about 70% in white muscle. The existence of the *RN* locus was confirmed by breeding experiment and was later mapped to chromosome 15 in the pig (Mariani *et al.*, 1996; Milan *et al.*, 1996; Looft *et al.*, 1996). Anonymous DNA markers genetically linked to the mutation were first used to begin to remove the negative allele. After several years and considerable effort, a consortium led by L. Andersson, D. Milan and C. Looft reported the identification of the causative mutation (Milan *et al.*, 2000). The gene involved is a new member of a gene family coding one of the regulatory subunits of the AMP-activated protein kinase complex (named *PRKAG3*). Interestingly, the same gene might explain certain forms of diabetes in humans and the consortium is looking at the opportunities for their research to benefit human health. The test for the *RN* mutation is being used to remove the defect from primarily Hampshire based lines and this genetic test represents another important additional tool to be used by pig breeders to improve meat quality. The *RN* allele has also been found to be associated with leaner carcasses (Le Roy *et al.*, 2000), which might explain its relatively high frequency in Hampshire based populations. Interestingly, additional mutations (Ciobanu

et al., 2001) within the gene have been discovered and are of importance to the industry (see later section of this paper).

Genomic Scanning

A significant number of QTL mapping programs have been developed in the pig over the last 5-8 years with most being associated with growth and performance traits. In most cases, pig QTL resource families were produced by crossing phenotypically divergent founder populations such as Meishan x Large White or Wild Boar x Large White. In a limited number of cases domestic breeds were used as parents for the cross. Statistical analyses were generally performed assuming that different QTL alleles were fixed in founder populations. The QTL identified are consequently those explaining the genetic differences between populations. These studies have been summarized by Bidanel and Rothschild (2002) and Rothschild *et al.* (2003) but are briefly presented here.

Backfat thickness QTL were detected on all porcine chromosomes except SSC 16 and 17, with genome-wide significant effects on 10 different chromosomes (Figure 1). Very clear results were obtained for the three same regions of chromosomes 1, 4 and 7 for growth traits (Andersson *et al.*, 1994; Knott *et al.*, 1998; Rohrer and Keele, 1998a,b; Walling *et al.*, 1998a, b; Wang *et al.*, 1998; de Koning *et al.*, 1999, 2001a; Rattink *et al.*, 2000; Rohrer, 2000; Pérez-Enciso *et al.*, 2000; Wada *et al.*, 2000; Bidanel *et al.*, 2001; Grindflek *et al.*, 2001; Malek *et al.*, 2001a). Other regions with backfat QTL include regions of chromosome 1 (Malek *et al.*, 2001a), the end of the short arm of chromosome 2 (Knott *et al.*, 1998; Jeon *et al.*, 1999; Nezer *et al.*, 1999; Rattink *et al.*, 2000; Bidanel *et al.*, 2001; de Koning *et al.*, 2001a), chromosome 5 (Bidanel *et al.*, 2001), chromosome 6 (Bidanel *et al.*, 2001; Ovilo *et al.*, 2000), chromosome 8 (Bidanel *et al.*, 2001), chromosome 9 (Rohrer, 2000), chromosome 13 (Yu *et al.*, 1995), chromosome 14 (Bidanel *et al.*, 2001) and the central region of chromosome X (Rohrer and Keele, 1998a; Rohrer, 2000; Bidanel *et al.*, 2001).

The chromosome X QTL has the largest effects, explaining up to 50% of the phenotypic variance of backfat thickness measurements based on one experiment (Rohrer and Keele, 1998a). The QTL located on chromosomes 1, 2, 4 and 7 respectively explain 5-23%, 2-20%, 2-17% and 6-33% of the phenotypic variance of backfat thickness. The other identified QTL explain less than 5% of backfat thickness variability. The important variations in QTL effects between experiments are, in some cases, related to the likely differences in the founder populations used. In a joint analysis of chromosome 4 effects in several QTL experiments, Walling *et al.* (2000) clearly showed that the effects of Wild Boar alleles on backfat thickness were significantly larger than those of Meishan alleles. On the whole, QTL allele effects are consistent with breed differences. However, favorable effects of Meishan (fatter breed) as compared to Large White alleles were obtained for the QTL located on chromosome 7 (Rohrer and Keele, 1998a; Wang *et al.*, 1998; de Koning *et al.*, 1999; 2001a; Rohrer, 2000; Bidanel *et al.*, 2001).

Of particular importance is whether these results will translate to useful findings in commercial lines. The results of Malek *et al.* (2001a,b) offer some information, since

QTL in that population have yielded results useful for the industry. A new study using 10 commercial pig populations from research herds and breeding companies has examined 11 chromosomal regions (1p, 1q, 2, 3, 4, 6, 7, 8, 9, 10, and 13). Of these 11 chromosomal regions studied three were considered control and eight as QTL regions to be verified (Evans *et al.*, 2003). Results confirmed a number of the fat QTL on chromosomes 1, 3, 4, 6, and 13 in some, but not all, of the commercial populations.

Chromosomal regions with significant effects on meat quality traits were detected on chromosomes 1, 5, 6, 7, 8, 12, 15, 17 and X (Figure 2). Significant effects on intramuscular fat content or marbling were detected on chromosome 1 in a Berkshire x Yorkshire (Malek *et al.*, 2001b), on chromosome 6 in a Landrace x Iberian cross (Ovilo *et al.*, 2000, 2002a,b), in a Landrace x Korean native cross (Kim *et al.*, 2002) and in a commercial population (Grindflek *et al.*, 2001), on chromosome 7 in Meishan x Large White pigs (Bidanel *et al.*, 2002) and on chromosome X in Meishan x Large White (Harlizius *et al.*, 2000) and Landrace x Iberian (Pérez-Enciso *et al.*, 2002) crosses. Two QTL affecting this same trait were also obtained on chromosome 6 by de Koning *et al.* (2001b), but a different location more than 40 cM from the previously reported QTL. The chromosome 6 and 7 QTL explain 14-18 % of the phenotypic variance. Large White or Landrace alleles have unfavorable additive effects as compared to Iberian, Korean native or Meishan alleles. Conversely, Yorkshire alleles have favorable effects as compared to Berkshire alleles for the chromosome 1 QTL, but this QTL only explains 3-4% of the phenotypic variance of intramuscular fat content or marbling.

Two QTL located on chromosomes 5 and 15 have significant effects on meat ultimate pH in Berkshire x Yorkshire F₂ pigs (Malek *et al.*, 2001b). The QTL located at the end of the long arm of chromosome 5 explains approximately 5% of the phenotypic variance and presents favorable dominant Large White alleles in this cross. The same chromosomal region also has suggestive effects on meat color. The chromosome 15 QTL explains 4-6% of ultimate pH variance and presents favorable, but partly recessive Berkshire alleles. This QTL, which also affects muscle glycolytic potential, is localized in the same region as the *RN* locus. The *RN* mutation evidenced by Milan *et al.* (2000) was not present in the population studied. This observed effect is due to additional mutations inside the *RN* locus that are discussed in the candidate gene section. Only one QTL for 24 hr postmortem pH was observed on chromosome 3 in the Iberian x Landrace (Olivo *et al.*, 2002a). Suggestive QTL on ultimate pH were also reported in the same region of chromosome 6 (Malek *et al.*, (2001b) in Berkshire x Yorkshire crosses and by Park *et al.* (2002) in Korean native x Landrace crosses. This region also has a suggestive effect on drip loss in Meishan x White pigs (de Koning *et al.*, 2001b). Confirmation of some of these QTL was demonstrated in commercial populations (Evans *et al.*, 2003). The QTL for pH at either 45 min or 24 hrs was seen on chromosomes 1, 2, 3, 4, 6, 7, 9, 10 and 13 for the two sets of traits.

Significant marker-trait associations were detected for meat color on chromosome 12, 15 and 17 in Berkshire x Yorkshire pigs (Malek *et al.*, 2001b). The chromosome 12 QTL explained about 10% of the variance of a subjective color score, with favorable Large White alleles for this cross, but does not seem to affect reflectance measurements. The

chromosome 17 QTL affects both color score and reflectance measurements. Berkshire alleles are favorable as compared to Large White alleles and explain approximately 4% of the phenotypic variance of both traits. Genome-wide significant Minolta reflectance (lightness) QTL were observed in Iberian x Landrace pigs on chromosomes 4 and 7 (Olivo et al., 2002a). The two same chromosomal regions also significantly affected muscle pigment (haematin) content. The QTL explained 11% and 4%, respectively, of the variance of Minolta reflectance, and 3% of the variance of haematin content, with positive effects of Iberian alleles on meat color and pigment content.

Conversely, no genome-wide significant QTL has so far been detected for water holding capacity, drip or cooking loss. Some suggestive QTL were reported for drip loss on chromosomes 1, 2 and 11 by Malek et al. (2001b) and on chromosomes 4, 6, 14 and 18 by de Koning et al. (2001b), for water holding capacity on chromosomes 2 and 13 (Malek et al., 2001b) and for cooking loss on chromosomes 6 (Park et al., 2002), 7 and 18 (de Koning et al., 2001b), but results are not consistent between traits and across experiments.

Two QTL, with significant effects on the number of muscle fibers of the semimembranosus muscle, were detected on chromosomes 7 and 8 by Bidanel et al. (unpublished results). They explain, respectively, 9 and 6% of the trait variance. Meishan alleles had a positive, but recessive, effect for the chromosome 7 QTL, and a negative and largely additive effect for the chromosome 8 QTL. This latter QTL also affects the relative surface of type I fibers, with a favorable dominant effects of Large White over Meishan alleles. A single experiment (Malek et al., 2001b) has carried out a genome scan for meat sensory quality traits, including sensory panel scores. Only suggestive QTL were obtained but they correlate well with more objective measures like pH or instron measures of tenderness. Some of them are close to significance, such as the QTL located at the end of the long arm of chromosome 2, which affects also tenderness and chewiness scores.

Candidate Genes

The candidate gene approach can be employed in several ways (Rothschild and Soller, 1997). The first uses genes that by their very nature are expected to be associated with certain physiological functions. The candidate gene approach also may use mutational candidates from other species. The third approach is to identify QTL regions and then use comparative genomics and genetic maps to identify positional candidates genes. These genes have important biological functions and are expected to be located in the region of interest.

To date several genes have been investigated. Many of these genes relate to fat level. Early work by Dutch researchers suggested that the porcine gene for heart fatty acid binding protein (*H-FABP*) might be associated with intramuscular fat. This gene's location is near the location of a QTL on chromosome 6 (Gerbens et al., 1997). A genetic test for this gene has been patented but results are of limited success in most populations.

Perhaps the largest single gene effect seen to date is that of the polymorphism located in the *MC4R* gene. This gene is part of the leptin pathway and codes for a receptor in the brain that affects feed intake. Results from Kim et al (2000) clearly demonstrate large effects on feed intake that in turn affect backfat and growth rate (5-8% differences). The mutation discovered has an effect in nearly all commercial lines studied (Kim et al., 2000). Recently, the causative nature of the mutation was demonstrated (Kim et al., in press). Recent results suggest that one allele (the high growth allele) is also associated with increased marbling (Kim et al., 2000).

Significant imprinting effects for backfat and heavy muscling were obtained for a QTL on the small arm of chromosome 2. Further analysis revealed that the causative mutation is likely associated with *IGF2*, which is known to be imprinted (Jeon et al., 1999; Nezer et al., 1999; de Koning et al., 2000). Latest scientific results have just been published (Van Laere et al., 2003). A genetic test for this mutation has been patented and used primarily for increased muscling.

The study of Malek et al. (2001b) demonstrated a significant QTL for pH and color traits in the region of the *RN* or *PRKAG3* gene. While the *RN* mutation was not present in these families, further study of chromosome 15 QTL effects revealed three additional mutations in the *RN* locus (Ciobanu et al., 2001). When these three mutations were combined into haplotypes they produce differences in pH that may be as high as 0.1 pH unit in all breeds (Table 1) except Berkshires in which the differences may exceed 0.2 units. Unlike the *RN* mutation, which is essentially only in Hampshires, these three new mutations are in all breeds and this makes them extremely important economically. This genetic test is in industry use and a patent is pending.

Table 1. Association results between the genotypes at I199V substitution site of the *PRKAG3* gene and meat quality traits across five commercial lines (Ciobanu et al., 2001)

Traits	Genotypes		
	II	IV	VV
Ham pH	5.81 (.01) ^e	5.74 (.01) ^{f,e}	5.71 (.01) ^f
Ham color	44.9 (.37) ^e	46.5 (.27) ^f	46.9 (.26) ^f
Loin pH	5.78 (.01) ^e	5.74 (.01) ^{f,e}	5.71 (.01) ^f
Loin color	44.2 (.26) ^e	44.7 (.18) ^a	45.2 (.18) ^{f,b}

Significant differences: a-b p<0.05; c-d p<0.005; e-f p<0.0005.

A small but distinct QTL for tenderness was detected in the middle of chromosome 2 by Malek *et al.* (2001b). Further investigation revealed that Calpastatin (*CAST*) which is a specific inhibitor of calpains, a Ca²⁺-activated protease family and considered to be the major cause of initiation of myofibrillar protein degradation in living muscle mapped under the QTL. Extensive analysis of the *CAST* gene revealed several polymorphisms which altered the protein and these had large effect on tenderness (see Table 2). Further analysis in many commercial lines has revealed significant differences in drip loss, pH and firmness (correlated to tenderness) measured in commercial facilities (Ciobanu *et al.*, 2002). The analysis using haplotypes (linked markers) points to one genotype that is associated with tenderness in fresh meat and increased yield. It had been suggested that the alternate genotype might be better for dry-cured meat. Results reveal that for one of the tested mutations, *CAST Hpy188I-* genotype 11 is best for yield but the genotype 22 that is worse for fresh meat is best for dry-cured properties. For properties like final product moisture, salt % and cured pH all favor the *CAST* genotype 22. Processors can then think of using genotype to sort carcasses or cuts of meat based on their use as fresh or cured products.

Table 2. Association results between genotypes of *CAST Hpy188I* substitution and meat quality traits in BxY F₂ animals ^{a,b}.

Traits	Genotype			P
	11	12	22	
Firmness	3.21 ^{e,c}	3.44 ^f	3.43 ^d	0.001
Juiciness	6.23 ^a	6.05	5.76 ^b	0.05
Tenderness	8.01 ^a	7.74 ^b	7.75	0.11
Chew score	2.32	2.51	2.54	0.11
Instron Force (kg)	4.39 ^a	4.45 ^a	4.63 ^b	0.05

^a n=136 (11), 228-233 (12) and 129-130 (22).

^b Significant differences: a-b, p<0.05; c-d, p<0.005; e-f, p<0.0005.

Table 3. Association results between genotypes of *CAST Hpy188I* substitution for fresh ham traits.^a

Trait	Genotype			Prob
	11	12	22	
Final Wt., kg	7.12 ± 0.08	7.15 ± 0.09	7.09 ± 0.18	0.95
Cut Wt., kg	6.85 ± 0.08	6.83 ± 0.09	6.70 ± 0.18	0.74
Fat, %	3.87 ± 0.20	4.26 ± 0.25	4.27 ± 0.47	0.39
Hunter L	44.5 ± 0.35	44.3 ± 0.43	44.0 ± 0.83	0.79
Hunter L Change	3.31 ± 1.37	1.27 ± 1.68	5.88 ± 3.20	0.38
Yield,%	78.9 ± 0.42	77.6 ± 0.52	77.9 ± 0.99	0.10
Moisture, %	75.9 ± 0.25	75.2 ± 0.32	75.8 ± 0.60	0.20
Wt. Loss, kg	4.02 ± 0.09	4.33 ± 0.11	4.19 ± 0.20	0.06
Final product moisture, %	63.4 ± 0.33	62.2 ± 0.40	61.0 ± 0.76	0.0037
Salt, %	4.16 ± 0.11	4.42 ± 0.13	4.63 ± 0.25	0.09
Cured pH	6.29 ± 0.02	6.30 ± 0.03	6.40 ± 0.06	0.21

^a n=74 (11), 42 (12) and 11 (22).

Given the increased knowledge of muscle physiology and the increasing number of QTL scans and positional candidate gene analyses it is likely that the discovery of other candidate genes will grow.

Future Research Approaches

New technical developments continue to provide novel tools that may yield exciting results. In particular, sequencing efforts in all species have now allowed the identification of tens to thousands of individual genes that may be responsible for the traits of interest. This technology is germane to studies focused on complex traits of carcass merit and meat quality. These projects involve the development of genomic libraries from specialized tissues. Using these specialized tissues including muscle tissue from the ham and loin in which specific genes are expected to be expressed, researchers can select expressed sequence tags or ESTs and sequence them. To date several such projects are underway in the pig and over 140,000 ESTs, from a variety of tissues, have been deposited but it is likely a million more could be deposited soon because of the large Chinese-Danish EST project. These include identification of ESTs from muscle tissue and a variety of other tissues. Public deposit of such partial gene sequences can be found in GenBank (<http://www.ncbi.nlm.nih.gov/Genbank/GenbankOverview.html>) or in more specialized databases (<http://pigest.genome.iastate.edu/data.html>). Many of these ESTs will be mapped so that the comparative map of the pig will advance rapidly allowing faster utilization of information from the human and mouse genomes.

The ESTs can also be used to examine gene expression. The genes or ESTs are placed on microarrays or gene chips so as to study the expression of many genes in parallel. RNA

from excellent or poor meat quality animals or other sets of treatments affecting meat quality is then hybridized to the arrays or chips and expression is compared. The genes that show significant differences between treatments or states become guides to candidate genes and pathways that are important for the trait of interest. Some companies have funded projects with specialized tissues from animals challenged by specific diseases. Such an example is the EC funded project called Quality Pork Genes (<http://www.qualityporkgenes.com/>). The US Pig genome Coordinator is sponsoring the production of arrays for pigs and these are commercially available now. The use of DNA chips or arrays to examine gene expression will offer new glimpses into the complex traits of economic importance in the pig.

Practical Applications in the Pig Industry

Information at DNA level can help producers, and pig breeders to select against specific major mutations such as the negative *HAL* allele or *RN⁻* allele (Table 4). DNA information can also be used to assist in the selection of quantitative traits including those that can be selected by traditional means (e.g., using *MC4R* marker to increase marbling). Molecular information can increase the accuracy of selection, allow for selection for sex limited traits or imprinted genes and allow for selection for traits like meat quality. Such opportunities using DNA technology can therefore increase the selection response in the population by as much as 60% since these DNA can be used in selection decisions much earlier compared to the collection of phenotypic measurements.

Table 4. Molecular Genetic Tests Used by the Swine Industry

HAL	meat quality - non exclusive use
KIT	white color - exclusive use (PIC)
MC1R	red/black color - exclusive use (PIC)
MC4R	growth and fatness – exclusive use (PIC)
RN ⁻	meat quality - non exclusive/exclusive tests (several companies).
PRKAG3	meat quality- exclusive use (PIC)
AFABP, HFABP	intramuscular fat - non exclusive (IPG)
CAST	tenderness – exclusive (PIC)
IGF2	carcass composition – exclusive use (Seghers)
Trade secret tests	several traits – many companies

A list of genetic companies providing routine genotyping in livestock can be seen at: <http://www.genome.iastate.edu/community/genetest.html>.

We anticipate that significant progress will be made by utilizing candidate genes and searching for population-wide linkage disequilibrium, using tools such as random markers and building up haplotype blocks covering interesting genomic areas. Overall, these approaches have led to a number of genes and markers being used in the swine industry as shown in Table 4. These and others developed genetic markers will be utilized at all levels of the pork chain to improve carcass composition, meat quality and

cooking properties. Such developments will help producers and packers but ultimately benefit the consumer most of all.

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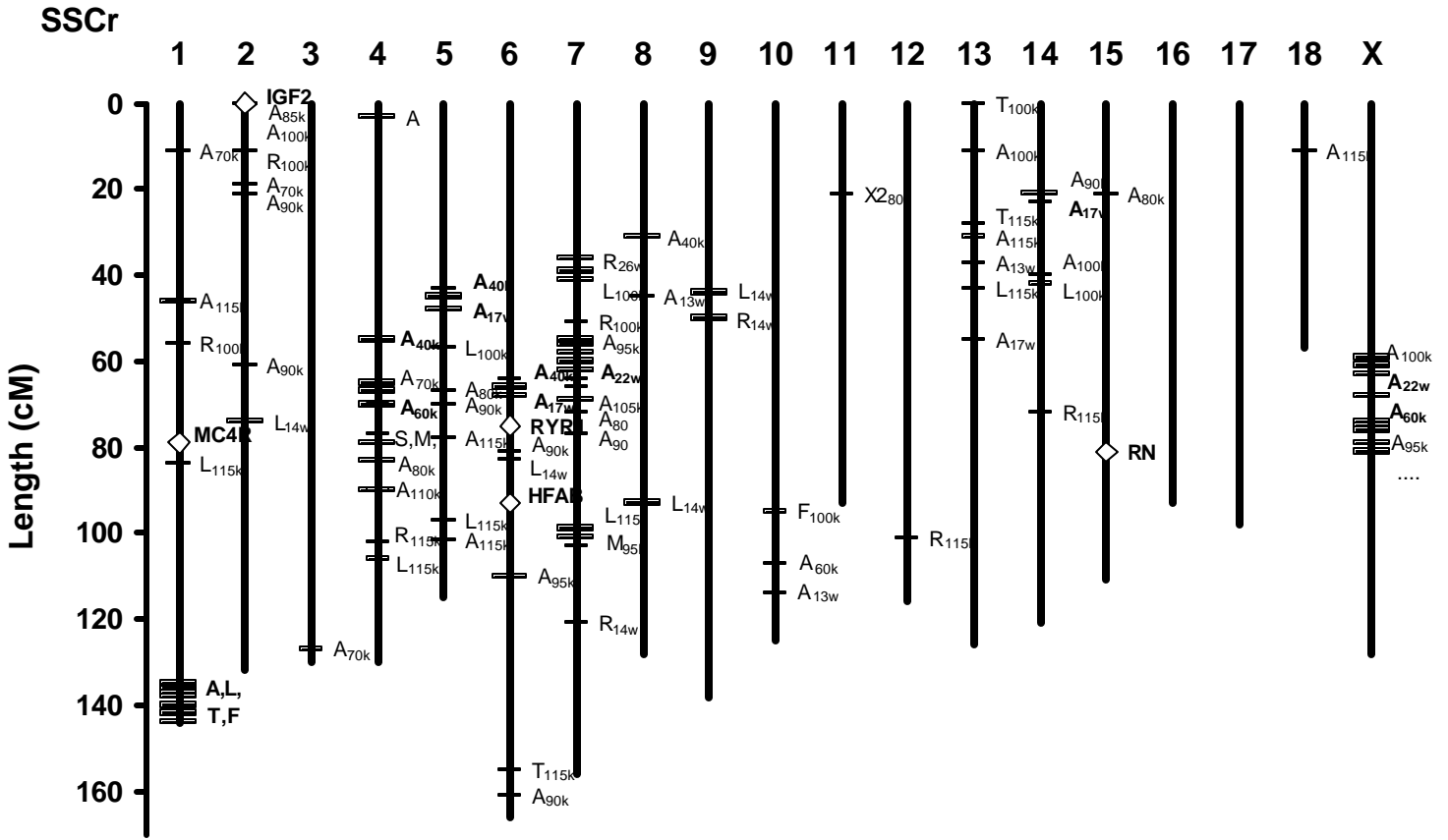


Figure 1. Candidate Genes and Quantitative Trait Loci Detected for Backfat Thickness

Xyz : X = A (average), L (lumbar), R (last rib), T (tenth-rib), S (shoulder), M (mid-back), F (first-rib) backfat thickness at xx kg (k) or xx weeks (w) of age; Locus names (in bold characters) : MC4R = melanocortin-4 receptor locus; IGF2 = insulin growth factor 2; RYR1 = ryanodine receptor locus ; HFAB = heart fatty acid binding protein locus; PIT1 = regulatory factor locus; RN = “acid meat” locus.

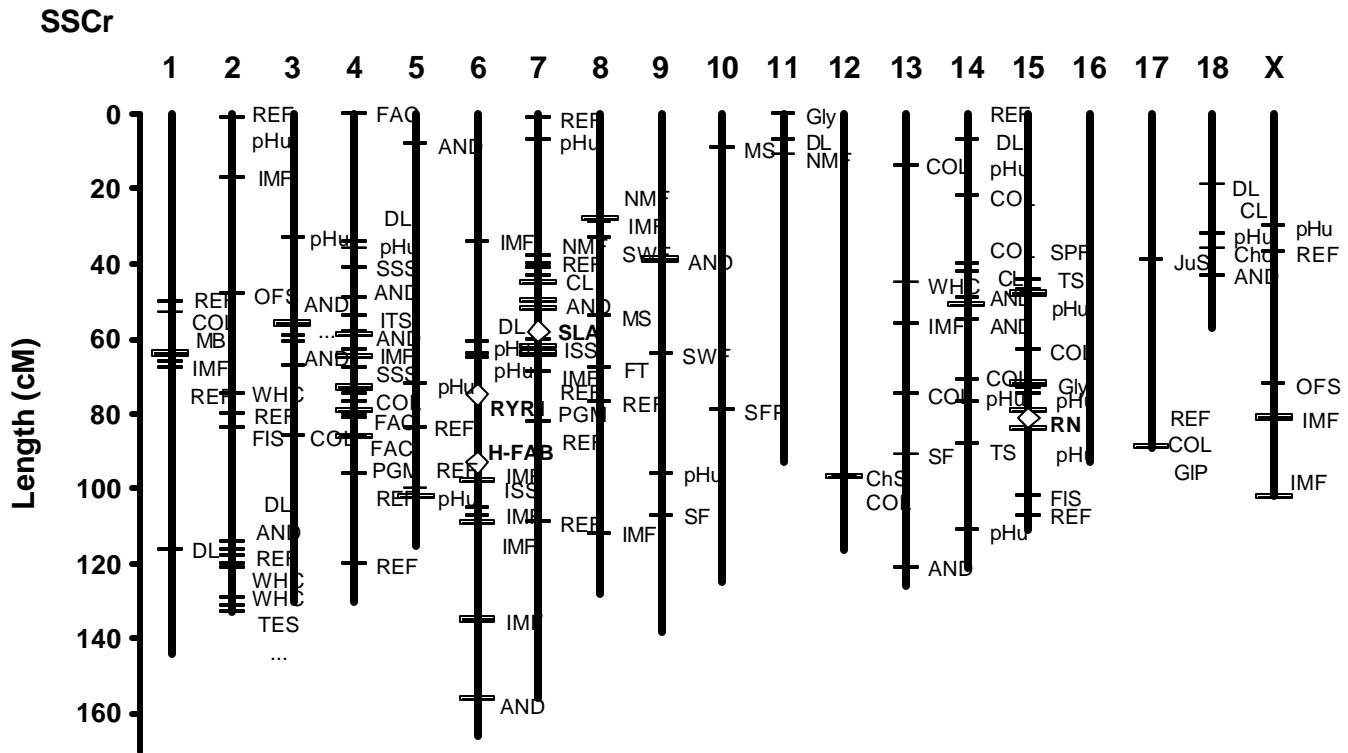


Figure 2. Candidate Genes and Quantitative Trait Loci Detected for Meat and Fat Quality Traits

AND = fat androstenone level; ChS = chewiness score; CL = cooking loss; COL = color score; Cho = muscle cholesterol content; DL = drip loss; FAC = fatty acid composition; FIS = flavor score; FT = fiber type; GIP = glycolytic potential ; Gly = muscle glycogen content; IMF = intramuscular fat content; ISS = intensity of smell score (trained score) ; ITS = intensity of taste score (trained panel test); JuS = Juiciness score (trained panel test); MS = marbling score; OFS = off-flavor score (trained panel test); PGM= muscle pigments; pHu = meat ultimate pH; REF = reflectance; SPF = star force probe, SSS= subacid smell score (trained panel test); TS = tenderness score; WHC = water holding capacity; Locus names (in bold characters) : **MC4R** = melanocortin-4 receptor locus; **IGF2** = insulin growth factor 2; **RYR1** = ryanodine receptor locus ; **HFAB** = heart fatty acid binding protein locus; **PIT1** = regulatory factor locus; **RN** = “acid meat” locus.