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Detection of Quantitative Trait Loci Affecting Muscle Histochemical Properties in the F_2 Progeny of a Cross Between Japanese Black and Limousin Breed

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Abstract: With a view towards, the genetic improvement of economically important traits, we previously generated a beef cattle F_2 resource population from a Japanese Black and Limousin cross. Here, we report on a genome-wide scan for QTLs affecting muscle fiber diameter and composition traits. The longissimus thoraces muscle samples from 150 F_2 animals were examined to determine muscle fiber type and diameter. At the same time, F_2 animals as well as the F_1 parents and F_0 grandparents were genotyped for 313 informative micro satellite markers that spanned 2.382 cM of the Bovine autosomes. The results of a genome scan using least-squares regression interval mapping provided evidence for a QTL affecting the diameter of the red muscle fiber (<5% chromosome-wide level) at 42 cM on BTA17; a QTL affecting the composition of the red and white muscle fibers (<5% chromosome-wide level) at 0 cM on BTA5 and a QTL affecting the composition of the red muscle fiber (<5% chromosome-wide level) at 106 cM on BTA8. Thus in this study, we detected 3 QTLs for 3 traits. The detected QTLs were either contiguous with or overlapped previously reported QTLs with effects on several traits assumed to be related to muscle histochemical properties.

Key words: QTL, Japanese black, limousin, meat quality, muscle fiber, beef

INTRODUCTION

The histochemical properties of muscle in beef cattle are of considerable interest with regard to their presumed effect on meat quality, for example, meat color, marbling and tenderness. In the muscles that contract in a fast or slow-twitch manner, fueled by energy from oxidative and glycolytic metabolisms, a heterogeneity of myofibers has been recognized (Peter and Starson, 1972, 1990). Myofibers can essentially be divided into 3 major categories, namely, red (correspond to type I, βR, Slow-twitch Oxidative; SO), intermediate (correspond to type IIA, αR, Fast-twitch Oxidative Glycolytic; FOG) and white (correspond to type IIB, αW, Fast-twitch Glycolytic; FG), depending on their histochemical, physiological and biochemical properties (Klont *et al*., 1998). A significant positive correlation has been demonstrated between beef muscle fiber diameter and shear force (Herring *et al*., 1965; Crouse *et al*., 1991). Crouse *et al*. (1991) have also revealed a negative correlation between sensory tenderness and the percentage of white muscle fiber area. Further, Calkins *et al*. (1981) reported a negative correlation between αW muscle fiber and marbling and tenderness, but a positive correlation between αR and βR muscle fibers and the same qualities. Whipple *et al*. (1990) also verified the relationship between muscle fiber traits and beef longissimus tenderness and reported the effect of αR and βR muscle fibers on this trait. Differences in these muscle fiber characteristics have been reported to be related to both growth and breed (Wegner *et al*., 2000). Moreover, compared with other breeds of cattle, the Japanese Black has been revealed to have a significantly higher percentage distribution and larger diameter of type I myofibers (Gotoh, 2003).

There have been several reports on the Quantitative Trait Loci (QTL) analysis of industrial animals. In particular, there have been several reports on the QTL mapping of muscle histochemical traits in pigs (Malek *et al*., 2001; Nii *et al*., 2005; Wimmers *et al*., 2006; Estellé *et al*., 2008). To the best of the knowledge, however, there have been no reports to date on the QTL mapping of these muscle properties in cattle.

In this study, we focused on the histochemical properties of muscle in beef cattle and used interval mapping to search for QTLs associated with these traits, using an F_2 resource population derived from a cross between Japanese Black and Limousin breed.

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MATERIALS AND METHODS

Animals and phenotypes: The F_2 population used in this study was described in detail in our previous report (Abe *et al*., 2008). A total 150 animals (78 steers, 72 heifers) were used for muscle fiber trait measurements.

The rib roast blocks of the seventh to 8th rib bones were sampled from these F_2 animals and the longissimus thoracis muscle was excised from the block. A 1×1×1 cm cube was then cut from the center of the rib eye, immediately frozen in liquid nitrogen and stored at -30°C, until used for analysis. Transverse serial sections (8 μm thick) were cut at -18°C using a cryostat microtome (HM505E; Microm International GmpH, Walldorf, Germany). Succinic dehydrogenase activity was localized using nitroblue tetrazolium as a substrate according to the method of Gauthier *et al*. (1968). Sections were incubated for 30 min at 37°C. The proportion of each fiber type (red, intermediate and white) was obtained by counting >200 fibers in 3 fields of view. The minor axis of each fiber was also measured. All image processing was carried out using WinROOF software (Mitani Corp., Tokyo, Japan).

Genotyping: DNA was extracted from blood using automatic extraction equipment (NA1000; Kurabo, Osaka, Japan) and the final DNA concentration was adjusted to 20 ng μL^{-1}. A genome screen was conducted using microsatellite markers (Kappes *et al*., 1997; Ihara *et al*., 2004). Polymerase Chain Reaction (PCR) amplification was performed in a volume of 15 μL containing 20 ng of genomic DNA, 1.67 mM $MgCl_2$, 6.25 pmol of each primer, 0.2 mM deoxynucleotides (dNTPs) and 0.375 U Taq DNA polymerase (ABgene, Epsom, UK). The annealing temperatures of each marker in the thermocycling steps were optimized in accordance with Ihara *et al*. (2004). Amplifications were performed under the following conditions: 5 min at 94°C; 30 cycles of 30 sec at 94°C, 30 sec at the annealing temperature and 30 sec at 72°C and a final extension of 7 min at 72°C. After PCR amplification, the reaction products were fractionated in an ABI377 DNA sequencer (Applied Biosystems, Foster City, CA) and fragment analysis was performed using GeneScan and Genotyper software (Applied Biosystems, Foster City, CA).

Linkage analysis and QTL mapping: Linkage maps for the 29 bovine autosomes were constructed using CRI-MAP (Green *et al*., 1990) and the constructed maps were used for the whole-genome QTL scan. The information content of markers was calculated using the method described by Knott *et al*. (1998).

The maps were then used for QTL detection on the 29 autosomes using QTL Express software (Seaton *et al*., 2002). The least-squares regression model (Haley *et al*., 1994) was used for QTL analysis, including individual sex, breed of the recipients and combinations of seasons and locations as the fixed effects and ages of the recipients as covariates, along with additive and dominance effects for the putative QTLs. Detection of QTLs was based on an F-statistic that was computed from sums of squares explained by the additive and dominance coefficients for the QTL. Significance thresholds for the F-statistic were derived at the chromosome and experiment-wide levels on a single-trait basis using a permutation test, with 1,000 repetitions for each trait. The percentage of F_2 variance explained by the model was calculated as follows:

$$\text{Variance (\%)} = \frac{\text{RMS-FMS}}{\text{RMS}} \times 100$$

Where:

RMS = The residual mean square from the reduced model, omitting the QTL but including all fixed effects

FMS = The RMS from the full model, including the QTL and all fixed effects

RESULTS AND DISCUSSION

Phenotype measurement: The longissimus thoracis muscle samples from 150 F_2 individuals were classified into 3 muscle fiber types (red, intermediate and white; Table 1). Significant differences were observed between steers and heifers with respect to the diameters of both intermediate and white muscle fibers ($p<0.001$), with heifers having larger diameters than steers. Gotoh (2003) reported gender differences in myofiber type distribution between steers and bulls and discussed the possibility of the effect of hormonal regulation differences. Although, the combination of genders differed in the present study, the same influences could still be at work.

Whole-genome QTL analyses of F_2 animals were successfully carried out. No QTLs at experiment-wide level were detected in this study, but 3 chromosome-wide significant QTLs for 3 muscle fiber traits were detected (Table 2).

QTL on BTA17: A QTL for the diameter of red muscle fiber was detected at 42 cM on BTA 17 (Fig. 1). F_2 individuals inheriting the Japanese Black allele had larger red muscle fiber diameters. A QTL for lean-to-fat ratio and marbling score have previously been mapped at 21 cM and 38 cM, respectively, on BTA17 (Casas *et al*., 2000, 2004). The composition of type I myofiber has been reported to be positively correlated with marbling

Table 1: Muscle fiber traits of F_2 animals from an inter cross of F_1 animals deribed from 2 Japanese Black and Limousin dams

		Diameter (um)[1]			Composition of myofibre type (%)[1]		
F_2	n	Red	Intermediate	White	Red	Intermediate	White
Steers	78	41.55±0.77	49.19±0.89	52.78±1.03	24.32±0.80	17.03±0.65	58.65±0.96
Heifers	72	43.12±0.65	53.96±0.78	57.61±0.97	23.60±0.72	16.21±0.64	60.15±1.02
In total[2]	150	42.36±0.50	51.67±0.62	55.29±0.73	23.95±0.54	16.60±0.45	59.43±0.70

[1]Mean±SE; [2]Total of all the F_2 population

Table 2: Summary of chromosome-wide significant QTL for muscle fiber traits

Traits	Muscle fiber type	Chromosome	F-value[1]	Location (cM)	Flanking markers	Additive effect	Dominance effect	Variance (%)
Diameter (μm)	Red	17	5.61	42	MB008-IDVGA-40	1.62±0.71	2.80±1.09	6.18
Composition (%)	Red	5	5.89	0	BMS1095-BMS610	-2.46±0.78	-1.80±1.08	6.53
	Red	8	5.58	106	DIK1169-BMS2629	-1.44±0.81	3.16±1.16	6.15
	White	5	5.72	0	BMS1095-BMS610	2.22±0.95	3.48±1.31	6.32

[1]All F-statistics inscribed in this column were significant at the 5% chromosome-wide level

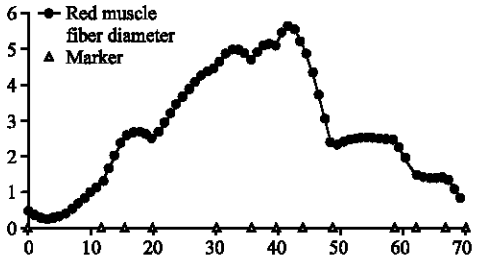

Fig. 1: Plot of the F-ratios from multilocus least square analisis (Haley *et al*., 1994) of the diameter of red muscle fiber on BTA17. The x-axis indicates the relative position on the linkage map and the y-axis represents the F-ratio. Triangles on the x-axis indicate marker positions. Markers were RM156, BMS2220, MNB-10, BMS941, BM305, TGLA231, MB008, IDVGA-40, BM8125, BM1862, DIK643, BM1233 and MS2263

(Calkins *et al*., 1981) and the percentage of intramuscular fat content (Gotoh, 2003). This suggests that the same latent gene may have an effect on each the QTL for lean-to-fat ratio, marbling score and our QTL for the diameter of red muscle fiber.

A QTL for feed-to-gain ratio has previously been reported at 40 cM on BTA 17 (Nkrumah *et al*., 2007). Given the fact that the differences in muscle fiber type originate from differences in energetic metabolism, this would appear to be a reasonable results. More interestingly, QTLs for average daily gain and post-weaning average daily gain were also detected at 43.5 and 35.1 cM, respectively, on BTA17 (Nkrumah *et al*., 2007; Alexander *et al*., 2007). These results might be summarized as follows. The difference in energetic metabolism of different muscle fiber types has an effect on feed efficiency and this in turn is reflected in average daily gain.

QTL on BTA5: A QTL for the composition of red and white muscle fibers was detected at 0 cM on BTA5 (Fig. 2). In this case, F_2 individuals that inherited the Limousin alleles had a higher percentage of red muscle fiber, whereas animals inheriting the Japanese Black allele had a higher percentage of white muscle fiber (Table 2). This finding is contrary to what we had earlier predicted, because it has previously been reported that the Japanese Black breed tends to develop a higher percentage of type I muscle fiber than the Japanese Red or Holstein breeds (Gotoh, 2003). In addition, there is a positive correlation between the percentage of type I muscle fiber and fat accumulation, whereas the type IIB muscle fiber tends to accumulate less intramuscular fat (Clakins *et al*., 1981; Gotoh, 2003). Gotoh (2003) deduced that Japanese Black cattle contain more type I myofibers compared to other breeds and thus, they have a greater propensity to accumulate intramuscular fat. Furthermore, approximately, 70% of semitendinosus muscle fiber in 16-months-old pure-bred Limousin bulls was typed as FG muscle fiber, which is equivalent to Type IIB muscle fiber (Jurie *et al*., 1995). Thus, the observations made in the present study tend to conflict with those made previously. The Limousin allele had an increasing effect on the percentage of red muscle fiber and therefore, if we were to introgress the Limousin allele into the Japanese Black, it may be possible to increase the percentage of red muscle fiber in the latter breed.

A QTL for average daily gain-related traits had been reported around the centromeric region of BTA5. Li *et al*. (2002) detected QTLs for both average daily gain and pre-weaning average daily gain at 6.05-17.28 cM on BTA5 in their Bos taurus cattle study. Therefore in this QTL, the same latent gene may have affects on both average daily gain and muscle fiber percentage.

QTL on BTA8: A QTL for the composition of red muscle fiber was detected at 106 cM on BTA8 (Fig. 3). F_2 individuals that inherited the Limousin allele had a higher percentage of red muscle fiber, which shown the same tendency as the QTL we detected on BTA5. Davis *et al*. (2007) reported a QTL for the adhesion properties of cattle

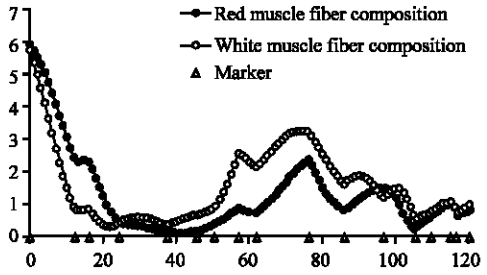

Fig. 2: Plot of the F-ratios from multilocus least square analisis (Haley *et al*., 1994) of the composition of red and white muscle fiber on BTA5. The x-axis indicates the relative position on the linkage map and the y-axis represents the F-ratio. Triangles on the x-axis indicate marker positions. Markers were BMS1095, BMS610, BP1, RM103, BMS1898, MS2106, CA084, ETH10, MNS-44, BMS1248, BM315, DIK2206, DIK2287, DIK2122, BM733, DIK2035 and BMS597

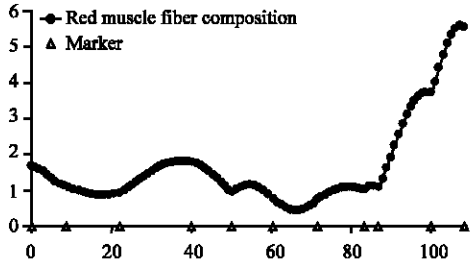

Fig. 3: Plot of the F-ratios from multilocus least square analisis (Haley *et al*., 1994) of the composition of red muscle fiber on BTA8. The x-axis indicates the relative position on the linkage map and the y-axis represents the F-ratio. Triangles on the x-axis indicate marker positions. Markers were BMS1864, INRA097, BMS1591, INRA180, DIK1174, BMS2072, IDVGA-52, BM711, DIK074, DIK1169 and BMS2629

longissimus lumborum muscle on BTA8. Briefly, adhesion is a measure of how easily a muscle can be pulled apart by a force applied perpendicular to the muscle fibers. Thus, this measurement represents connective tissue toughness, which was reflected by collagen cross-linking. To date, however, there have been no reports that have directly discussed the relationship between connective tissues and muscle fiber types, not only in cattle but also in other mammalian species. Nevertheless, it seems unlikely that adhesion is related to muscle fiber type composition. Furthermore, according to the linkage map constructed by Ihara *et al*. (2004), the interval between the highest peak of each of these 2 QTLs was estimated to be approximately 30 cM, suggesting them to be different QTLs with different effects.

Presumable relationship with calving ease: The QTLs detected on BTA8 and 17 in this study overlap with the previously reported QTLs for calving ease and percentage difficult birth (CE_PDB) traits (Ashwell *et al*., 2005). On BTA8, the QTL for CE_PDB was mapped at 116 cM, spanning the makers BMS2847 and BMS2629. The QTL for the composition of red muscle fiber on BTA8 in this study spanned DIK1169 and BMS2629. Consequently, the QTL for red muscle fiber composition covers the entire CE_PDB QTL. Furthermore, the QTL for CE_PDB on BTA17 was mapped at 69 cM and spanned BM305 and URB002. The QTL for the diameter of red muscle fiber on BTA17 in this study spanned MB008 and IDVGA-40. Consequently, the QTL for CE_PDB covers the entire QTL for the diameter of red muscle fiber. The foregoing results were completely unexpected. It is widely understood that Double Muscle (DM) cattle exhibit a high frequency of calving difficulty (Casas *et al*., 1999) and that they also have a higher percentage of Type IIB muscle fiber (Wegner *et al*., 2000). However, since the DM animals are an extreme case, we should perhaps not infer that this relationship is typical of all breeds. Nevertheless, the relationship between muscle fiber type and calving ease traits can be readily imaged. Considering the importance of calving ease traits, further studies should be conducted on this matter.

CONCLUSION

In this study, we identified 3 QTLs with effects on 4 muscle fiber traits. These QTLs may be of potential value in marker-assisted introgression; however, further studies will be required in order to establish their reliabilities.

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REFERENCES

Abe, T., J. Saburi, H. Hasebe, T. Nakagawa, T. Kawamura, K. Saito, T. Nade, S. Misumi, T. Okumura, K. Kuchida, T. Hayashi, S. Nakane, T. Mitsuhasi, K. Nirasawa, Y. Sugimoto and E. Kobayashi, 2008. Bovine QTL analysis for growth, carcass and meat quality traits in an F_2 population from a cross between Japanese Black and Limousin. J. Anim. Sci., 86: 2821-2832. DOI: 10.2527/jas.2007-0676. PMID: 18599673. http://jas.fass.org/cgi/content/full/86/11/2821.

Alexander, L.J.T.W.G., W.M. Snelling and M.D. Macneil, 2007. Quantitative trait loci with additive effects on growth and carcass traits in a Wagyu-Limousin F_2 population. Amim. Genet., 38: 413-416. DOI: 10.1111/j.1365-2052.2007.01616.x. PMID: 17596127. http://www3.interscience.wiley.com/journal/118504321/abstract.

Ashwell, M.S., D.W. Heyen, J.I. Weller, M. Ron, T.A. Sonstegard, C.P. Van Tassell and H.A. Lewin, 2005. Detection of quantitative trait loci influencing conformation traits and calvingease in Holstein-Friesian cattle. J. Dairy Sci., 88: 4111-4119. PMID: 16230715. http://jds.fass.org/cgi/reprint/88/11/4111.

Calkins, C.R., T.R. Dutson, G.C. Smith, Z.L. Carpenter and G.W. Davis, 1981. Relationship of Fiber Type Compositon to Marbling and Tenderness of Bovine Muscle. J. Food Sci., 46: 708-710. DOI: 10.1111/j.1365-2621.1981.tb15331.x. http://www3.interscience.wiley.com/journal/119571376/abstract.

Casas, E., J.W. Keele, S.C. Fahrenkrug, T.P. Smith, L.V. Cundiff and R.T. Stone, 1999. Quantitative analysis of birth, weaning and yearling weights and calving difficulty in Piedmontese crossbreds segregating an inactive myostatin allele. J. Anim. Sci., 77: 1686-1692. PMID: 10438013. http://jas.fass.org/cgi/content/abstract/77/7/1686.

Casas, E., S.D. Shackelford, J.W. Keele, R.T. Stone, S.M. Kappes and M. Koohmaraie, 2000. Quantitative trait loci affecting growth and carcass composition of cattle segregating alternate forms of myostatin. J. Anim. Sci., 78: 560-569. PMID: 1076-4062. http://jas.fass.org/cgi/reprint/78/3/560.

Casas, E., J.W. Keele, S.D. Shackelford, M. Koohmaraie and R.T. Stone, 2004. Identification of quantitative trait loci for growth and carcass composition. Anim. Genet., 35: 2-6. DOI: 10.1046/j.1365-2052.2003.01067.x. PMID: 14731222.http://www3.interscience.wiley.com/journal/118773900/abstract?CRETRY=1&SRETRY=0.

Crouse, J.D., M. Koohmaraie and S.D. Seidman, 1991. The relationship of muscle fibre size to tenderness of beef. Meat Sci., 30: 295-302. DOI: 10.1016/0309-1740(91)90039-S. http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6T9G-49NX785-5G&_user=2467816&_coverDate=12%2F31%2F1991&_fmt=abstract&_orig=search&_cdi=5114&view=c&_acct=C000057441&_version=1&_urlVersion=0&_userid=2467816&md5=d24d56b1a497a90c0c39b84092c31873&ref=full.

Davis, G.P., S.S. Moore, R.D. Drinkwater, W.R. Shorthose, I.D. Loxton, W. Barendse and D.J.S. Hetzel, 2007. QTL for meat tenderness in the *M. longissimus* lumborum of cattle. Amim. Genet., 38: 40-45. DOI: 10.1111/j.1365-2052.2007.01677.x. PMID: 18162103. http://www3.interscience.wiley.com/journal/119401059/abstract?CRETRY=1&SRETRY=0.

Estellé, J., F. Gil, J.M. Vazquez, R. Latorre, G. Ramírez, M.C. Barragan, J.M. Folch, J.L. Noguera, M.A. Toro and M. Pérez-Enciso, 2008. A quantitative trait locus genome scan for porcine muscle fiber traits reveals overdominance and epistasis. J. Anim. Sci., pp: 86. DOI: 10.2527/jas.2008-1034. PMID: 18641172. http://jas.fass.org/cgi/content/full/86/12/3290.

Gauthier, G.F., 1968. On the relationship of ultrastructural and cytochemical features to color in mammalian skeletal muscle. Z. Zellforsch., 95: 462-482. DOI: 10.1007/BF00995217. PMID: 5785841. http://www.springerlink.com/content/t16w8424j7797453.

Gotoh, T., 2003. Histochemical properties of skeltal muscles in Japanese cattle and their meat production ability. Anim. Sci. J., 74: 339-354. DOI: 10.1046/j.1344-3941.2003.00125.x. http://www3.interscience.wiley.com/journal/118895017/abstract.

Green, P., K. Falls and S. Crooks, 1990. Documentation for CRI-MAP, version 2.4. Washington Univ. School of Med., St. Louis, MO. http://linkage.rockefeller.edu/soft/crimap.

Haley, C.S., S.A. Knott and M. Elsen, 1994. Mapping quantitative trait loci in crosses between outbred lines using least squares. Genetics, 136: 1195-1207. PMID: 8005424. http://www.genetics.org/cgi/reprint/136/3/1195.

Herring, H.K., R.G. Cassens and E.J. Briskey, 1965. Further studies on bovine muscle tenderness as influenced by carcass position, sarcomere length and fiber diameter. Food Sci., 30: 1049-1054. DOI: 10.1111/j.1365-2621.1965.tb01885.x. http://www3.interscience.wiley.com/journal/119731077/abstract?CRETRY=1&SRETRY=0.

Ihara, N., A. Takasuga, K. Mizoshita, H. Takeda, M. Sugimoto, Y. Mizoguchi, T. Hirano, T. Itoh, T. Watanabe, K.M. Reed, W.M. Snelling, S.M. Kappes, C.W. Beattie, G.L. Bennett and Y. Sugimoto, 2004. A comprehensive genetic map of the cattle genome based on 3802 microsatellites. Genome Res., 14: 1987-1998. DOI: 10.1101/gr.2741704. PMID: 1546 6297. http://genome.cshlp.org/content/14/10a/1987.long.

Jurie, C., J. Robelin, B. Picard and Y. Geay, 1995. Post-natal changes in the biological characteristics of Semitendinosus muscle in male Limousin cattle. Meat Sci., 41: 125-135. DOI: 10.1016/0309-1740(94)00074-H. http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6T9G-3YS8DGK-11&_user=2467816&_rdoc=1&_fmt=&_orig=search&_sort=d&view=c&_acct=C000057441&_version=1&_urlVersion=0&_userid=2467816&md5=99c85640f387c0082032ebae4cf5c309.

Kappes, S.M., J.W. Keele, R.T. Stone, R.A. McGraw, T.S. Sonstegard, T.P. Smith, N.L. Lopez-Corrales and C.W. Beattie, 1997. A second-generation linkage map of the bovine genome. Genome. Res., 7: 235-249. DOI: 10.1101/gr.7.3.235. PMID: 9074927. http://genome.cshlp.org/content/7/3/235.long.

Klont, R.E., L. Brocks and G. Eikelenboom, 1998. Muscle fibre type and meat quality. Meat Sci., 49: 219-229. DOI: 10.1016/S0309-1740(98)90050-X. http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6T9G-49T53RN-N&_user=2467816&_rdoc=1&_fmt=&_orig=search&_sort=d&view=c&_acct=C000057441&_version=1&_urlVersion=0&_userid=2467816&md5=2f8966ef258cbda061cc34ca06b26080.

Knott, S.A., L. Marklund, C.S. Haley, K. Andersson, W. Davis, H. Ellegren, M. Fredholm, I. Hansson, B. Hoyheim, K. Lundstrom, M. Moller and L. Andersson, 1998. Multiple marker mapping of quantitative trait loci in a cross between outbred wild boar and large white pigs. Genetics, 149: 1069-1080. PMID: 9611214. http://www.genetics.org/cgi/content/abstract/149/2/1069.

Li, C., J. Basarab, W.M. Snelling, B. Benkel, B. Murdoch and S.S. Moore, 2002. The identification of common haplotypes on bovine chromosome 5 within commercial lines of Bos taurus and their associations with growth traits. J. Anim. Sci., 80: 1187-1194. PMID: 12019605. http://jas.fass.org/cgi/reprint/80/5/1187.

Malek, M., J.C.M. Dekkers, H.K. Lee, T.J. Baas, K. Prusa, E. Huff-Lonergen and M.F. Rothschild, 2001. A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. II meat and Muscle composition. Mamm. Genome, 12: 637-645. DOI: 10.1007/s003350020019. PMID: 11471059. http://www.springerlink.com/content/rxf2tc8en911l0421.

Nii, M., T. Hayashi, S. Mikawa, F. Tani, A. Niki, N. Mori, Y. Uchida, N. Fujishima-Kanayama, M. Komatsu and T. Awata, 2005. Quantitative trait loci mapping for meat quality and muscle fiber traits in Japanese wild boar × Large White intercross. J. Anim. Sci., 83: 308-315. PMID: 15644501. http://jas.fass.org/cgi/content/full/83/2/308.

Nkrumah, J.D., E.L. Sherman, C. Li, E. Marques, D.H. Crews, R. Bartusiak, B. Murdoch, Z. Wang, J.A. Basarab and S.S. Moore, 2007. Primary genome scan to identify putative quantitative trait loci for feedlot growth rate, feed intake and feed efficiency of beef cattle. J. Anim. Sci., 85: 3170-3181. DOI: 10.2527/jas.2007-0234. PMID: 17709790. http://jas.fass.org/cgi/content/full/85/12/3170.

Peter, J.B. and R.S. Starson, 1972. Metabolic profiles of three fiber types of skeltal muscle in guinea-pigs and rabbits. Biochemistry, 11: 2627-2633. DOI: 10.1021/bi00764a013. PMID: 4261555. http://pubs.acs.org/doi/abs/10.1021/bi00764a013.

Pette, D. and R.S. Staron, 1990. Cellular and molecular diversities of mammalian skeltal muscle fibers. Rev. Physiol. Biochem. Pharmacol., 116: 1-76. DOI: 10.1007/3540528806_3. PMID: 2149884. http://www.springerlink.com/content/p43t8v4807574248.

Seaton, G., C.S. Haley, S.A. Knott, M. Kearsey and P.M. Visscher, 2002. QTL express: Mapping quantitative trait loci in simple and complex pedigrees. Bioinformatics, 18. PMID: 11847090. http://bioinformatics.oxfordjournals.org/cgi/reprint/18/2/339.

Wegner, J., E. Albrecht, I. Fiedler, F. Teuscher, H.J. Papstein and K. Ender, 2000. Growth and breed related changes of muscle fiber characteristics in cattle. J. Anim. Sci., 78: 1485-1496. PMID: 10875630. http://jas.fass.org/cgi/reprint/78/6/1485.

Whipple, G., M. Koohmaraie, M.E. Dikeman and J.D. Crouse, 1990. Predicting Beef-Longissimus tenderness from various biochemical and histological muscle traits. J. Anim. Sci., 68: 4193-4199. PMID: 2286561. http://www.animal-science.org/cgi/content/abstract/68/12/4193.

Wimmers, K., I. Fiedler, T. Hardge, E. Murani, K. Schellander and S. Ponsuksili, 2006. QTL for microstructural and biophysical muscle properties and body composition in pigs. BMC Genet., 7: 15. DOI: 10.1186/1471-2156-7-15. PMID: 16526961. http://www.biomedcentral.com/1471-2156/7/15.