

**Scotland's Rural College****Effect of the Texel muscling QTL (TM-QTL) on spine characteristics in purebred Texel lambs**

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*Published in:*  
Small Ruminant Research

*DOI:*  
[10.1016/j.smallrumres.2013.11.020](https://doi.org/10.1016/j.smallrumres.2013.11.020)

Print publication: 01/01/2014

*Document Version*  
Peer reviewed version

[Link to publication](#)

*Citation for published version (APA):*

Donaldson, CL., Lambe, NR., Maltin, CA., Knott, S., & Bungler, L. (2014). Effect of the Texel muscling QTL (TM-QTL) on spine characteristics in purebred Texel lambs. *Small Ruminant Research*, 117(1), 34 - 40.  
<https://doi.org/10.1016/j.smallrumres.2013.11.020>

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1 **Effect of the Texel muscling QTL (TM-QTL) on spine characteristics in purebred Texel**  
2 **lambs**

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24 **Abstract**

25

26 Previous work showed that the Texel muscling QTL (TM-QTL) results in pronounced  
27 hypertrophy in the loin muscle, with the largest phenotypic effects observed in lambs  
28 inheriting a single copy of the allele from the sire. As the loin runs parallel to the spinal  
29 vertebrae, and the development of muscle and bone are closely linked, the primary aim of this  
30 study was to investigate if there were any subsequent associations between TM-QTL  
31 inheritance and underlying spine characteristics (vertebrae number, VN; spine region length,  
32 SPL; average length of individual vertebrae, VL) of the thoracic, lumbar, and thoracolumbar  
33 spine regions. Spine characteristics were measured from x-ray computed tomography (CT)  
34 scans for 142 purebred Texel lambs which had been previously genotyped. Least-squares  
35 means were significantly different between genotype groups for lumbar and thoracic VN and  
36 lumbar SPL. Similarly for these traits, contrasts were shown to be significant for particular  
37 modes of gene action but overall were inconclusive. In general, the results showed little  
38 evidence that spine trait phenotypes were associated with differences in loin muscling  
39 associated with the different TM-QTL genotypes.

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41 **Keywords:**

42 Vertebrae, Spine, Texel, Loin, Muscling

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## 49 **1. Introduction**

50

51 Walling et al. (2004) reported evidence of a quantitative trait locus (QTL) segregating in the  
52 United Kingdom's Texel sheep population which significantly increased *longissimus dorsi*  
53 (loin) muscle depth (up to +1.15 – +2.00 mm, as measured ultrasonically over the third  
54 lumbar vertebra). Observing similar results (QTL effect of +2.57 mm) from an analysis  
55 including existing and new Texel family data, the QTL, later termed the Texel muscling QTL  
56 (TM-QTL), was further verified by Matika et al. (2006). Located on the distal end of the  
57 ovine chromosome 18 (OAR18) (Walling et al., 2004; Matika et al., 2006), the TM-QTL sits  
58 in the same region as the *Callipyge* (*CLPG*) and Carwell loci (Cockett et al., 1994; Nicoll et  
59 al., 1998) which are also known to affect carcass muscling; the *CLPG* mutation leads to  
60 greater muscle mass most pronounced in the hind quarters (loin, pelvis, leg) (Cockett et al.,  
61 1994; Koohmaraie et al., 1995; Jackson et al., 1997a, 1997b; Freking et al., 2002), while  
62 carriers of Carwell exhibit a larger loin muscle area and weight (Nicoll et al., 1998).

63 Such QTL are of economic interest as there is the potential to utilise their effects through  
64 selection programmes to gain greater carcass value (e.g. reducing fat deposition and  
65 increasing lean meat production). In the case of the TM-QTL, the proportion of the high  
66 value loin cut may be increased e.g. two-dimensional measurements (estimated from cross-  
67 sectional computed tomography (CT) scans, taken at the fifth lumbar vertebra) describing  
68 loin depth, width, and area were found to be ~ 0.5 – 11% greater in TM carrier lambs than  
69 non-carrier lambs (Macfarlane et al., 2010).

70 Moreover, taking the QTL's mode of inheritance into consideration allows the opportunity to  
71 exploit the TM-QTL more fully and appropriately in a commercial situation. Similar to  
72 *CLPG* (Cockett et al., 1994; Freking et al., 1998a), expression of the Texel muscling  
73 phenotype has been suggested to follow the complex parent-of-origin-dependent pattern of

74 inheritance termed polar overdominance (Macfarlane et al., 2010; Matika et al., 2011). This  
75 unique type of inheritance is characterised by the instance where heterozygous progeny that  
76 inherit a single copy of the allele from the sire exhibit the superior phenotype (Cockett et al.,  
77 1996). Indeed, Macfarlane et al. (2010) observed that the largest phenotypic effects of the  
78 TM-QTL were particularly apparent in the TM carrier lambs that had inherited a single copy  
79 of the TM allele from the sire and the wild type (+) from the dam (genotype  $TM^S/+^D$ ; where  
80 superscripts S (sire) and D (dam) denote the paternal and maternal origin of the alleles,  
81 respectively), with loin depth, width, and area measures ~ 2 – 11% greater in these  $TM^S/+^D$   
82 genotype lambs than in the other three genotype groups (homozygote non-carriers,  $+^S/+^D$ ;  
83 heterozygote carriers inheriting TM-QTL from the dam,  $+^S/TM^D$ ; homozygote carriers,  
84  $TM^S/TM^D$ ).

85 Essentially, muscle hypertrophy from TM allele segregation appears to be localised to the  
86 loin muscle (Macfarlane et al., 2010), which is found along the length of the thoracolumbar  
87 (thoracic plus lumbar) spine region. Given that development of muscle and bone are closely  
88 linked, it is of further interest to investigate, across genotype groups, if the increased loin  
89 muscling is associated with any change to characteristics of the underlying spine section i.e.  
90 is there a subsequent effect on spine characteristics in relation to the pattern of TM allele  
91 inheritance? Freking et al. (1998b), for instance, found that the spinal column was  
92 significantly shorter in *CLPG* genotype lambs (-2.5 cm; when all animals compared at the  
93 same carcass weight) and the carcasses more compact in skeletal structure in comparison to  
94 normal genotype lambs. Given its chromosomal position, it may be a similar condition for  
95 the TM-QTL. This is a particularly relevant point to assess in terms of a possible ‘trade-off’  
96 between increasing loin muscle size (e.g. depth) but, in consequence, shortening the spinal  
97 column.

98 The thoracolumbar spine region, on which the loin is located, encompasses the ‘body’ (or  
99 trunk) vertebrae and the total length of this region (as with any spine region) is a product of  
100 the number and length of vertebrae which comprise it. Hence, the difference in body (and  
101 carcass) lengths observed from individual to individual is contributed to the variation in these  
102 vertebral factors. Recent work has demonstrated that the spine characteristics (vertebrae  
103 number, vertebrae length), of the thoracolumbar region, can be reliably measured from CT  
104 scans. Using such method, it was also identified that these characteristics exhibit significant  
105 intra-breed variation in Texel sheep, for example, thoracolumbar vertebrae number was  
106 observed to range from 17 to 21 (Donaldson et al., 2013). Therefore, it may be reasonable to  
107 use CT measured spine traits to investigate if any association exists between the pattern of  
108 TM allele inheritance and spine characteristics.

109

110

## 111 **2. Materials and Methods**

112

### 113 *2.1. Animals sampled*

114

115 The present study used a subset of the 209 available purebred Texel lamb records previously  
116 used by Macfarlane et al. (2010) and Lambe et al. (2011). Lambs were sired by seven  
117 different rams that were previously identified as carriers of at least one copy of TM-QTL; all  
118 209 lambs were blood-sampled soon after birth (born 2009) in order to classify their TM-  
119 QTL genotype (homozygote non-carrier,  $+^S/+^D$ ; heterozygote carrier inheriting TM-QTL  
120 from the sire,  $TM^S/+^D$ ; heterozygote carrier inheriting TM-QTL from the dam,  $+^S/TM^D$ ;  
121 homozygote carrier,  $TM^S/TM^D$ ); detailed information on the genotyping of the animals can  
122 be found in Macfarlane et al. (2010). However, for a number of animals the genotype could

123 not be fully classified. These unknowns were excluded from this study's analysis, leaving a  
124 total of 142 lamb records in the subset, which divided into the TM-QTL genotype groups as  
125 follows: 39  $+^S/+^D$ , 52  $TM^S/+^D$ , 17  $+^S/TM^D$ , 34  $TM^S/TM^D$ . These 142 lamb records included  
126 59 entire males and 83 female lambs from the purebred population of Texel sheep kept across  
127 two sites, one in Scotland and one in Wales, which were reared as either singles (n = 97),  
128 twins (n = 34), or artificially (pet; n = 11) (further details on the management of these  
129 animals can be found in Macfarlane et al. (2010) and Lambe et al. (2011)).

130

## 131 2.2. Computed tomography (CT) measurements

132

133 Lambs were CT scanned at ~ 126 days of age (ranging from 93 to 145 days) and their  
134 topogram images (produced from the CT process) used to quantify spine characteristics for  
135 each, details provided in Donaldson et al. (2013). In short, spine traits measured directly  
136 from the scans included counts of vertebrae in the thoracic and lumbar regions ( $VN_{THOR}$  and  
137  $VN_{LUM}$  respectively) and length (mm) of the thoracic and lumbar spine region ( $SPL_{THOR}$  and  
138  $SPL_{LUM}$  respectively). These measures were used to calculate the average length (mm) of  
139 individual vertebrae in the thoracic and lumbar regions ( $VL_{THOR}$  ( $SPL_{THOR}/VN_{THOR}$ ) and  
140  $VL_{LUM}$  ( $SPL_{LUM}/VN_{LUM}$ ) respectively). The results for the thoracic and lumbar spine  
141 regions were further used to provide the number of thoracolumbar vertebrae ( $VN_{T+L}$   
142 ( $VN_{THOR}+VN_{LUM}$ )), and the length (mm) of the thoracolumbar region ( $SPL_{T+L}$   
143 ( $SPL_{THOR}+SPL_{LUM}$ )). These thoracolumbar spine traits were then used to calculate the  
144 average length (mm) of individual vertebrae across the thoracolumbar region ( $VL_{T+L}$   
145 ( $SPL_{T+L}/VN_{T+L}$ )).

146 For each lamb, the dimensions, width (mm), depth (mm), and area ( $mm^2$ ), of the *longissimus*  
147 *lumborum* (CT\_MLL\_W, CT\_MLL\_D, and CT\_MLL\_A respectively), were estimated (from

148 cross-sectional CT scans taken at the fifth lumbar vertebra) by Macfarlane et al. (2010) and  
149 included in this study's analysis of the genotypic effect. Essentially, these traits were  
150 included to, (i) determine if analysis of the reduced sample of animals shows genotype effects  
151 on loin traits similar to that observed for the larger sample, and, (ii) assess, from further  
152 analysis of the smaller data set, if the same or similar pattern of TM expression (polar  
153 overdominance) can be considered as a source for any genotype differences.

154

### 155 2.3. Statistical Analysis

156

157 Data were analysed using the GLM procedure in SAS (SAS Institute Inc., Cary, NC, USA) to  
158 determine the effects of genotype on the collated loin traits and measured spine traits. Fixed  
159 effects fitted in the model for loin dimensions (CT\_MLL\_W, CT\_MLL\_D, CT\_MLL\_A),  
160 spine length traits (SPL<sub>THOR</sub>, SPL<sub>LUM</sub>, SPL<sub>T+L</sub>, VL<sub>THOR</sub>, VL<sub>LUM</sub>, VL<sub>T+L</sub>) and spine count  
161 traits (VN<sub>THOR</sub>, VN<sub>LUM</sub>, VN<sub>T+L</sub>) were site, with two levels (Scotland and Wales), sex, with  
162 two levels (male and female), rearing rank, with three levels (single, twin, or pet), and TM-  
163 QTL-genotype, with four levels ( $+^S/+^D$ ,  $TM^{S/+^D}$ ,  $+^S/TM^D$  and  $TM^S/TM^D$ ). The model was  
164 run with and without covariate adjustments for live weight (LWT); where any of the traits  
165 differed significantly between genotype groups, it was of interest to assess if, by testing the  
166 groups at a standard live weight, the differences were removed.

167 A set of orthogonal contrasts, as described by Freking et al. (1998a), (additive (-1 0 0 1),  
168 dominance (-1 1 1 -1), and reciprocal heterozygote (0 1 -1 0)) was fitted to the  $+^S/+^D$ ,  
169  $TM^{S/+^D}$ ,  $+^S/TM^D$ ,  $TM^S/TM^D$  genotypes, respectively. The contrasts test for any distinct  
170 pattern in the differences amongst the genotype group's least-squares means (for loin and  
171 spine traits), from which, a particular model for TM gene action might be suggested. Due to  
172 the previous evidence supporting the expression of the TM muscling phenotype through a

173 polar overdominant mode of inheritance (Macfarlane et al., 2010), if significant differences  
174 were found between the heterozygote groups (reciprocal heterozygote test) a further set of  
175 orthogonal contrasts was fitted to the genotypes to include a test for the paternally derived  
176 polar overdominant mode of inheritance. Again following that from Freking (1998a), this  
177 second set of orthogonal contrasts included additive (-1 0 0 1), maternal dominance (-1 0 2 -  
178 1), and polar overdominance (-1 3 -1 -1) models of gene action which were fitted to the  
179  $+^S/+^D$ ,  $TM^S/+^D$ ,  $+^S/TM^D$ ,  $TM^S/TM^D$  genotypes, respectively. Contrasts were performed on  
180 the spine count data which was not adjusted for LWT and on the loin muscle and spine length  
181 data after the adjustment for LWT.

182

183

### 184 **3. Results**

185

186 In the context of this work it is useful to note that an earlier study (Macfarlane et al., 2012)  
187 found that least-squares means for LWT (measured at birth, 5, 10, 15, and 20 weeks of age)  
188 and carcass weight for  $TM^S/TM^D$  animals were consistently larger than that measured for  
189  $+^S/+^D$ ,  $+^S/TM^D$ , and  $TM^S/+^D$  genotype lambs (these differences were significant between  
190  $TM^S/TM^D$  and  $+^S/+^D$  lambs for LWT at birth, 5, and 10 weeks of age, and carcass weight). In  
191 the present study, statistical models were first run without an adjustment of LWT but, given  
192 the above, to remove, as far as possible, any misinterpretation of TM-QTL effects, statistical  
193 models were run again with certain traits (loin dimensions, spine length) adjusted for LWT.  
194 The following sections discussing these traits will therefore focus only on the LWT adjusted  
195 results.

196

#### 197 *3.1. Loin dimensions*

198

199 Similar to the findings of Macfarlane et al. (2010),  $TM^{S/+^D}$  genotype lambs were observed to  
200 generally have the largest loin width, depth, and area, on average (Table 1). The differences  
201 in loin dimensions between  $TM^{S/+^D}$  and  $+^S/+^D$  genotype lambs were consistently significant,  
202 however, the larger trait averages observed for the  $TM^{S/+^D}$  group were not all significantly  
203 different from those averages observed for the  $+^S/TM^D$  and  $TM^S/TM^D$  genotype groups. For  
204 example, the  $TM^{S/+^D}$  group was significantly different from the  $+^S/TM^D$  group in regards to  
205 loin area (CT\_MLL\_A\_LWT) but the groups were not significantly different for loin width  
206 and depth measures (CT\_MLL\_W\_LWT and CT\_MLL\_D\_LWT, respectively). Further to  
207 this, and in contrast to Macfarlane et al. (2010), the  $TM^{S/+^D}$  group in this smaller data set was  
208 not significantly different from  $TM^S/TM^D$  in regards to all three loin dimension traits.

209 In general, the pattern of results from the analysis of the full data set (Macfarlane et al., 2010)  
210 suggested that the effect of the TM allele on these loin dimensions is expressed through a  
211 non-additive mode of inheritance (paternal polar overdominance). Analysis of the subset of  
212 records suggests a more general paternal TM-QTL effect on the loin with little evidence of a  
213 polar overdominance effect.

214

### 215 3.2. Spine length traits

216

217 Overall, there was no significant effect of the TM-QTL on the thoracic region length traits  
218 ( $SPL_{THOR}$ ,  $VL_{THOR}$ ). Nor was there an effect of TM-QTL genotype on the average length of  
219 individual lumbar vertebrae ( $VL_{LUM}$ ), however, associations were shown to exist between  
220 TM-QTL genotype groups and length of the lumber region ( $SPL_{LUM}$ ) (Table 1). Least-  
221 squares means showed that, on average,  $+^S/+^D$  and  $TM^{S/+^D}$  genotype lambs had a longer  
222 lumbar length compared to  $+^S/TM^D$  and  $TM^S/TM^D$  genotype lambs. However, when

223 considering the combined length of the thoracic and lumbar regions ( $SPL_{T+L}$ ), the genotype  
224 effect is negligible (Table 1).

225

### 226 3.3. Spine count traits

227

228 The segmentation and anatomical regionalisation of the spinal elements (vertebrae) is  
229 established in early development (Wellik, 2007; Imura et al., 2009), hence, it should not be  
230 affected by varying LWT. In running the statistical model with the inclusion and omission of  
231 a covariate adjustment of LWT, little difference was found between the least-squares means  
232 for each model (Table 1), lending support to the previous statement. Therefore, only the  
233 results obtained from the model without LWT adjustment will be discussed (results from the  
234 model with LWT covariate adjustment are not shown).

235 Regarding vertebrae number in the separate thoracic and lumbar spine regions first ( $VN_{THOR}$   
236 and  $VN_{LUM}$  respectively), there were some significant differences between the genotype  
237 groups, however, the magnitude of these differences was relatively small (Table 1). In more  
238 detail, it can be seen from the least-squares means that there is much overlap between the  
239 genotype classes with regards to  $VN_{THOR}$ . The  $+^S/TM^D$  and  $TM^S/TM^D$  genotype lambs had,  
240 on average, a greater number of thoracic vertebrae than  $+^S/+^D$  and  $TM^S/+^D$  genotype lambs,  
241 however  $+^S/TM^D$  and  $+^S/+^D$  genotype lambs were not significantly different from each other.  
242 With regards to  $VN_{LUM}$ , the  $+^S/+^D$  and  $TM^S/+^D$  genotype lambs were significantly different  
243 from the  $+^S/TM^D$  and  $TM^S/TM^D$  genotype lambs. While observed to possess fewer thoracic  
244 vertebrae,  $+^S/+^D$  and  $TM^S/+^D$  genotype lambs had a greater number of lumbar vertebrae, on  
245 average.

246 Although significant differences occurred between the genotype groups for the two spine  
247 regions when considered separately, when examining the results for the combined thoracic

248 and lumbar vertebrae number ( $VN_{T+L}$ ), there were no significant differences between the  
249 groups (Table 1).

250

### 251 *3.4. Orthogonal contrasts*

252

253 Previous work on loin dimensions had shown strong evidence that the mode of inheritance  
254 for the TM-QTL deviates from a simple additive model (Macfarlane et al., 2010). Although  
255 the results obtained in this study's subset of data did not fully provide the same results, there  
256 was certainly an indication for superior loin dimensions in TM-QTL carrier lambs, especially  
257 in those with a paternal copy of the TM-QTL. Due to this, sets of orthogonal contrasts were  
258 fitted to the genotypes to investigate the situation further. These contrasts allowed testing for  
259 any particular patterns in the differences among the TM-QTL genotype (least-squares)  
260 means, for loin and spine traits, in order to define if certain modes of gene action may be  
261 present.

262 The first set of orthogonal contrasts was fitted to the genotypes to test for additive,  
263 dominance, and reciprocal heterozygote models of gene action (Table 2; only traits where  
264 TM-QTL genotype had a significant effect are shown).

265 The additive inheritance model was fitted as  $-1\ 0\ 0\ 1$  to the  $+^S/+^D$ ,  $TM^S/+^D$ ,  $+^S/TM^D$ , and  
266  $TM^S/TM^D$  genotypes respectively; testing the difference between the means of the  
267 homozygote genotypes. Where the contrast value was positive this showed that  $TM^S/TM^D$   
268 had a larger mean than  $+^S/+^D$  for that particular trait and vice versa if the contrast value was  
269 negative. The difference between  $+^S/+^D$  and  $TM^S/TM^D$  genotype means was significant for  
270 all three loin traits  $CT\_MLL\_W\_LWT$ ,  $CT\_MLL\_D\_LWT$ , and  $CT\_MLL\_A\_LWT$ , and  
271 spine traits,  $VN_{THOR}$ ,  $VN_{LUM}$ , and  $SPL_{LUM\_LWT}$ . The dominance inheritance model was  
272 fitted as  $-1\ 1\ 1\ -1$  to the  $+^S/+^D$ ,  $TM^S/+^D$ ,  $+^S/TM^D$ , and  $TM^S/TM^D$  genotypes respectively;

273 testing the combined means of the heterozygote genotypes ( $TM^{S/+^D}$ ,  $+^S/TM^D$ ) with the  
274 combined means of the homozygote genotypes ( $+^S/+^D$ ,  $TM^S/TM^D$ ). However, none of the  
275 differences between genotype means were significant, providing no evidence of a dominance  
276 effect on any of the traits. The reciprocal heterozygote model of gene action was fitted as 0 1  
277 -1 0 to the  $+^S/+^D$ ,  $TM^S/+^D$ ,  $+^S/TM^D$ , and  $TM^S/TM^D$  genotypes respectively. This contrast  
278 tested the difference between the means of the two heterozygote genotypes ( $TM^S/+^D$  and  
279  $+^S/TM^D$ ), which were significant for traits CT\_MLL\_A\_LWT, VN<sub>THOR</sub>, VN<sub>LUM</sub>, and  
280 SPL<sub>LUM</sub>\_LWT.

281 Freking et al. (1998a) previously commented that in such a case where the reciprocal  
282 heterozygote contrast is shown to be significant, the dominance contrast may be misleading  
283 i.e. under and over-estimation of heterozygote genotypes, and further analysis required.  
284 Therefore, due to this, and with the previous observation of the TM allele's expression  
285 through a non-additive mode of inheritance, a further set of orthogonal contrasts, [additive](#),  
286 [maternal dominance](#), and [polar overdominance](#), were fitted to the genotypes as (1 0 0 -1) (-1  
287 0 2 -1) (-1 3 -1 -1), respectively. Results for the additive model have been discussed above,  
288 and with no significant results for a maternal dominance effect only the results for the polar  
289 overdominance model from this set of contrasts were shown (Table 2) and discussed further.

290 The polar overdominance inheritance model was fitted as -1 3 -1 -1 to the  $+^S/+^D$ ,  $TM^S/+^D$ ,  
291  $+^S/TM^D$ , and  $TM^S/TM^D$  genotypes respectively and used to test the difference between the  
292 mean of the  $TM^S/+^D$  group with each of the means calculated for  $+^S/+^D$ ,  $+^S/TM^D$ , and  
293  $TM^S/TM^D$  genotype groups. Contrast values for the paternal polar overdominance model are  
294 the combined differences between genotype means (condition as defined above) and were  
295 shown to be significant for all traits tested (Table 2); with the exception of VN<sub>THOR</sub>,  $TM^S/+^D$   
296 genotype lambs had a larger mean compared with each of the other genotype groups.

297

298

## 299 **4. Discussion**

300

301 It should be noted that the data set used in the present report was limited in its size, largely  
302 due to the restricted availability of sires (identified as TM-QTL carriers) which could be used  
303 to produce a study group of lambs. Nonetheless, to date, it is the only available data set  
304 which provides detail of the TM-QTL status for a sufficient number of purebred Texel  
305 animals, from which, the effects of TM-QTL on carcass, meat quality, and production traits  
306 could be assessed.

307 The analysis in the present report made use of lamb records, where TM-QTL genotype was  
308 unambiguously known, to, (i) determine if similar conclusions for loin dimensions could be  
309 formulated using only a subset of data in the analysis, repeating, as close as possible, the  
310 model described by Macfarlane et al. (2010), (ii) extend this test to determine if there is an  
311 effect of TM-QTL on underlying spine characteristics as the loin muscle is located parallel to  
312 spinal vertebrae, and, (iii) fit sets of contrasts to the TM-QTL genotype groups in order to  
313 determine the inheritance pattern of the TM-QTL.

314 It should also be noted that the following discussion will [continue to](#) refer only to loin  
315 [dimension](#) and spine length trait results generated from the model where all lamb records  
316 were adjusted for LWT.

317

### 318 *4.1. TM-QTL and loin dimensions*

319

320 Regarding the loin dimensions, CT\_MLL\_W, CT\_MLL\_D, and CT\_MLL\_A, the least-  
321 squares means for these traits reported by Macfarlane et al. (2010) are in strong agreement  
322 with an overdominance mode of expression of the TM allele; there is evidence of both

323 heterozygote groups lying outside, in this case above, the phenotypic range of the  
324 homozygote groups. The results of Macfarlane et al. (2010) even suggested, more  
325 specifically, a paternally expressed polar overdominance effect as  $TM^{S/+^D}$  genotype lambs  
326 consistently exceeded  $+^S/TM^D$  genotype lambs in trait means; the difference between  
327 heterozygote groups, however, only appeared to be significant for the loin area  
328 (CT\_MLL\_A).

329 From the present study, the polar overdominance test (Table 2) did show significance, but the  
330 pattern of differences between the  $TM^{S/+^D}$  genotype least-squares means and the least-  
331 squares means for  $+^S/+^D$ ,  $+^S/TM^D$ , and  $TM^S/TM^D$  genotype groups (Table 1) conflicts with  
332 this outcome and could not support a polar overdominance mode of TM gene action i.e. trait  
333 means for  $TM^{S/+^D}$  genotype lambs did not appear to significantly ‘out-perform’ over all (or  
334 the majority) of the other genotype groups (Table 1). Nonetheless, the pattern of least-  
335 squares means did still infer TM expression which could not be explained by simple additive  
336 gene action, and though an overdominance model could not be supported, there was still  
337 indication towards some paternal influence of the TM allele; genotype groups which inherited  
338 a copy of the TM allele from the sire ( $TM^{S/+^D}$  and  $TM^S/TM^D$ ) were observed to have, on  
339 average, larger loin width (CT\_MLL\_W\_LWT), depth (CT\_MLL\_D\_LWT), and area  
340 (CT\_MLL\_A\_LWT) measures.

341

#### 342 4.2. TM-QTL and spine characteristics

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344 Three out of the nine spine traits ( $VN_{THOR}$ ,  $VN_{LUM}$ , and  $SPL_{LUM}$ ) were observed to be  
345 significantly different amongst the TM-QTL genotype groups (Table 1).

346 The least-squares means for vertebrae number traits ( $VN_{THOR}$ ,  $VN_{LUM}$ ) followed a curious  
347 pattern; means for  $+^S/+^D$  and  $TM^{S/+^D}$  genotype lambs were similar and significantly different,

348 in most instances, to the means for  $+^S/TM^D$  and  $TM^S/TM^D$  genotype lambs, the latter of  
349 which were also similar to each other in their mean values. The  $+^S/+^D$  and  $TM^S/+^D$  groups  
350 had, on average, fewer thoracic vertebrae ( $VN_{THOR}$ ) but more lumbar vertebrae ( $VN_{LUM}$ ),  
351 with the situation reversed for the  $+^S/TM^D$  and  $TM^S/TM^D$  groups. However, the overall  
352 number of thoracolumbar vertebrae ( $VN_{T+L}$ ) across the four genotype groups was not  
353 different. It appeared that TM-QTL inheritance patterns had no substantial effect on the total  
354 number of thoracolumbar vertebrae but may have some influence on the thoracic-lumbar  
355 vertebral arrangement in the spine, but this remains uncertain as the size of difference  
356 between genotype groups is small.

357 Similarly, the total length of the thoracolumbar region ( $SPL_{T+L}$ ) was not drastically different  
358 between the genotype groups. Freking et al. (1998b) observed shorter spinal columns in  
359 *CPLG* genotype lambs, and given that TM-QTL falls close to its position on the  
360 chromosome, it was an important point to investigate further in connection with TM  
361 inheritance. Least-squares means for spine length traits ( $SPL$ ,  $VL$ ) from the present study,  
362 however, do not suggest any such negative effects of TM-QTL on spine length. The  $TM^S/+^D$   
363 genotype lambs, which express the muscle hypertrophy phenotype, in fact, were observed to  
364 have, on average, longer thoracolumbar vertebrae ( $VL_{T+L\_LWT}$ ), and subsequently longer  
365 thoracolumbar spine regions ( $SPL_{T+L\_LWT}$ ), but these trait values (23.22mm; 442.0mm  
366 respectively) were not significantly different from the other three groups. It is interesting that  
367 in the animals which were observed to have the largest loin dimension measures ( $TM^S/+^D$ ),  
368 there is not much of a change to the structure on which it lies.

369 Given that differences in spine traits are largely non-significant between the genotype groups,  
370 and that the overall pattern of least-squares means is indistinct, interpreting the models of  
371 gene action should be done with reservation. For example, the contrast tests showed  
372 significance for the polar overdominant model of TM gene action on  $VN_{THOR}$ ,  $VN_{LUM}$ , and

373 SPL<sub>LUM</sub> spine traits. These results should, again, be carefully considered alongside least-  
374 squares means (Table 1) as, though slightly larger (for VN<sub>LUM</sub> and SPL<sub>LUM</sub>), the means for  
375 TM<sup>S/+<sup>D</sup></sup> genotype lambs did not significantly ‘out-perform’ over all other genotype groups  
376 for these spine traits. Hence, there was no strong indication that the observed differences in  
377 spine trait phenotypes were associated with increased loin muscling specific to TM gene  
378 action.

379 What is important to take from the present study is that increased loin muscling, particularly  
380 associated with TM<sup>S/+<sup>D</sup></sup> genotype lambs, has been shown to have little associated effect on  
381 the underlying spine characteristics. Information on spine characteristics, in general, could  
382 potentially be used to improve loin production i.e. through increasing the size and/or number  
383 of loin chops (Donaldson et al., 2013). Hence, it would be interesting to investigate further  
384 the potential size of increase in loin production from those TM<sup>S/+<sup>D</sup></sup> animals which possess a  
385 greater number of thoracolumbar vertebrae.

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## 388 **5. Conclusion**

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390 Given the results from the present study, it was evident that some effect of the TM allele on  
391 loin dimension phenotypes was linked to a paternal genetic influence, but, with a weaker data  
392 set (67 fewer records) this study could not provide further evidence for a specific polar  
393 overdominance inheritance pattern. With regards to spine characteristics, in general terms,  
394 the analysis of the subset of data did not reveal any obvious (advantageous or  
395 disadvantageous) associations with TM-QTL inheritance. **There did not appear to be any**  
396 **effect on spine/vertebrae length and** detailing how, or if, the TM allele interacts in the  
397 vertebral patterning process (given the thoracic-lumbar vertebral combinations across

398 genotype groups) would require analysing a substantially larger data set than what was  
399 available at present.

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401

## 402 **Acknowledgements**

403 The authors gratefully acknowledge funding from BBSRC and Defra under the Sustainable  
404 Livestock Production LINK programme. We thank our industry sponsors and project  
405 partners: EBLEX, HCC, QMS, LMCNI, Pfizer Animal Genetics, Innovis Genetics Ltd, Vion  
406 Food Group, E+V, ASDA and SAMW, and are grateful for contributions of colleagues,  
407 especially from the CT unit providing the topograms. C. L. Donaldson is funded by a  
408 BBSRC CASE Studentship award to the University of Edinburgh with contributions from  
409 ASDA and QMS.

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482 **Table 1.** Least-squares means (and standard errors) for **live weight**, loin dimensions<sup>1</sup> and spine traits<sup>2</sup> for Texel lambs of each TM-QTL  
 483 genotype<sup>3</sup>

Trait	Genotype				Site	Sex	Rearing rank	TM-QTL genotype	Live weight	R <sup>2</sup>
	<sup>S/+<sup>D</sup></sup> n = 39*	TM <sup>S/+<sup>D</sup></sup> n = 52*	<sup>S/TM<sup>D</sup></sup> n = 17	TM <sup>S/TM<sup>D</sup></sup> n = 34						
Live Weight	30.53 (1.004)	31.78 (0.855)	30.59 (1.402)	31.45 (1.094)	< .001	0.104	< .001	0.672	.	0.253
CT_MLL_W	66.27 <sup>b</sup> (1.034)	69.49 <sup>a</sup> (0.881)	67.12 <sup>a,b</sup> (1.444)	68.82 <sup>a</sup> (1.127)	0.084	0.069	0.199	<b>0.034</b>	.	0.126
CT_MLL_D	28.45 <sup>b</sup> (0.779)	30.96 <sup>a</sup> (0.663)	29.28 <sup>a,b</sup> (1.087)	30.44 <sup>a</sup> (0.848)	0.234	0.411	<b>0.001</b>	<b>0.029</b>	.	0.163
CT_MLL_A	1684 <sup>c</sup> (64.94)	1883 <sup>a</sup> (55.33)	1689 <sup>b,c</sup> (90.68)	1851 <sup>a,b</sup> (70.76)	0.385	0.633	< .001	<b>0.021</b>	.	0.157
CT_MLL_W_LWT	66.27 <sup>b</sup> (0.591)	68.43 <sup>a</sup> (0.507)	67.06 <sup>a,b</sup> (0.825)	68.04 <sup>a</sup> (0.646)	< .001	0.400	0.059	<b>0.001</b>	< .001	0.716
CT_MLL_D_LWT	28.45 <sup>b</sup> (0.560)	30.28 <sup>a</sup> (0.481)	29.25 <sup>a,b</sup> (0.782)	29.94 <sup>a</sup> (0.612)	<b>0.007</b>	<b>0.008</b>	0.148	<b>0.029</b>	< .001	0.570
CT_MLL_A_LWT	1684 <sup>c</sup> (37.68)	1817 <sup>a</sup> (32.36)	1685 <sup>b,c</sup> (52.63)	1803 <sup>a,b</sup> (41.17)	< .001	<b>0.002</b>	<b>0.353</b>	<b>0.004</b>	< .001	0.718
VN <sub>THOR</sub>	12.69 <sup>b,c</sup> (0.064)	12.65 <sup>c</sup> (0.055)	12.89 <sup>a,b</sup> (0.090)	12.88 <sup>a</sup> (0.070)	<b>0.026</b>	0.350	<b>0.044</b>	<b>0.006</b>	.	0.174
VN <sub>LUM</sub>	6.356 <sup>a</sup> (0.074)	6.387 <sup>a</sup> (0.063)	6.111 <sup>b</sup> (0.104)	6.143 <sup>b</sup> (0.081)	0.092	0.427	0.061	<b>0.009</b>	.	0.149
VN <sub>T+L</sub>	19.05 (0.063)	19.04 (0.054)	19.00 (0.088)	19.02 (0.069)	0.759	0.981	0.645	0.967	.	0.011
SPL <sub>THOR</sub>	255.6 (3.941)	260.7 (3.358)	257.9 (5.504)	262.5 (4.295)	<b>0.003</b>	0.429	<b>0.034</b>	0.503	.	0.122
SPL <sub>LUM</sub>	184.4 <sup>a,b</sup> (2.411)	186.8 <sup>a</sup> (2.054)	176.6 <sup>c</sup> (3.366)	180.3 <sup>b,c</sup> (2.627)	0.208	0.742	<b>0.029</b>	<b>0.018</b>	.	0.125
SPL <sub>T+L</sub>	440.0 (5.138)	447.5 (4.378)	434.5 (7.176)	442.8 (5.599)	<b>0.004</b>	0.447	<b>0.015</b>	0.329	.	0.128
VL <sub>THOR</sub>	20.13 (0.276)	20.60 (0.235)	20.00 (0.386)	20.38 (0.301)	<b>0.009</b>	0.246	<b>0.007</b>	0.352	.	0.133
VL <sub>LUM</sub>	29.03 (0.292)	29.29 (0.249)	28.91 (0.408)	29.36 (0.319)	< .001	0.702	<b>0.045</b>	0.657	.	0.124
VL <sub>T+L</sub>	23.10 (0.265)	23.51 (0.226)	22.86 (0.370)	23.28 (0.289)	<b>0.004</b>	0.443	<b>0.007</b>	0.332	.	0.135
SPL <sub>THOR_LWT</sub>	255.6 (2.495)	256.9 (2.143)	257.7 (3.485)	259.7 (2.726)	0.379	0.456	0.088	0.610	< .001	0.650
SPL <sub>LUM_LWT</sub>	184.4 <sup>a</sup> (2.033)	185.2 <sup>a</sup> (1.746)	176.5 <sup>b</sup> (2.839)	179.1 <sup>b</sup> (2.221)	0.151	0.513	0.333	<b>0.007</b>	< .001	0.382
SPL <sub>T+L_LWT</sub>	440.0 (2.720)	442.0 (2.336)	434.2 (3.798)	438.8 (2.971)	0.061	0.241	0.575	0.289	< .001	0.758
VL <sub>THOR_LWT</sub>	20.13 (0.160)	20.32 (0.138)	19.99 (0.224)	20.18 (0.175)	0.051	0.772	0.595	0.531	< .001	0.710
VL <sub>LUM_LWT</sub>	29.03 (0.147)	28.97 (0.126)	28.89 (0.205)	29.13 (0.160)	0.350	< .001	<b>0.011</b>	0.721	< .001	0.781
VL <sub>T+L_LWT</sub>	23.10 (0.130)	23.22 (0.112)	22.85 (0.182)	23.07 (0.142)	<b>0.023</b>	0.185	0.488	0.297	< .001	0.793

484 <sup>a-c</sup> Within a row, means with common letters, or no letters, in their superscript are not significantly different ( $P > 0.05$ )

485 LWT = live weight (kg) fitted as a covariate in model

486 <sup>1</sup> CT\_MLL\_W = width of *M. longissimus lumborum* (mm); CT\_MLL\_D = depth of *M. longissimus lumborum* (mm); CT\_MLL\_A = area of *M. longissimus lumborum* (mm<sup>2</sup>)

487 <sup>2</sup> VN<sub>THOR</sub> = number of thoracic vertebrae; VN<sub>LUM</sub> = number of lumbar vertebrae; VN<sub>T+L</sub> = number of thoracolumbar vertebrae; SPL<sub>THOR</sub> = length of thoracic spine region  
488 (mm); SPL<sub>LUM</sub> = length of lumbar spine region (mm); SPL<sub>T+L</sub> = length of thoracolumbar spine region (mm); VL<sub>THOR</sub> = average length of individual thoracic vertebrae (mm);  
489 VL<sub>LUM</sub> = average length of individual lumbar vertebrae (mm); VL<sub>T+L</sub> = average length of individual thoracolumbar vertebrae (mm)  
490 <sup>3</sup> +<sup>S</sup>/<sup>D</sup> = homozygote non-carrier; TM<sup>S</sup>/<sup>D</sup> = heterozygote carrier inheriting TM-QTL from sire; +<sup>S</sup>/TM<sup>D</sup> = heterozygote carrier inheriting TM-QTL from dam; TM<sup>S</sup>/TM<sup>D</sup> =  
491 homozygote carrier

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504 **Table 2.** Estimates of TM-QTL genotype contrasts (and standard errors) and significance levels (*P-value*) for additive, dominance, reciprocal  
505 heterozygote, and paternally derived polar overdominant effects on loin dimensions<sup>1</sup> and spine traits<sup>2</sup>

Trait	Additive			Dominance			Reciprocal heterozygote			Polar overdominance		
	Contrast		<i>P-value</i>	Contrast		<i>P-value</i>	Contrast		<i>P-value</i>	Contrast		<i>P-value</i>
CT_MLL_W_LWT	1.767	(0.736)	<b>0.017</b>	1.184	(1.151)	0.305	1.368	(0.893)	0.128	3.919	(1.698)	<b>0.023</b>
CT_MLL_D_LWT	1.496	(0.697)	<b>0.034</b>	1.142	(1.090)	0.297	1.032	(0.847)	0.225	3.207	(1.609)	<b>0.048</b>
CT_MLL_A_LWT	118.9	(46.92)	<b>0.013</b>	15.90	(73.38)	0.829	131.5	(56.98)	<b>0.023</b>	279.0	(108.3)	<b>0.011</b>
VN <sub>THOR</sub>	0.186	(0.080)	<b>0.022</b>	-0.032	(0.126)	0.800	-0.243	(0.097)	<b>0.014</b>	-0.518	(0.185)	<b>0.006</b>
VN <sub>LUM</sub>	-0.213	(0.092)	<b>0.022</b>	-0.001	(0.144)	0.994	0.275	(0.112)	<b>0.015</b>	0.550	(0.212)	<b>0.012</b>
SPL <sub>LUM</sub> _LWT	-5.321	(2.531)	<b>0.037</b>	-1.857	(3.958)	0.640	8.675	(3.073)	<b>0.006</b>	15.49	(5.840)	<b>0.009</b>

506 First set of orthogonal contrasts was fitted as -1 0 0 1(additive), -1 1 1 -1(dominance), and 0 1 -1 0(reciprocal heterozygote) to the +<sup>S</sup>/<sub>+<sup>D</sup></sub>, TM<sup>S</sup>/<sub>+<sup>D</sup></sub>, +<sup>S</sup>/TM<sup>D</sup>, and TM<sup>S</sup>/TM<sup>D</sup>  
507 genotypes, respectively. Second set of orthogonal contrasts was fitted as -1 0 0 1(additive), -1 0 2 -1(maternal dominance), and -1 3 -1 -1(polar overdominance) to the +<sup>S</sup>/<sub>+<sup>D</sup></sub>,  
508 TM<sup>S</sup>/<sub>+<sup>D</sup></sub>, +<sup>S</sup>/TM<sup>D</sup>, and TM<sup>S</sup>/TM<sup>D</sup> genotypes, respectively. From the second set of contrasts, only the results from the polar overdominance test are shown; additive results  
509 previously reported with first set of contrasts and the maternal dominance test was not significant for any of the traits.

510 LWT = live weight (kg) fitted as a covariate in model

511 <sup>1</sup> CT\_MLL\_W = width of *M. longissimus lumborum* (mm); CT\_MLL\_D = depth of *M. longissimus lumborum* (mm); CT\_MLL\_A = area of *M. longissimus lumborum* (mm<sup>2</sup>)

512 <sup>2</sup> VN<sub>THOR</sub> = number of thoracic vertebrae; VN<sub>LUM</sub> = number of lumbar vertebrae; VN<sub>T+L</sub> = number of thoracolumbar vertebrae; SPL<sub>THOR</sub> = length of thoracic spine region  
513 (mm); SPL<sub>LUM</sub> = length of lumbar spine region (mm); SPL<sub>T+L</sub> = length of thoracolumbar spin region (mm); VL<sub>THOR</sub> = average length of individual thoracic vertebrae (mm);

514 VL<sub>LUM</sub> = average length of individual lumbar vertebrae (mm); VL<sub>T+L</sub> = average length of individual thoracolumbar vertebrae (mm)

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