Association of the Muscle Hypertrophy Locus with Carcass Traits in Beef Cattle[1,2]

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ABSTRACT: A locus near the centromere of bovine chromosome 2 is responsible for muscle hypertrophy (*mh*) in cattle. The objectives of this study were to refine the genomic region in which the locus resides and to assess the effects of a single copy of the *mh* allele on carcass and birth traits. Two half-sib families were developed using a Belgian Blue × MARC III (n = 246) or a Piedmontese × Angus (n = 209) sire. Traits analyzed were calving ease (CE), birth weight (BWT, kg), longissimus rib eye area (REA), retail product yield (RPYD), USDA yield grade (YG), marbling (MAR), fat thickness (FAT), estimated kidney, pelvic, and heart fat (KPH), and longissimus tenderness measured as Warner-Bratzler shear force at 3 (S3) and 14 (S14) d postmortem. Six microsatellites were used to determine the presence or absence of the *mh* allele and to confirm the location of the locus affecting the traits, which was assessed to be 4 cM from the beginning of the linkage group, with the 95% confidence interval between 2 and 6 cM. Cattle with an *mh* allele had increased ($P < .01$) REA, RPYD, and BWT and decreased MAR, YG, FAT, and KPH, compared with those without the allele. The effects of the *mh* allele (*mh*/+ vs +/+) were 1.35, 1.6, .41, –1.01, –1.42, –.84, and –.86 residual standard deviations, respectively. There were no effects ($P > .10$) for CE, S3, and S14. Allelic differences due to the *mh* locus were similar for both sources (Belgian Blue or Piedmontese). Individuals inheriting a single *mh* allele had a leaner, more heavily muscled carcass compared with those inheriting the alternative allele. Thus, mating schemes that maximize production of *mh*/+ genotypes provide a viable approach for improving carcass composition.

Key Words: Double Muscling, Carcasses, Beef, Genetic Markers

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Introduction

Double-muscled animals are known to have leaner carcasses than normal animals. This phenotype is characterized by greater muscle mass with less fat, reduced feed intake, and improved feed conversion (Hanset et al., 1987; Arthur, 1995; Cundiff et al., 1996; Wheeler et al., 1996; Wheeler et al., 1997). These characteristics have led to the selection of this phenotype for specific uses in Europe despite its association with reduced female fertility, susceptibility to respiratory illness, and the need for Caesarian section due to high incidence of dystocia (Hanset, 1991). Most studies support the notion that a single copy of the allele (*mh*/+) has relatively large effects on carcass characteristics, without a negative effect on fertility, compared with no copies (+/+) of the allele (Arthur, 1995).

The locus causing double muscling in cattle has been mapped to the centromeric end of bovine chromosome 2 (**BTA2**; Charlier et al., 1995; Dunner et al., 1997). This map position was located 2 and 3 centimorgans (cM) beyond the most centromeric marker available on BTA2 at the time these studies were conducted (Charlier et al., 1995; Dunner et al., 1997, respectively). Recently, additional markers in this region have been developed (Sonstegard et al., 1997). Thus, the objectives of the present study were to refine the location of the *mh* locus and to assess the effects of a single copy of the *mh* allele on birth and carcass traits.

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[2]Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by the USDA and does not imply approval to the exclusion of other products that may be suitable.

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Materials and Methods

Animals

Two half-sib families were developed using a Belgian Blue × MARC III (¼ Angus, ¼ Hereford, ¼ Red Poll, ¼ Pinzgauer) sire and a Piedmontese × Angus sire. A total of 246 ¼ Belgian Blue (**BB**) and 209 ¼ Piedmontese (**P**) offspring were produced by matings primarily to MARC III dams. The paternal grandsires displayed double muscling phenotype and were presumed to be homozygous for the *mh* allele. Thus, we expected that one-half of the progeny of the two sires used in this study would inherit one copy of the *mh* allele (*mh*/+), and the other half would inherit zero copies (+/+). Dams were artificially inseminated, and the offspring were born during the spring of 1995. Calves were weaned at an average of 200 d and raised from weaning to slaughter on a corn-corn silage diet. At a commercial beef processing facility, steers were slaughtered after 194 to 312 d, and heifers were slaughtered after 207 to 287 d of feed.

Markers

A total of six microsatellite markers were used (Figure 1). The first four microsatellite markers at the beginning of BTA2 linkage group were used to assess inheritance of the *mh* allele from Belgian Blue or Piedmontese. Two additional markers, TGLA377 at 28 cM and BMS1300 at 47 cM (Kappes et al., 1997), were used to confirm that the locus affecting the traits was in the proximal region of BTA2. Primer sequences were obtained from the MARC bovine genome map (Kappes et al., 1997; http://sol.marc.usda.gov), an updated version of BTA2 (Sonstegard et al., 1997), or developed from yeast artificial chromosome (**YAC**) clones. The most centromeric, BMC9007 (Figure 1), was developed from a cosmid clone containing Protein C (Sonstegard et al., 1997). Markers TGLA44 and INRA40 are, respectively, 1.2 and 9 cM (Figure 1) from BMC9007 (Kappes et al., 1997). Primers for INRA40 were redesigned: INRA40F: 5′-TGA AAG GGG GTG TGT GGG-3′; INRA40R: 5′-CTG CCC TGG GGA TGA TTG-3′.

To increase the informativeness in the area of the locus, an additional closely linked microsatellite (BY5) was isolated from YAC clones containing TGLA44 using an adaptation of the vectorette PCR (Pandolfo, 1992). This marker maps to the same position as TGLA44 (Figure 1). Pulse field electrophoresis was used to isolate DNA from a YAC and digested with *Sau*3AI. After YAC/vectorette ligation, PCR was done using the universal primer 224 (Riley et al., 1990) and either a G4(GT)11 or G4(CA)11 primer. Products were ligated into a dT-tailed vector (Marchuk et al., 1991) and sequenced. Compatible primers developed from the sequences on either side of the microsatellite were obtained by testing primer pair combinations on undigested YAC DNA. Sequences for the forward and reverse primers that were found to consistently yield amplified products were as follows: BY5F: 5′-TCA AAT CCA ACC CAG TCT CC-3′; BY5R: 5′-GAT CAA AGC TGC TCC TAA TGT T-3′.

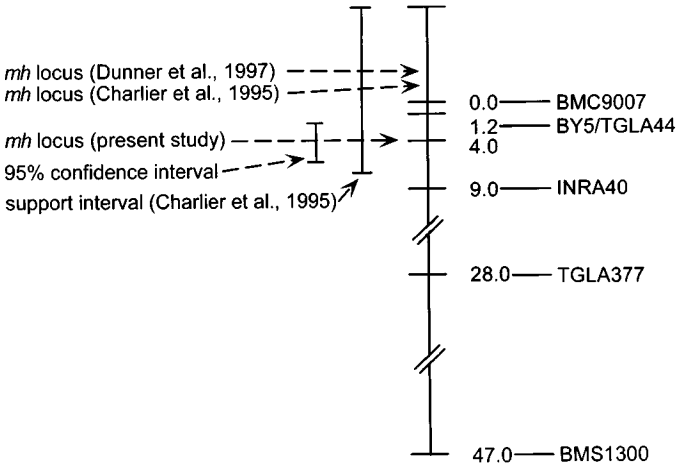

Figure 1. Markers and linkage distances used. Position of the *mh* locus according to previous studies (Charlier et al., 1995; Dunner et al., 1997) and the present study are indicated.

Analytical Procedure

Marker Inheritance. Microsatellite markers were amplified under conditions described elsewhere (Bishop et al., 1994). A saturated salt procedure was used to extract DNA (Miller et al., 1988) from white blood cells obtained from all the offspring, dams, sires, and one grandparent of each family. Genotyping was done by examining offspring, paternal, and paternal grandparent genotypes, and linkage analysis was done using the program CRIMAP ver. 2.4 (Green et al., 1989). Linkage distances and marker order were obtained by genotyping the USDA reference family (Kappes et al., 1997). To minimize genotyping errors, two individuals scored each genotype independently. When discrepancies occurred, consensus was attempted. If discrepancy remained, the sample was reamplified and scored again. If discrepancy remained after this, the genotype was discarded from the analysis.

The probability of inheriting the *mh* allele from the sire was estimated using a similar procedure as described by Haley and Knott (1992). Linkage data for the six markers were analyzed using CRIMAP (Green et al., 1989). The CHROMPIC option was used to identify crossovers and to establish the alleles at the markers inherited from the Belgian Blue and Piedmontese grandsires. These marker alleles were assumed to be associated with the *mh* allele, and the conditional probabilities of inheriting it were calculated with a FORTRAN program.

Traits Analyzed. Offspring of the two sires were evaluated for birth and carcass traits. Birth weight (**BWT**) was recorded and calving ease (**CE**) scored as previously described (Gregory et al., 1991). Carcass information was obtained according to the procedure outlined by Shackelford et al. (1995). Briefly, at 36 h postmortem, carcasses were ribbed between the 12th and 13th ribs and marbling score was determined. The wholesale rib was obtained from the right side of the carcass and transported to MARC. The wholesale rib was separated into a rib eye roll, 80% lean trim, fat trim, bone, and short rib according to Wheeler et al. (1997). Retail product was estimated according to Shackelford et al. (1995). The rib eye roll was sliced to yield 2.54-cm-thick steaks. Longissimus Warner-Bratzler shear force was assessed at 3 and 14 d postmortem (AMSA, 1995). Carcass traits evaluated were retail product yield (**RPYD**), USDA yield grade (**YG**), longissimus rib eye area (**REA**), marbling (**MAR**), fat thickness (**FAT**), estimated kidney, pelvic, and heart fat (**KPH**), and longissimus tenderness measured as shear force at 3 (**S3**) and 14 (**S14**) d postmortem (AMSA, 1995).

Statistical Analysis. Data were analyzed using the approach suggested by Haley and Knott (1992) with the following statistical model: $Yijklm = \mu + Si + Gj + SGij + Mk + Bl + \beta cov\ Xcov + \epsilon ijklm$, where Yijklm = phenotypic observations, μ = overall mean, Si = effect of the i^{th} sire, Gj = effect of the j^{th} sex, SGij = effect of the sire × sex interaction, Mk = regression of the phenotype on the probability of inheriting the *mh* allele given the marker genotypes and recombination distances, Bl = effect of the maternal breed inheritance, βcov = regression coefficient of age of dam for BWT and CE and hot carcass weight for carcass traits, Xcov = age of dam for BWT and CE and hot carcass weight for carcass traits, and ϵijklm = random error.

To identify the position of the *mh* locus and determine the magnitude of its effect on the traits, *F*-statistics were generated at 1-cM intervals. In addition, the interaction between the sire and *mh* allele was included in the model to test for the differences in *mh* allele effect and position between the two sires. A 95% confidence interval was constructed to establish whether differences in magnitude and position between Belgian Blue and Piedmontese *mh* allele origin were different from zero.

The length of a 95% confidence interval for the location of the *mh* locus was obtained by simulation. The midpoint of the 95% confidence interval was established at the position corresponding to the maximum *F*-statistic. Retail product yield was used as the basis for obtaining the confidence interval because it provided the most information for resolving the *mh* locus. A simulated quantitative trait locus (**QTL**) was randomly assigned to any location within the linkage group, and the most likely position was identified with the marker information available. The difference between both positions was obtained and the process was repeated 10,000 times. For each 5-cM interval, approximately 1,000 repetitions were obtained.

The experiment-wise threshold value was calculated according to the equation indicated by Lander and Kruglyak (1995), using the values of 30 chromosomes and 30 Morgans of genome length. A threshold value of 16.9 for the *F*-statistic was obtained for evidence of association. Declaring a significant QTL only if the *F*-statistic is at, or exceeds, 16.9 ensures that the occurrence of false positives in whole genome scans will be 5% or less. This corresponds to a nominal type I error of .00005.

Results

Position of the mh Locus. The position of the maximum *F*-statistic obtained for all the traits ranged from 2 to 7 cM from the beginning of the linkage group (Figures 1, 2, and 3). The most likely map position of the locus is at the 4 cM position, and the simulation procedure, based on RPYD, suggests that the 95% confidence limit is between 2 and 6 cM. This information indicates that *mh* is located between TGLA44/BY5 and INRA40, which have been mapped to 1.2 and 9.0 cM distal to BMC9007 (0 cM), respectively (Figure 1). The simulation procedure provided additional support for the locus being in this

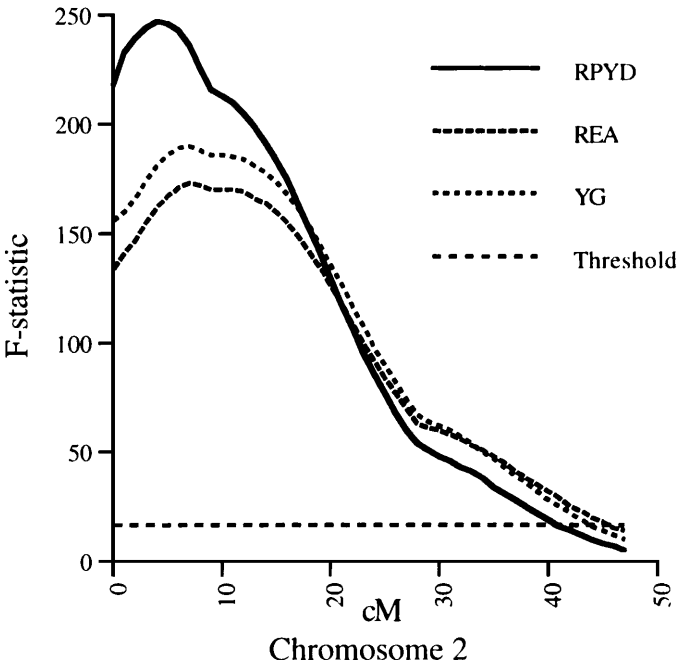

Figure 2. *F*-statistic profile for retail product yield (RPYD, %), rib eye area (REA, cm^2), and yield grade (YG) on proximal region of bovine chromosome 2. Significant threshold (F = 16.9; P < .01) according to Lander and Kruglyak (1995)

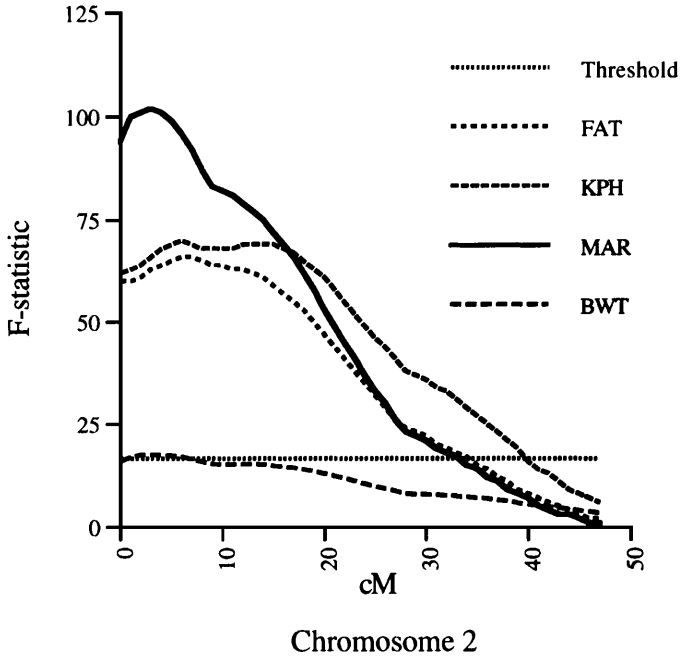

Figure 3. *F*-statistic profile for fat thickness (FAT, cm), estimated kidney, pelvic, and heart content (KPH, %), marbling (MAR), and birth weight (BWT, kg) on the proximal region of bovine chromosome 2. Significant threshold (F = 16.9; P < .01) according to Lander and Kruglyak (1995).

interval and suggested that it is approximately 2.8 cM distal to TGLA44/BY5.

Association of mh Allele with Carcass Traits. The *F*-statistics indicate an association (P < .001) of the proximal region of chromosome 2 with BWT, RPYD, REA, YG, MAR, FAT, and KPH (Figures 2 and 3). No association (P > .10) was observed for CE, S3, and S14. Age of dam was not significant (P > .10), and in all cases sex and hot carcass weight were important sources of variation (P < .05). The mean, SE, maximum *F*-statistic, and effect of the *mh* allele for each trait are summarized in Table 1. Relative to the alternative allele, the *mh* allele increased REA, RPYD, and BWT and decreased MAR, YG, FAT, and KPH. The effect of the *mh* allele (*mh*/+ vs +/+) was 1.35, 1.60, .41, –1.01, –1.42, –.84, and –.86 residual standard deviations, respectively (Table 1). The difference between groups is also indicated on Table 1. The effect of the *mh* allele was not influenced by source (Belgian Blue or Piedmontese; Table 2). The small differences observed between alternate sources of the *mh* allele are likely due to sampling.

Discussion

Charlier et al. (1995) and Dunner et al. (1997) mapped the *mh* locus to BTA2 between TGLA44 and the centromere (Figure 1). More recently, a more centromeric marker, BMC9007, has been developed, and informativeness has been increased in the region by the development of an additional marker, BY5, from a YAC containing TGLA44 (Kappes et al., 1997; Sonstegard et al., 1997). The analysis, using the additional marker information, showed the maximal *F*-statistic for all the traits to be between 3 and 7 cM. The data suggest a map location of approximately 2.8 cM distal to TGLA44. This estimate is not precise; however, the simulation procedure using RPYD as a model trait allowed us to predict with more than 95% certainty that the locus is between BMC9007 and INRA40 or between 2 and 6 cM of the linkage map (Figure 1).

The map position of the *mh* locus in the centromeric region of BTA2 is similar to reports from previous studies (Charlier et al., 1995; Dunner et al., 1997). Charlier et al. (1995) mapped the *mh* locus to 2 cM centromeric to TGLA44, and Dunner et al. (1997) mapped it to 3.1 cM in the same direction. Charlier et al. (1995) gave a support interval of 12 cM centered on TGLA44. The confidence interval obtained in the present study is included in the support interval postulated by Charlier et al. (1995). There is no indication of conflict between studies, given that the most likely position of the *mh* locus established in this study lies within the boundaries of the support interval (Charlier et al., 1995); however, the resolution of the confidence interval in this study is more refined.

A strong positional candidate gene for the *mh* locus has been identified (Smith et al., 1997). Myostatin, a gene that causes muscle hypertrophy in mice (McPherron et al., 1997), has been positioned within the boundaries of the 95% confidence interval reported herein. The results of the present study and future genotypic data from these animals based on sequence variation in the myostatin gene will provide critical information for establishing myostatin as a candidate gene for the *mh* locus.

Historical evidence has led to the conclusion that double muscling is a major gene in beef cattle causing the same physiological events in all breeds expressing the condition (Menissier, 1982; Arthur, 1995). A comparison was made to assess whether there were differences in magnitude at the maximal *F*-statistic between the two origins of the *mh* allele (Belgian Blue or Piedmontese). In all traits associated with the *mh* allele, the difference between sires was close to zero. Furthermore, all the 95% confidence intervals calculated for this difference included zero. This result is consistent with the conclusion that the effect of the *mh* allele on carcass traits is independent of breed origin.

Inheritance of the *mh* allele from the F_1 sires resulted in distinct differences in carcass composition compared to those inheriting the alternative allele. Individuals inheriting the *mh* allele, from either the Belgian Blue or Piedmontese sire, had a higher proportion of muscle mass and were leaner. These

Table 1. Mean and standard errors for birth weight (BWT), retail product yield (RPYD), rib eye area (REA), yield grade (YG), marbling (MAR), fat thickness (FAT), estimated kidney, pelvic, and heart fat (KPH), calving ease (CE), and tenderness measured as shear force at 3 (S3) and 14 (S14) d postmortem, and the effect of the *mh* allele [(*mh*/+) – (+/+)] as proportion of the residual standard deviation

			(*mh*/+) – (+/+)	
Trait	Mean ± SE	Maximum *F*-statistic	Difference[a]	Residual SD units
BWT, kg	40.3 ± .2813	17.5	4.56	.41
RPYD, %	66.4 ± .199	247	4.39	1.60
REA, cm^2	85.2 ± .48	173	1.3	1.35
YG	2.13 ± .035	190	–.74	–1.42
MAR	500 ± 3.14	102	–50.92	–1.01
FAT, cm	.7 ± .018	66	–.099	–.84
KPH, %	2.8 ± .033	70	–.43	–.86
CE	1.2 ± .05	2	NS	NS
S3	4.6 ± .05	5	NS	NS
S14	3.5 ± .033	2	NS	NS

[a]Differences are presented in the units for the traits in the first column.
NS = not significant ($P > .05$).

differences in carcass composition between the alternative groups follow a pattern similar to those previously reported in which homozygous double-muscled cattle were compared to normal animals (Menissier, 1982; Hanset and Michaux, 1985; Arthur, 1995). Double-muscled animals generally have a higher dressing percentage, a larger proportion of muscle, and lower proportion of fat and bone (for review see Arthur, 1995). Arthur (1995) stressed that studies evaluating a single copy of the *mh* allele have been limited to offspring of homozygous purebred sires or have relied on subjective criteria to determine the presence or absence of the allele. Thus, it has not been possible to accurately separate overall breed effect from the effect of the *mh* allele. We have used microsatellite markers flanking the *mh* allele to follow its segregation in ¼ Belgian Blue or ¼ Piedmontese animals and establish its effects on carcass traits in a composite genetic background and a conventional production system. This is one of the first examples of markers being used to evaluate the effect of a segregating allele for which phenotypic data are difficult to obtain. Future production systems using alleles such as *mh* can be more efficient because breeding decisions can be based on genotypes with less reliance on subjective phenotypes.

The largest estimated effects of the *mh* allele were on RPYD (4.4% between genotypes or 1.6 residual SD) and YG (–.74 units of YG or –1.42 residual SD). In most breeds of cattle, the majority of the variation in RPYD and YG is attributable to variation in fat content (Shackelford et al., 1995). In cattle inheriting the *mh* allele, RPYD and YG are influenced by a decrease in fat and an increase in muscularity. Although early reports indicated that double-muscled animals produced tough meat, recent studies indicate that meat from double-muscled animals is more tender than meat from animals with the alternative alleles (Arthur, 1995); however, the results of the present study suggest that a single copy of the *mh* allele had no effect on tenderness, measured as longissimus shear force at 3 and 14 d postmortem.

When birth weight and calving ease were analyzed as traits of the calf, individuals inheriting the *mh* allele were slightly heavier at birth ($P < .05$), and there was no association with calving ease ($P > .05$). These results were expected, because previous reports indicated that birth weight was not increased in individuals inheriting a single copy of the *mh* allele (Menissier, 1982; Hanset, 1991). Calving difficulty has been associated with double muscling when compared in dams with alternative phenotypes (Hanset et al., 1989; Hanset, 1991). The design of the

Table 2. Difference between effect of Belgian Blue or Piedmontese origin of *mh* allele and 95% confidence interval for birth weight (BWT), retail product yield (RPYD), rib eye area (REA), yield grade (YG), marbling (MAR), fat thickness (FAT), and estimated kidney, pelvic, and heart fat (KPH)

		Confidence interval	
Trait	Difference	Lower boundary	Upper boundary
BWT, kg	–.045	–1.1	.92
RPYD, %	.47	–.088	1.03
REA, cm^2	.157	–.042	.36
YG	–.101	–.21	.007
MAR	–2.05	–12.2	8.1
Fat, cm	–.04	–.098	.025
KPH, %	–.075	–.18	.028

present study was unable to estimate the effect of the *mh* allele on calving ease as a characteristic of the dam; however, calving difficulty was unaffected by the inheritance of a single copy of the *mh* allele from the sire. This indicates that calves heterozygous for the double-muscled phenotype are slightly heavier at birth but have calving ease comparable to that of calves without the allele.

Implications

Mating schemes that maximize production of individuals heterozygous for the *mh* allele (*mh*/+ genotypes), while avoiding the production of *mh*/*mh*, provide a viable approach for producing leaner, more heavily muscled carcasses. The use of microsatellite markers permits the identification of individuals with double muscling characteristics at an early stage in life, thus allowing flexibility in mating schemes using the *mh* allele to influence carcass characteristics.

Literature Cited

AMSA. 1995. Research guidelines for cookery, sensory evaluation and instrumental tenderness measurements of fresh meat. American Meat Science Association, Chicago, IL.

Arthur, P. F. 1995. Double muscling in cattle: A review. Aust. J. Agric. Res. 46:1493–1515.

Bishop, M. D., S. M. Kappes, J. W. Keele, R. T. Stone, S. L. Sunden, G. A. Hawkins, S. S. Toldo, R. Fries, M. D. Grosz, J. Yoo, and C. W. Beattie. 1994. A genetic linkage map for cattle. Genetics 136:619–639.

Charlier, C., W. Coppetiers, F. Farnir, L. Grobert, P. L. Leroy, C. Michaux, M. Mni, A. Schwers, P. Vanmanshoven, R. Hanset, and M. Georges. 1995. The mh gene causing double-muscling in cattle maps to bovine chromosome 2. Mamm. Genome 6: 788–792.

Cundiff, L. V., K. E. Gregory, T. L. Wheeler, S. D. Shackelford, M. Koohmaraie, H. C. Freetly, and D. D. Lunstra. 1996. Preliminary results from cycle V of the Cattle Germplasm Evaluation Program at the Roman L. Hruska U.S. Meat Animal Research Center. Germplasm Evaluation Program Progress Report No. 15. USDA-ARS, Clay Center, NE.

Dunner, S., C. Charlier, F. Farnir, B. Brouwers, J. Canon, and M. Georges. 1997. Towards interbred IBD fine mapping of the mh locus: Double-muscling in the Asturiana de los Valles breed involves the same locus as in the Belgian Blue cattle breed. Mamm. Genome 8:430–435.

Green, P., K. Falls, and S. Crooks. 1989. Documentation for CRI-MAP, version 2.4. Washington University School of Medicine, St. Louis, MO.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for birth weight, birth date, dystocia, and survival as traits of dam in beef cattle. J. Anim. Sci. 69:3574–3589.

Haley, C. S., and S. A. Knott. 1992. A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. Heredity 69:315–324.

Hanset, R. 1991. The major gene of muscular hypertrophy in the Belgian Blue cattle breed. In: J. B. Owen and R.F.E. Axford (Ed.) Breeding for Disease Resistance in Farm Animals. pp 467–478. CAB International, Bangor, U.K.

Hanset, R., and C. Michaux. 1985. On the genetic determinism of muscular hypertrophy in the Belgian White and Blue cattle breeds. Genet. Sel. Evol. 17:359–368.

Hanset, R., C. Michaux, and G. Detal. 1989. Genetic analysis of some maternal reproductive traits in the Belgian Blue cattle breed. Livest. Prod. Sci. 23:79–96.

Hanset, R., C. Michaux, and A. Stasse. 1987. Relationship between growth rate carcass composition, feed intake, feed conversion ratio and income in four biological types of cattle. Genet. Sel. Evol. 19:225–248.

Kappes, S. M., J. W. Keele, R. T. Stone, R. A. McGraw, T. S. Sonstegard, T.P.L. Smith, N. L. Lopez-Corrales, and C. W. Beattie. 1997. A second generation linkage map of the bovine genome. Genome Res. 7:235–249.

Lander, E., and L. Kruglyak. 1995. Genetic dissection of complex traits: Guidelines for interpreting and reporting linkage results. Nat. Genet. 11:241–247.

Marchuk, D., M. Drumm, A. Saulino, and F. S. Collins. 1991. Construction of T-vectors, a rapid and general system for direct cloning of unmodified PCR products. Nucleic Acids Res. 19: 1154.

McPherron, A. C., A. M. Lawler, and S.-J. Lee. 1997. Regulation of skeletal muscle mass in mice by a new TGF-β superfamily member. Nature (Lond.) 387:83–90.

Menissier, F. 1982. General survey of the effect of double muscling on cattle performance. In: J.W.B. King and F. Messinier (Ed.) Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production. pp 23–53. Martinus Nijhoff Publishers, The Netherlands.

Miller, S. A., D. D. Dykes, and H. F. Polesky. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. Nucleic Acids Res. 16:1215.

Pandolfo, M. 1992. A rapid method to isolate (GT)n repeats from yeast artificial chromosomes. Nucleic Acids Res. 20:1154.

Riley J., R. Butler, D. Ogilvie, R. Finniear, D. Jenner, S. Powell, R. Anand, J. C. Smith, and A. F. Markham. 1990. A novel, rapid method for the isolation of terminal sequences from yeast artificial chromosome (YAC) clones. Nucleic Acids Res. 18: 2887–2894.

Shackelford, S. D., L. V. Cundiff, K. E. Gregory, and M. Koohmaraie. 1995. Predicting beef carcass cutability. J. Anim. Sci. 73: 406–413.

Smith, T.P.L., N. Lopez-Corrales, S. M. Kappes, and T. S. Sonstegard. 1997. Myostatin maps to the interval containing the bovine mh locus. Mamm. Genome 8:742–744.

Sonstegard, T. S., N. L. Lopez-Corrales, S. M. Kappes, C. W. Beattie, and T.P.L. Smith. 1997. Comparative mapping of human chromosome 2 identifies segments of conserved synteny near the bovine mh locus. Mamm. Genome 8:751–755.

Wheeler, T. L., L. V. Cundiff, R. M. Koch, and J. D. Crouse. 1996. Characterization of biological types of cattle (Cycle IV): Carcass traits and longissimus palatability. J. Anim. Sci. 74: 1023–1035.

Wheeler, T. L., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and J. D. Crouse. 1997. Characterization of different biological types of steers (Cycle IV): Wholesale, subprimal, and retail product yields. J. Anim. Sci. 75:2389–2403.