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1 **Genome Wide Association Study on beef production Traits in Marchigiana**

2 **Cattle breed**

3

4 Silvia Sorbolini¹, Silvia Bongiorno², Massimo Cellesi¹, Giustino Gaspa¹, Corrado Dimauro¹, Alessio
5 Valentini, and Nicolò Pietro Paolo Macciotta^{1*}.

6

7 ¹ Dipartimento di Agraria, Sezione di Scienze Zootecniche, Università degli Studi di Sassari, 07100,
8 Sassari, Italy;

9 ² Dipartimento per l'Innovazione dei Sistemi Biologici Agroalimentari e Forestali DIBAF,
10 Università della Tuscia, Viterbo, Italy.

11

12 *corresponding author: Nicolò Pietro Paolo Macciotta, Dipartimento di Agraria, Sezione di Scienze
13 Zootecniche Università degli Studi di Sassari, 07100, Sassari, Italy. E-mail: macciott@uniss.it

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24 **Summary**

25 A genome-wide association study was carried out on a sample of Marchigiana breed cattle to detect
26 markers significantly associated with carcass and meat traits. Four hundred and nine young bulls
27 from 117 commercial herds were genotyped by Illumina 50K BeadChip assay. Eight growth and
28 carcass traits (average daily gain, carcass weight, dressing percentage, body weight, skin weight,
29 shank circumference, head weight, carcass conformation) and two meat quality traits (pH at
30 slaughter and pH 24 hours after slaughter) were measured. Data were analyzed with a linear mixed
31 model that included fixed effects of herd, slaughter date, fixed covariables of age at slaughter and
32 SNP genotype, and random effects of herd and of animal. A permutation test was performed to
33 correct SNP genotype significance level for multiple testing. A total of 96 SNPs were
34 significantly associated at genome-wide level with one or more of the considered traits. Gene search
35 was performed on genomic regions identified on the basis of significant SNP position and level of
36 linkage disequilibrium. Interesting loci affecting lipid metabolism (*SOAT1*), bone (*BMP4*) and
37 muscle (*MYOF*) biology were highlighted. These results may be useful to better understand the
38 genetic architecture of growth and body composition in cattle.

39

40 **Keywords:** SNP chip, GWAS, bovine, productive traits

41

42 **Introduction**

43 The recent availability of high throughput SNP platforms for several livestock species has
44 revitalized the search for DNA markers associated to phenotypic variation in complex traits of
45 economic importance (Bush and Moore 2012). Genome-wide association studies (GWAS)
46 represent a first step toward the understanding of molecular and cellular mechanisms underlying
47 phenotypic expression of complex traits (Jiang *et al.* 2010; Korte and Farlow 2013).

48 Genomic approaches are expected to have a great impact on traits that are difficult and expensive to
49 measure. An example are *post-mortem* traits in beef cattle. Dressing percentage, carcass
50 composition, and meat quality are difficult to obtain and relate to animals retained for selection.
51 Recent GWAS studies have detected associations between SNPs and beef traits, suggesting
52 *myostatin*, *DGAT1* and *leptin receptor* as candidate genes (Jiang *et al.* 2010).

53 Local beef breeds are important for typical production systems and for crossbreeding with
54 specialized breeds. GWAS carried out on local breeds may provide useful insights in the genetic
55 determinism of meat traits by picking up genetic variation no longer detectable in cosmopolitan
56 breeds. In Italy there are several local beef cattle breeds. They differ in selection history, trait
57 phenotypic expression, and genetic background (Sorbolini *et al.*, 2015). The Marchigiana breed is a
58 typical example. It originated from the Asiatic long-horned (*Bos primigenius*) cattle and moved to
59 Italy from Central Asian steppes during invasions in the sixth/seventh century C.E. (Trombetta *et*
60 *al.* 2005). Beef traits were improved by crosses with Chianina and Romagnola cattle in the second
61 half of the nineteenth century. The current Marchigiana is the result of a breeding program started
62 after the above mentioned cross-breeding. At present, it is the second beef breed of Italy with about
63 52,344 hd registered in the Herdbook. It is characterized by a strong adaptability to harsh
64 environmental conditions, great precocity, fertility and a remarkable aptitude for meat production
65 (Balasini 1981) due to well-pronounced muscle development and fine bone structure and skin. For
66 these reasons it has also been exported to countries such as United States, Canada, Brazil,
67 Argentina and Australia (“<http://www.anabic.it/>”)

68 In the present work, a GWAS was carried out on a sample of 409 Marchigiana young bulls farmed
69 in commercial herds, genotyped with the Illumina Bovine SNP50 BeadChip. The study was aimed
70 at identifying chromosome regions harbouring new putative candidate genes affecting meat and
71 carcass quality traits in beef cattle.

72

73 **Material and Methods**

74 Animals and phenotypic data

75 Four hundred and nine Marchigiana young bulls from 117 commercial herds were slaughtered
76 between 16 and 24 months of age. Phenotypes of ten different growth, carcass and meat quality
77 traits were recorded at the slaughter house: body weight (BW), average daily gain (ADG), carcass
78 weight (CW), dressing percentage (DP), skin weight (SW), shank circumference (SC), head weight
79 (HW), carcass conformation according to the European grid based on muscularity and fat content
80 (SEUROPE) evaluation system (CC), pH at slaughter (pH) and pH 24 hours after slaughter
81 (pH24h). pH at slaughter and 24h after slaughter were measured on the *longissimus dorsii* muscle
82 with the HI 99 163 pHmeter (Hanna instruments).

83

84 Genotypic data

85 Genomic DNA was extracted from whole blood samples gathered immediately before slaughter
86 using the NucleoSpin 96 Blood Kit (Macherey-Nagel) according to manufacturer's instructions.
87 All 409 animals were genotyped using the Illumina 50K BeadChip assay. SNP editing was on call
88 rate (>99%) and minor allele frequency (>1%). Animals having more than 2,5% of missing
89 genotypes were discarded. A total of 43,313 markers were retained after edits.

90

91 Statistical Analysis

92 Data were analyzed using the following mixed linear model:

$$93 \quad Y = D + bAGE + bSNP + a + h + e \quad [1]$$

94 where:

95 Y = record for the the considered trait;

96 D = fixed effect of slaughter date (46 levels);

97 bAGE = fixed covariable of age at slaughter in months ;

98 bSNP = fixed covariable of SNP genotype (coded as 0, 1, 2 according to the number of second
99 allele)

100 a = random additive genetic effect of the animal.

101 h = random effect of the herd (114 levels);

102 e = random residual.

103 The animal effect was assumed to be normally distributed $\sim N(0, \mathbf{G}\sigma_a^2)$ where \mathbf{G} is the genomic
104 relationship matrix and σ_a^2 is the additive genetic variance. \mathbf{G} was calculated according to
105 VanRaden (2008) as:

106
$$\mathbf{G} = \frac{\mathbf{ZZ}'}{2\sum p_i(1-p_i)}$$

107 where \mathbf{Z} is the matrix of individual genotypes scaled by allele frequencies (p_i) expressed as
108 differences from 0.5.

109 A modified version of the experimentwise empirical threshold proposed by Churchill and Doerge
110 (1994) was used to correct SNP statistical significance for multiple testing. In a first step, single
111 marker analysis was performed with model [1]. Significant markers ($P < 0.01$) were retained. In the
112 second step, 10,000 permutations were performed for each significant marker by shuffling SNPs
113 across animals, while keeping invariant the other factors included in model [1] (Anderson and Ter
114 Braak 2003). The bottom 5% of α probabilities of test statistics for each marker (SNP_ALPHA)
115 were retained. Then SNP_ALPHA for all SNPs were put in the same column, and the 5th percentile
116 was kept as a critical threshold for declaring significant at $P < 0.05$ tests performed in the first step.
117 Statistical analyses were performed using SAS 9.2 (SAS/STAT software version 9.2, SAS Institute,
118 Inc. Cary, NC, USA).

119

120 Putative candidate genes identification

121 Gene search was performed on chromosome regions defined by positions of significant SNPs
122 according to the sixth draft of bovine genome assembly (UMD3.1/bosTau 6) UCSC Genome
123 Browser Gateway (<http://genome.ucsc.edu/>). Windows of variable amplitude in Mb were defined
124 based on linkage disequilibrium of the specific genomic region (Macciotta *et al.* 2015). For each
125 significant SNP the squared coefficient (r^2) statistic with all other SNPs positioned in the same
126 chromosome was calculated (Table S1). Distance between the significant SNP and the furthest SNP
127 having an $r^2 > 0.10$ was calculated and added upstream and downstream to the position of
128 significant marker. SNP not in LD with other markers were not considered for gene discovery.
129 Finally, specific functional analysis and biological roles of annotated genes were investigated by an
130 accurate literature search and databases consultation such as GeneCards (www.genecards.org),
131 National Centre for Biotechnology Information (www.ncbi.nlm.nih.gov), Proteinatlas
132 (www.proteinatlas.org). Gene names and symbols were derived from HUGO Gene nomenclature
133 database (www.genenames.org).

134

135 **Results**

136 Significant SNPs and association analyses

137 A total of 96 SNPs were found to be associated with seven out of ten considered traits (ADG,
138 CW, DP, BW, HW, SC and pH) (Table S1). As an example, figure 1 reports the Manhattan plot for
139 ADG.

140 No significant SNP were found for pH24h, SW and CC. The largest number of significant markers
141 associated with different traits was found on BTA2 (14 SNPs), followed by BTA6 (11 SNPs) and 8
142 (10 SNPs). Chromosomes 9, 11, 12, 18, 19, 23, and 29 showed only one significant marker. BTAs
143 13, and 27 did not show any associated marker.

144 Significant markers of BTA2 were associated with five different traits (ADG, CW, DP, pH, and
145 SC) followed by BTA8 with four (ADG, HW, SC, pH) and 26 with three (HW, SC, pH). Finally, a

146 total of two SNPs resulted associated with two traits (ADG and BW); rs43272238 on BTA1, and
147 rs41662409 on BTA16.

148

149 Average Daily Gain

150 Forty-five significant markers were detected for ADG. Chromosome 6 showed the highest number
151 of SNP associated with this trait (10). BTAs 5, 15, 22, 24 and 28 contained only one significant
152 marker associated with ADG. A SNP located on BTA10 between 65,7 and 67,5 Mb (*rs41568676*)
153 flagged a region where the *bone morphogenetic protein 4 (BMP4)* gene maps (Table1). On BTA14
154 the rs41631408 at 57469150 bp pointed out the *thyrotropin-releasing hormone receptor (THRH)*
155 locus. Other significant markers associated with ADG identified several distinct genes involved
156 primarily in cellular processes such as growth and proliferation (*IFRD1, CGRRF1, TGFB2*), but
157 also genes involved in general metabolic pathways such as (*SPTLC1, UTG1A6* and *UTG1A1*) or
158 specific pathways such as carbohydrate metabolism (*ALDOA*) and lipid metabolism (*SOAT1*)
159 (Table1).

160

161 Shank circumference

162 Table S1 reports the 13 significant markers found to be associated with SC. After ADG, it was the
163 trait with the highest number of significant associated markers. Three of them were found on
164 BTA14 and two on BTA8. However, no annotated genes were retrieved in the corresponding
165 chromosomal regions.

166

167 Dressing Percentage

168 Twelve SNPs were found significantly associated with DP. Eight out of 12 were located in a large
169 chromosomal region between 1,0-5,2 Mb on BTA2. These SNPs were in close proximity with a

170 QTL that contains the *myostatin* (*MSTN*) locus and two other genes that have a role in muscle
171 biology (*SLC40A1* and *COL5A2*.) On BTA9 at 288595 bp from the significant SNP *rs 41662464*
172 map the *connective tissue growth factor* (*CTGF*), a gene involved in chondrocyte proliferation.

173

174 Carcass Weight

175 In this study, 9 significant markers distributed over seven different autosomes were associated
176 with CW. Four SNPs were found on BTA5 (Table S1). On BTA2 the SNP *rs109168082* at 129,8
177 Mb tagged to the *PNRC2*, *GALE* genes (Table 1). On BTA23 the validated mRNA sequence of
178 *ATP-binding cassette, subfamily F (GCN20), member 1 (ABCF1)* is annotated close to the
179 *rs110277462* marker.

180

181 Head Weight

182 A total of 7 significant SNPs were associated with HW. BTA7 harbored the largest number of
183 markers (n = 2) associated with this trait (Table S1) whereas BTAs 5,11,16,20 and 26 showed a
184 single significant marker.

185

186

187 Body weight

188 A total of 5 significant SNPs were found associated with BW (Table S1). Few annotated genes were
189 retrieved in the intervals surrounding these SNPs. Three significant markers were shared with other
190 traits examined in this study. On BTA7, a significant marker (*rs42691441*) associated to the BW
191 and located at 68,070,311 bp was also associated with HW. The annotated sequence nearest the
192 marker was the *CCR4-NOT transcription complex, subunit 8 mRNA (CNOT8)*.

193

194 pH at slaughter

195 Five significant markers were found to be associated with pH at slaughter (Table S1). A single
196 associated SNP was on BTAs 2, 3, 14, 17, and 26. No suggestive genes were found for this trait.

197

198 **Discussion**

199 Growth performance and growth-related traits such as body size and weight or average daily gain,
200 have a crucial role in livestock due to their influence on meat production. Average daily weight gain
201 is one of the most important traits for assessment of animal growth and it is a component of most
202 economic indices. In livestock, discovering and understanding genes and molecular mechanisms
203 underlying differences in ADG could clarify relationships among weight gain and other important
204 traits such as body composition or feed intake (Santana *et al.* 2014).

205 Marchigiana cattle have been selected for meat production (a trait with a medium to high
206 heritability) over the last twenty years. Aim of this study was to identify candidate genes associated
207 with beef production traits in this breed. The total number of significant associations detected in this
208 GWAS was in general agreement with literature (Snelling *et al.* 2010; Rolf *et al.* 2012).

209 SNPs significantly associated to ADG flagged regions where genes involved in the metabolism of
210 sugars and lipids are located. This is in general agreement with cattle physiology because these
211 metabolic pathways may have a significant influence on average daily gain. An interesting
212 outcome of the present study is represented by the association between ADG and two markers
213 (*rs41662409* and *rs110397182*) located on BTA 16. These associations underline *Sterol-O-*
214 *Acyltransferase 1 (SOAT1)* and *transforming growth factor, beta 2 (TGFB2)* genes, respectively. In
215 particular *SOAT1* was already reported as a candidate gene in beef cattle (Jiang *et al.* 2009). *SOAT1*
216 encodes for an enzyme that is involved in steroidogenesis and lipogenesis/lipolysis network.

217 Another promising candidate gene for ADG was *TGFB2*. This gene regulates cell proliferation and
218 differentiation and it was already reported as a locus involved in extracellular matrix organization
219 of muscle development (Guo *et al.* 2015). Moreover, polymorphisms at *TGFB2* were associated

220 with growth traits in chicken (Mojtaba *et al.* 2013). A significant marker (*rs41631408*) located on
221 BTA14 between 57,4-57,5 Mb highlighted the *thyrotropin-releasing hormone receptor (TRHR)*.
222 This gene encodes for the receptor responsible of thyrotropin hormone (TRH) release. In mammals
223 *THR* is involved in somatotropin (GH) secretion, regulation and activity (Harvey 1990). The
224 relationship between blood concentration of GH and growth has long been known and positive
225 effects of THRH on growth and carcass characteristics in beef cattle performances were already
226 reported by Enright *et al.* (1993).
227 Finally, the marker *rs43395215* found to be associated associated with ADG tagged a putative
228 candidate gene, *interferon-related development regulator (IFRDI)*, involved in adipocyte
229 proliferation, growth and differentiation.
230 Carcass weight and dressing percentage represent economically important traits for livestock
231 production. However, in recent years, meat quality has also received more attention as economically
232 important. Phenotypic traits such as tenderness, marbling and unsaturated fat content are
233 considered essential in the beef industry. Dressing percentage trait is an estimate of amount of
234 saleable product derived from a given carcass (Casas *et al.* 2003). The *MSTN* locus, encoding
235 myostatin, is one of the most studied genes in beef cattle (Djari *et al.* 2013). Polymorphism at this
236 single autosomal locus causes double muscle phenotype. Several mutations have been previously
237 reported in many cattle breeds for *MSTN* (Djari *et al.* 2013). In mammals, polymorphisms in this
238 locus result in muscle hyperplasia caused by inactivation of the negative regulator of myogenesis
239 (McPherron and Lee 1997). *MSTN* mutations are associated with increased muscle mass, carcass
240 yield, meat tenderness and a reduction of collagen content in cattle (Esmailzadeh *et al.* 2008).
241 Besides economic benefits, double muscled phenotype implies undesirable consequences such as
242 reduced fertility, low calf viability and dystocia (Bellinge *et al.* 2005). A point mutation consisting
243 of a G/T transversion in the third exon of *MSTN* has been reported in Marchigiana (Marchitelli *et*
244 *al.* 2003). This variant has a rather low frequency in the population, probably due to the careful

245 breeding policy of breeders that want to avoid negative effects on reproduction. However extreme
246 double-muscling individuals are still observed (Marchitelli *et al.* 2003). Also SNP in the promoter
247 region of this gene may influence muscularity and therefore DP (Crisà *et al.* 2003). Significant
248 markers found in this study identify a QTL region where *MSTN* and other neighboring genes such
249 as *Collagen, type V, alpha 2 (COL5A2)* and *Solute carrier family 40, member A1 (SLC40A1)*
250 involved in muscle biology and collagen biosynthesis were located. This result is in agreement with
251 previous reports for beef cattle (Pintus *et al.* 2014, Saatchi *et al.* 2014).

252

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349 Supporting Information

350 Table S1: List of significant markers associated with the traits under study.

351

352 **Tables**

353 **Table 1.**

354

355

356 **Figures**

357 **Figure 1.**

358 **Captions for Tables**

359 **Table 1: Putative candidate genes associated with *in vivo* and *post mortem* phenotypes under**
360 **study.**

361

362 **Captions for Figures**

363 **Figure 1. Genome-wide association study of average daily gain. The dashed line corresponds**
364 **to a permutation treshold of 0.05.**

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