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1 **Effect and mode of action of the Texel Muscling QTL (TM-QTL) on carcass**
2 **traits in purebred Texel lambs**

3

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15

16 **Running head:** Effect and mode of action of a muscling QTL in Texels

17

18 **Abstract**

19 TM-QTL is a quantitative trait locus (QTL) on ovine chromosome 18 (OAR18) known
20 to affect loin muscling in Texel sheep. Previous work suggested that its mode of
21 inheritance is consistent with paternal polar overdominance, but this has yet to be
22 formally demonstrated. This study used purebred Texel sheep segregating for TM-
23 QTL to confirm its presence in the chromosomal region in which it was first reported
24 and to determine its pattern of inheritance. To do so, this study used the first
25 available data from a Texel flock, which included homozygote TM-QTL carriers

26 (TM/TM; n = 34) in addition to homozygote non-carriers (+/+; n=40 and,
27 heterozygote TM-QTL-carriers inheriting TM-QTL from their sire (TM/+; n=53) or
28 their dam (+/TM; n=17). Phenotypes included a wide range of loin muscling, carcass
29 composition and tissue distribution traits. The presence of a QTL affecting ultrasound
30 d muscle depth on OAR18 was confirmed with a paternal QTL effect ranging from
31 +0.54 to +2.82 mm UMD (s.e. 0.37 to 0.57 mm) across the sires segregating for TM-
32 QTL. Loin muscle width, depth and area, loin muscle volume and dissected *M.*
33 *longissimus lumborum* weight were significantly greater for TM/+ than +/+ lambs
34 (+2.9 to +7.9%; $P < 0.05$). There was significant evidence that the effect of TM-QTL
35 on the various loin muscling traits measured was paternally polar overdominant
36 ($P < 0.05$). In contrast, there was an additive effect of TM-QTL on both live weight at
37 20 weeks and carcass weight; TM/TM animals were significantly ($P < 0.05$) heavier
38 than +/+ (+11.1% and +7.3%, respectively) and +/TM animals (+11.9% and +11.7%,
39 respectively), with TM/+ intermediate. Weights of the leg, saddle and shoulder region
40 (corrected for carcass weight) were similar in the genotypic groups. There was a
41 tendency for lambs inheriting TM-QTL from their sire to be less fat with slightly more
42 muscle than non-carriers. For example, carcass muscle weight measured by live
43 animal CT-scanning was 2.8% higher in TM/TM than +/+ lambs ($P < 0.05$), carcass
44 muscle weight measured by carcass CT-scanning was 1.36% higher in TM/+ than
45 +/+ lambs ($P < 0.05$), and weight of fat trimmed from the carcass cuts was significantly
46 lower for TM/+ than +/+ lambs (-11.2%; $P < 0.05$). No negative effects of TM-QTL on
47 carcass traits were found. Optimal commercial use of TM-QTL within the sheep
48 industry would require some consideration, due to the apparently different mode of
49 action of the two main effects of TM-QTL (on growth and muscling).

50

51 **Keywords:** genetics, QTL, sheep, Texel, muscling

52

53 **Implications**

54 There are two contrasting direct effects of TM-QTL: (i) on loin muscling (4-11%
55 increase in highly priced part of the carcass) exhibiting polar overdominance, and (ii)
56 an additive effect on live and carcass weight. This makes TM-QTL an interesting
57 candidate for exploitation within the UK sheep industry and beyond, especially since
58 no major negative impacts on eating quality have been observed. However, there
59 are two main aspects to consider before commercial exploitation is feasible: (i) the
60 development of a commercial genotyping test and (ii) an optimal plan for exploitation
61 in the industry.

62

63 **Introduction**

64 A quantitative trait locus (QTL) for muscle depth on OAR18, termed the TM-QTL,
65 was first identified in purebred Texel sheep in the UK by Walling *et al.* (2004). In this
66 original study, the effect of carrying a single copy of TM-QTL inherited from the sire
67 was a 1-2mm increase in ultrasound muscle depth (+ 4 to +11%). In a further study
68 using crossbred lambs sired by Texel rams heterozygous for TM-QTL, with Mules or
69 Welsh Mountain ewes as their dams (Macfarlane *et al.*, 2009; Masri *et al.*, 2011)
70 reported a 4 to 11% effect on muscling, specific to the loin region, of carrying a
71 single copy of the QTL. No effect was observed on other carcass traits.

72

73 There is evidence that QTL or mutations affecting muscling that lie in the area of
74 OAR18 where TM-QTL is located may show imprinting, specifically polar
75 overdominance in which the QTL effect is expressed only if the QTL is inherited from
76 the sire and not from the dam. This mode of inheritance was first observed for the
77 Callipyge mutation, which has substantial muscling effect in sheep and lies in a
78 similar region of OAR18 to TM-QTL (Cockett *et al.*, 1994b; 1996a; Cockett *et al.*,
79 1996b, Georges and Cockett, 1996). Additionally, the Carwell QTL (synonymous
80 with LM-QTL, LoinMax) (Nicoll, 2007), which also lies in the region of OAR18 and
81 affects loin muscling to a similar degree as TM-QTL, also appears to have a non-
82 additive mode of inheritance (Jopson *et al.*, 2001, Nicoll, 2007). Lastly, previous work
83 on TM-QTL by Matika *et al.* (2011), examining maternal and paternal variance
84 components for the TM-QTL in commercial Texel lambs, using ultrasound muscle
85 depth as their phenotype, reported results that were also consistent with paternal
86 polar overdominance.

87

88 Interestingly, alongside its effect on muscling, TM-QTL appears to have an additive
89 effect on live- and carcass weights; animals carrying 2 copies of TM-QTL were
90 substantially heavier at a fixed age than wildtype animals (Macfarlane *et al.*, 2012).
91 Although no effects have been reported on carcass traits other than in the loin
92 region, given the effect on live and carcass weights seen in homozygote carriers, it is
93 important to know whether overall carcass composition and tissue distribution traits
94 are affected by TM-QTL, and the nature of any effects on these traits.

95

96 The aim of this study was to investigate the effect of TM-QTL, in purebred Texel
97 lambs on a range of carcass trait. These included traits measured by ultrasound
98 scanning (muscle and fat depths in the loin region), by x-ray computed tomography
99 (CT) scanning (carcass and joint composition, muscularity) and by commercially
100 relevant butchery (lean meat yields, tissue weight distribution). Critically, for the first
101 time, the experimental group included representatives of all TM-QTL genotypes
102 (wildtype, heterozygotes inheriting TM-QTL from either the sire or the dam, and
103 homozygote carriers), enabling formal testing of the hypothesis that TM-QTL
104 displays polar overdominance for a range of muscling traits. Testing this hypothesis
105 was the third aim of this study.

106

107 **Materials & Methods**

108 All procedures involving animals were approved by the Scotland's Rural College
109 (SRUC) Animal Ethics Committee and were performed under UK Home Office
110 licence, following the regulations of the Animals (Scientific Procedures) Act 1986.

111

112 *Position of TM-QTL*

113 A population of Texel sheep located across two farms, one in Wales (IBERS) and
114 one in Scotland (SRUC), was recorded and monitored over 4 years from 2005 to
115 2009. The SRUC Texel flock had been purchased from The Roslin Institute in 2002
116 and the presence of TM-QTL, an OAR18 QTL for muscle depth reported by Walling
117 *et al.* (2004), was maintained and its frequency increased in the flock between 2002
118 and 2005. Sires that had been previously identified as likely carriers of TM-QTL
119 were also mated to existing Texel ewes on the IBERS farm, with some sires used on
120 both farms. All progeny born from 2006 onwards were weighed and ultrasound
121 scanned to measure muscle depth (UMD) at 20 weeks of age.

122 All animals (sires, dams and lambs) born from 2006 onwards were blood sampled
123 and blood-spotted onto FTA^R cards, and these samples were used for genotyping. In
124 addition blood samples were collected via venepuncture into EDTA-vacutainers and
125 conserved at -40⁰; these samples were used if a repeated genotyping test was
126 required. Because the causal mutation responsible for the TM-QTL is still unknown,
127 it was necessary to use markers around the region of interest to classify the likely
128 TM-QTL genotype for each animal. Blood samples were genotyped for five
129 microsatellite markers on OAR18 (MCMA26, CSSM18, OY5, OY3 and OARTMR1)
130 at the Animal Genomics Group, AgResearch Invermay, New Zealand. Marker data
131 collected each year were used along with previously collected data to classify all
132 animals for genotype status for TM-QTL, as described by Macfarlane *et al.* (2009,
133 2010). The information produced was used each year to plan matings within the
134 flocks, in order to increase the frequency of TM-QTL whilst limiting inbreeding.
135 Between 2005 and 2009, 33 sires were used. Of these, 5 were used across both
136 sites and 7 were used in three or more years. In each year, ewe lambs fit for
137 breeding were retained within the flock and selected ram lambs identified as likely

138 TM-QTL carriers were also retained. In total, 1731 purebred Texel lambs contributed
139 to this dataset, comprising 759 entire male and 972 female lambs.

140

141 Lambs were grazed with the ewes at pasture as either singles (about one third) or
142 twins (about two thirds) up to ultrasound scanning at 20 weeks, except for any hand-
143 reared lambs ($n = 42$), which were raised indoors until the age of approximately 8
144 weeks and then grazed and creep-fed up to ultrasound scanning at 20 weeks. All
145 lambs were weighed and ultrasound scanned to measure loin muscle depth (UMD),
146 as described below, at around 20 weeks of age (average age = 138 days, min = 119
147 days, max = 151 days), before being slaughtered (average age 144 days, min = 126,
148 max = 155).

149

150 Microsatellite marker genotypes, UMD and marker map information were used to run
151 single QTL analyses using QTL Express software at <http://QTL.cap.ed.ac.uk> (Seaton
152 *et al.*, 2002). QTL Express used a multi-marker approach to interval mapping in half
153 sib families (Knott *et al.*, 1996). The probability of a QTL affecting UMD being
154 present was estimated at 1 cM intervals conditional on marker genotypes and
155 recombination fraction/distance from marker. Across families, a test statistic was
156 calculated as an F ratio for every map position obtained using the ratio of mean
157 squares of a model fitting a QTL to not fitting a QTL. Empirical significance
158 thresholds were estimated by using permutation tests (Churchill and Doerge, 1994)
159 involving 10,000 randomisations to estimate the 5 and 1% thresholds. Heterogeneity
160 of QTL position was also explored by estimating the putative position of the QTL
161 indicated by each of the main half-sib families in turn. The models fitted included a

162 covariate of live weight at scanning and fixed effects of age of dam, rearing rank,
163 farm, sex and year born.

164

165 *2009-born animals, their management and genotypes*

166 The population of Texel sheep described above was used to produce a total of 211
167 purebred Texel lambs in 2009 at SRUC and IBERS which were used for detailed
168 phenotyping. These 211 were out of 181 Texel dams mated to 7 different Texel sires
169 that had previously been identified as carrying at least one copy of TM-QTL. Three of
170 these sires were used on both sites. Of the lambs, 87 were out of dams that had
171 been previously identified as carrying TM-QTL, 65 out of dams not carrying TM-QTL
172 and the remaining 59 out of dams with unknown TM-QTL status. Lambs were either
173 reared as a single (n=126) or a twin (n=73), or hand-reared (n=12), and were either
174 entire male (n=96) or female (n=115). There were 73 lambs at IBERS and 138 at
175 SRUC. Lamb management was as described above, with grazing (supplemented
176 with creep feeding for hand reared lambs) until transportation to slaughter.

177

178 Of the 211 lambs used in this study, it was possible to unequivocally assign TM-QTL
179 genotypes to 144: 40 non-carriers (+/+), 17 heterozygote carriers inheriting TM-QTL
180 from the dam (+/TM), 53 heterozygote carriers inheriting TM-QTL from the sire
181 (TM/+) and 34 homozygote carriers (TM/TM). The numbers of lambs of each known
182 genotype from each sire used are shown in Table 1.

183

184 **Please insert table 1 about here**

185 *Pre-slaughter measurements on 2009-born lambs*

186 All lambs were ultrasound scanned at approximately 20 weeks of age (average age
187 = 138 days, max = 151, min = 119) using a Dynamic Imaging Concept MLV
188 ultrasonic scanner with a 3.5 MHz transducer at the third lumbar vertebra to measure
189 muscle depth and fat depth. Muscle depth was measured vertically at the deepest
190 point. Three fat depths were measured on each scan: the first above the boundary
191 between *M. longissimus lumborum* (MLL) and the vertebral spinous process, and the
192 others at progressively lateral intervals of around 2 cm. This resulted in fat depths
193 that, for most animals, spanned the *longissimus* muscle. These fat depths were
194 averaged to provide a single measure of ultrasound fat depth for use in the analyses.

195

196 Lambs were CT scanned in three batches. The first batch of lambs (n = 40; all from
197 SRUC) were CT scanned with a Siemens Somatom Esprit CT scanner at the SRUC-
198 BioSS CT Scanning Unit near Edinburgh at approximately 16 weeks of age (average
199 age = 112 days, max = 118, min = 93). Meat from these lambs was due to go for
200 taste panel assessment (results reported by Lambe *et al.*, 2011) so they had to be
201 CT scanned at least 28 days prior to slaughter to allow for a withdrawal period from
202 the sedative used for CT scanning. The other two batches of lambs were CT
203 scanned at approximately 20 weeks of age. The first of these two batches, the
204 IBERS lambs (n = 73), were scanned using a mobile General Electric CT scanner at
205 IBERS (average age = 131 days, max = 141, min = 119). The last batch, the
206 remaining SRUC lambs (n = 98), were scanned with the Siemens Somatom Esprit
207 CT scanner (average age = 136 days, max = 145, min = 121).

208

209 All lambs were spiral CT scanned (Navajas *et al.*, 2006; Bunger *et al.*, 2011). Two
210 spiral scans were taken: one from the proximal third of the tibia to the last rib and the

211 second from the last rib to the fourth to fifth cervical vertebra. These spiral scans
212 were used to provide a series of approximately 60 cross-sectional images through
213 the carcass, each 8mm apart. The cross-sectional images were analysed using
214 STAR software (Mann *et al.*, 2003) to provide total carcass tissue volumes and
215 densities (Hounsfield units) (fat, lean and bone), and tissue volumes and densities
216 (fat, lean and bone) in the leg, saddle and shoulder regions, as well as two-
217 dimensional (2D) and three-dimensional (3D) measurements in the loin region and
218 the leg region. Total tissue weights in the carcass or region of interest were
219 calculated over all images for each tissue in the image by multiplying tissue volume
220 by the weighted mean density of the tissue: $(\Sigma(\text{area} \times \text{density}) / \Sigma\text{area})$. For bone,
221 because the density of bone cannot be well estimated from images analysed using
222 STAR, a fixed value of bone density ($1.55\text{g}/\text{cm}^3$) was used.

223

224 The carcass was virtually split into the leg (equivalent to hind-quarter), saddle and
225 shoulder (equivalent to fore-quarter) regions using in-house algorithms (unpublished
226 data). 2D-CT measurements taken in the loin were depth (D), width (W) and area (A)
227 of the MLL in a cross-sectional scan taken at the fifth lumbar vertebra (Jones *et al.*,
228 2002). Both left and right sides were measured and the average of these used in
229 analyses. In the leg, the 2D CT measurements were width (W) and length (L) of the
230 hind leg (HL) muscle on a cross-sectional scan taken at the ischium as described by
231 Jones *et al.* (2002). Measurements were made on both right (r) and left (l) legs and
232 the average used in analyses. A 2D gigot shape score was also calculated as
233 $10(\text{HLWr} + \text{HLWI})/(\text{HLLr} + \text{HLLI})$. Measurements taken using the 3D capabilities of
234 the CT scanner were loin region muscle volume (LRMV), lumbar spine length (LSL),
235 hind leg muscle volume (HLMV) and femur length (FL). These allowed calculation of

236 a muscularity index, as described by Navajas *et al.* (2007), for both the loin and hind
237 leg regions. This index relates the weight of muscle in a region (equivalent to muscle
238 volume because muscle density is close to 1 g/cm³) to the length of the bone in that
239 region and thus provides a dimensionless assessment of muscularity, independent
240 of fatness, at a constant carcass weight. The CT muscularity index for the hind leg
241 (HLMI) was calculated as $10\sqrt{(HLMV/FL^3)}$ and that for the loin region (LRMI) was
242 calculated as $10\sqrt{(LRMV/LSL^3)}$.

243

244 *Post-slaughter measurements on 2009-born lambs*

245 Mean age at slaughter was 144 days (s.d. 7.5, range 126–155 days) and mean hot
246 carcass weight was 15.2 kg (s.d. 3.1, range 8–25 kg). Post-slaughter, carcasses
247 were chilled for 7-9 days then CT scanned using spiral CT scanning. The CT
248 scanning was similar to that performed on live animals except that thresholds
249 suitable for meat were used (unpublished data), the analysis was simpler as there
250 was no need to edit the images to remove non-carcass parts, and only carcass and
251 regional tissue weights were calculated, not muscularity data. Following CT scanning
252 of the carcasses, they were cut into fore-quarter, saddle and hind-quarter and each
253 of these split into two along the spine. These were weighed and butchered into lean
254 meat yield (LMY), fat trim and bone. Using these data, proportions of LMY, fat trim
255 and bone in the carcass and in each region (fore-quarter, saddle, hind-quarter) were
256 calculated. The proportions of total carcass weight contained in each region were
257 also calculated. During butchery, left and right knuckle muscles were removed from
258 the leg joints and left and right *M. longissimus lumborum* (lamb loin fillet or strip loin)
259 were removed from the loin joint and these muscles weighed individually.

260

261 *Statistical analyses*

262 General linear models were run in Genstat (GenStat 11 Committee, 2008; linear
263 mixed models, REML) to identify the effect of TM-QTL on the traits described above.
264 The model used included TM-QTL genotype (+/+, +/-, TM/+, TM/TM or unknown),
265 sex (entire male or female), rearing rank (single, twin or hand-reared), farm (SRUC
266 or IBERS) and dam age (2, 3, 4 years or older) as fixed effects, and sire as a
267 random effect (7 levels, 3 common across farms). A covariate of age at scanning
268 was included to adjust the analyses rams
269 to an equal age. For all traits, including proportion traits, a covariate of live weight at
270 measurement (for pre-slaughter traits) or carcass weight (for post-slaughter traits)
271 was included. For proportion variables a significant relationship was observed
272 between the proportions and live or carcass weight, and these were used as
273 covariates where applicable.

274

275 To partition variation due to TM-QTL genotype effects, after adjusting for all other
276 effects in the model in a GLM analysis, orthogonal contrasts were fitted for +/+,
277 +/-, TM/+ and TM/TM as defined by Freking et al. (1998) for additive (1, 0, 0 and -
278 1), dominance (-1, 1, 1 and -1) and reciprocal heterozygote (0, 1, -1, and 0) models
279 of gene action. The hypothesis of a paternal polar overdominant action of TM-QTL
280 was tested for (-1, -1, 3, -1) as well as maternal dominance (-1, 2, 0, -1), in a second
281 set of orthogonal contrasts, alongside the additive effect (Freking *et al.*, 1999). The
282 polar overdominance contrast tests whether animals inheriting the QTL from their
283 sire, but not their dam, are significantly different from the mean of the other three
284 genotype categories, whereas the maternal dominance contrast compares the

285 animals inheriting the QTL from their dam, but not their sire, with the average of the
286 two homozygote genotypes.

287

288 **Results**

289 *Position of TM-QTL*

290 Figure 1 shows the F-ratio for the probability from QTL Express of a QTL for UMD
291 being located at each cM along the 23cM segment of OAR18 between MCMA26 and
292 OARTMR1, confirming the presence of a QTL affecting ultrasound muscle depth
293 (adjusted for live weight) in this segment of OAR 18. This interval mapping approach
294 showed that the most likely position of TM-QTL is at 19cM from MCMA26, which is
295 between microsatellite markers OY3 and OARTMR1. However, because relatively
296 few markers define the region tested, no confidence interval for this position is given.
297 There was some variation in the magnitude of the effect of TM-QTL with the effect
298 ranging from 0.54 mm to 2.82 mm UMD (s.e. 0.37 mm to 0.57 mm) across the sires
299 that were segregating for TM-QTL. These analyses assume an additive effect of the
300 QTL and ignore the possibility of paternal polar overdominance.

301

302 **Figure 1 about here**

303

304 *Ultrasound muscle and fat depths and live weight at 20 weeks*

305 Live weight at 20 weeks was significantly higher in TM/TM animals than either +/+
306 (+7.3%) or +/TM animals (+11.7%), with TM/+ animals intermediate (Table 2).
307 Ultrasound muscle depth, when corrected for live weight, was significantly higher in
308 TM/+ than +/+ animals (+6.3%), but when not corrected for live weight, it was similar
309 in TM/TM and TM/+ animals, with both significantly higher than +/+ animals (+8.1%

310 and +8.4% respectively). Ultrasound fat depth corrected for live weight was highest
311 in TM/TM animals and lowest in TM/+ animals, with these two groups being
312 significantly different from each other (+10.2%), but not from +/+ or +/TM animals.
313 When not corrected for live weight, TM/TM animals had the highest fat depth. The
314 evidence for an additive effect of TM-QTL on live weight was not quite significant (P
315 = 0.08), but there was significant evidence that the effect of TM-QTL on live weight
316 corrected UMD showed paternal polar overdominance ($P = 0.05$).

317 **Table 2 about here**

318

319 *CT measured muscularity and dissected loin muscle weight*

320 Loin muscle width, depth and area, loin muscle volume and dissected *M.*
321 *longissimus lumborum* weight were significantly greater for TM/+ than +/+ animals
322 (+2.9 to +7.9%), and for depth, area and muscle volume were also significantly
323 greater for TM/+ than +/TM animals (+6.9 to +11.3%) (Table 3). Lumbar spine
324 length was highest for TM/+, significantly higher than +/TM and TM/TM but not
325 significantly different to +/+, but loin muscularity index was not significantly different
326 between groups. There was significant evidence that TM-QTL had a paternal polar
327 overdominant action on CT measured loin muscle area, depth and width and loin
328 region muscle volume and dissected *M. longissimus lumborum* weight. There were
329 no significant effects of TM-QTL on hind leg muscle dimensions or muscularity or
330 femur length (results not shown).

331

332 **Table 3 about here**

333

334 *Carcass weight and composition*

335 There was an additive effect of TM-QTL on carcass weight with TM/TM being
336 significantly heavier than +/+ (+11.1%) and +/TM animals (+11.9%), with TM/+
337 intermediate (Table 4). Carcass fat, muscle and bone weights shown in Table 4 are
338 those measured using carcass CT scanning and are adjusted for total carcass
339 weight. TM/+ had higher carcass muscle weights than +/+ (+1.36%) and for this trait
340 the test for paternal polar overdominance was close to significance ($P = 0.066$). The
341 carcass CT scanning results are shown here as these are believed to be the more
342 accurate reflection of carcass composition. However, the butchery results (shown in
343 supplementary table S1) are the commercially relevant ones. When measured using
344 live animal CT, muscle weight was slightly higher in TM/TM than +/+ animals (+2.8%,
345 $P = 0.047$). When measured using butchery, weight of lean meat yield was also
346 slightly higher in TM/TM than +/TM animals (+3.0%, $P = 0.045$). There were no
347 significant effects on CT predicted fat or bone weights in either live animals or
348 carcasses. The butchery results (supplementary table S1) showed no effect on bone
349 weight, but weight of fat trimmed from the carcass cuts was significantly lower for
350 TM/+ than +/+ animals (-11.2%; $P = 0.036$).

351 Table 4 about here

352

353 *Weight and composition of joints*

354 Weights of the leg, saddle and shoulder region and proportion of carcass weight
355 contained in each of these regions did not differ significantly between genotypic
356 groups (data in supplementary table S2). For the carcass CT scanning data,
357 composition of leg, saddle and shoulder regions showed significant differences
358 between genotypic groups for 4 traits (data in supplementary table S3). The leg
359 region had significantly less fat in TM/+ than +/+ lambs (27g; -5.1%; $P = 0.04$) and

360 +/TM had significantly less muscle than the other genotypic groups (130g-144g;
361 ~3%; $P < 0.03$). For the saddle region, TM/+ animals were less fat than +/TM
362 animals (84g; -13.5%; $P = 0.049$), and ++ had significantly less muscle than either
363 +/TM (136g; -7.16%; $P = 0.009$) or TM/+ (86g; -4.53%; $P = 0.016$). For the live CT
364 scanning data, there were no significant differences between genotypic groups for
365 composition of the leg, saddle or shoulder regions (data not shown). In the butchery
366 data (supplementary table S4), +/TM animals had significantly less LMY in the leg
367 region than both TM/+ (77g; -5.70%; $P = 0.019$) or TM/TM animals (78g; -5.77%; $P =$
368 0.026). TM/TM had significantly less bone in the leg region than the other three
369 groups (-3.24% to -3.99%; $P = 0.008$ to $P = 0.028$), although in real terms this was a
370 difference of only 22.6-28.1g. A significant negative maternal dominance effect was
371 found for LMY in the leg and a significant dominance effect was observed for bone
372 weight in the leg.

373

374

375 **Discussion**

376 The work reported here comprises results arising from a comprehensive experiment
377 to evaluate the effect of TM-QTL on carcass traits in purebred Texel lambs. TM-QTL
378 was first reported by Walling *et al.* (2004) on OAR18, located between microsatellite
379 markers MCMA26 and OARTMR1, and the current study has confirmed the
380 presence of TM-QTL on this segment of OAR18. Using the microsatellite markers
381 available to us at the time, it would have been difficult to more accurately position the
382 TM-QTL. There is a possibility that other QTL in this region of OAR18, such as the
383 Carwell QTL, are allelic to TM-QTL. Further work to fine-map this region would be

384 required to more accurately position TM-QTL and, ultimately, determine whether the
385 other QTL lying in this region are different from or allelic to TM-QTL.

386

387 TM-QTL affects loin muscling in Texel sheep. The initial study by Walling *et al.* 2004
388 showed an effect of +4 to +7% on ultrasound muscle depth, and in a larger
389 population in a follow-on study Matika *et al.* (2011) showed an effect of +8 to +17%
390 in 6 out of 36 Texel families. This effect was confirmed in Texel sired crossbred
391 lambs out of Mule ewes (Macfarlane *et al.*, 2009) and also out of Welsh Mountain
392 ewes (Masri *et al.*, 2011). Macfarlane *et al.* (2009) also noted that loin muscle (*M.*
393 *longissimus lumborum*) width, area, volume and weight were also higher in lambs
394 inheriting TM-QTL from their sire.

395

396 These earlier studies all used heterozygote carriers of TM-QTL where TM-QTL was
397 inherited from the sire. Based on the maternal and paternal variance components for
398 muscle depth in their data Matika *et al.* (2011) hypothesised that the TM-QTL is
399 characterised by a paternal polar overdominant pattern of expression, although the
400 structure of their study could not provide direct evidence of this form of imprinting.
401 The present study reports, for the first time, the effect of the inheritance of TM-QTL
402 from the dam, either alone or together with TM-QTL from the sire and provides
403 supporting evidence for a polar overdominant pattern of expression for the TM-QTL's
404 effect on loin muscling (ultrasound muscle depth, CT muscle depth, width, area and
405 volume and dissected weight). This mode of inheritance will have an important
406 impact on optimal utilisation of the TM-QTL within the sheep industry, since the TM-
407 QTL phenotype is only expressed in carriers of a single copy of TM-QTL inherited
408 from the sire. Imprinting tends to affect a region of a chromosome and it is therefore

409 not unexpected that TM-QTL would be imprinted, given its position within the same
410 region as both Carwell (Nicoll, 2007) and Callipyge (Cockett *et al.*, 1994a, Charlier
411 *et al.*, 2001a; Freking *et al.*, 2002) and the cluster of imprinted genes around
412 Callipyge (Charlier *et al.*, 2001b, Cockett *et al.*, 1996b).

413

414 The results of Macfarlane *et al.* (2012), showing an apparent additive effect of TM-
415 QTL on live and carcass weights, were replicated here. Of further interest was the
416 effect TM-QTL had on carcass and joint composition. In previous work looking at the
417 effect of a single copy of TM-QTL in crossbred Texel-sired lambs, there did not
418 appear be an effect on other carcass traits (out of Mule ewes, Macfarlane *et al.*,
419 2009; out of Welsh Mountain ewes, Masri *et al.*, 2011). In the present study, lambs
420 inheriting TM-QTL from their sire (either homozygote or heterozygote carriers),
421 tended to be less fat than wild-type homozygotes and this translated to a
422 commercially relevant significant difference in weight of fat trimmed from the carcass
423 during butchery (-11%) between homozygote wild-types and heterozygotes inheriting
424 TM-QTL from the sire. Furthermore, although the differences were small and not
425 always significant, muscle weight and lean meat yield tended to be higher in lambs
426 inheriting TM-QTL from their sire (either homozygote or heterozygote carriers) than
427 in wild-type homozygotes or lambs inheriting TM-QTL from their dam. This indicates
428 that animals inheriting TM-QTL from their sires are likely to produce carcasses with
429 slightly greater lean meat yield and require less work for fat trimming during
430 butchery, in addition to the greater weight of the high value loin muscle. There did
431 not appear to be any unfavourable effects of TM-QTL on carcass traits and Lambe *et*
432 *al.* (2011) has shown that there are no significant effects of TM-QTL on meat quality
433 when meat was conditioned for a period of 7-9 days.

434

435 In summary, the direct effects of TM-QTL on loin muscling (4-11% increase in highly
436 priced part of the carcass) and growth make it an interesting candidate for
437 exploitation within the UK sheep industry and beyond, especially since it does not
438 have any major negative impacts on eating quality. However, there are two main
439 aspects to consider before commercial exploitation is feasible: (i) a commercial
440 genotyping test and (ii) a usage plan.

441 (i) Commercial genotyping test: Exploitation of this QTL will require development
442 of a suitable and affordable DNA test to identify carrier animals, as usage of
443 microsatellite marker panels with family-specific linkage phases is not feasible
444 in practice. This will necessitate further research to fine map and identify
445 closely linked markers or even the specific mutation(s) involved, so that a
446 commercial SNP test can be developed. However, in the case of Parent-of-
447 origin (PofO) effects, such as polar overdominance, the homologous
448 chromosomes exhibit differential gene expression and conventional
449 association studies generally ignore such inheritance patterns, considering
450 maternal and paternal alleles to be equivalent (e.g. Garg *et al.*, 2012). The
451 problems caused by PofO on genome-wide association (GWA) analyses has
452 been discussed in detail by Rowe *et al.* (2012) and it is obvious that this
453 remains challenging, as the recent standard approach for fine mapping using
454 dense SNPs may not work well. Typically, GWA studies regress the
455 phenotype on the number of (minor) alleles present at the locus, however,
456 with polar overdominance and an allele frequency approaching 0.5, the
457 regression of a trait showing polar overdominance on allele count will be close
458 to zero (see Rowe *et al.*, 2012). Hence standard GWA analyses miss the

459 effect. To overcome this problem, one would need phased haplotypes, i.e.
460 knowledge of the PofO, and specifically fit phased-haplotype-derived
461 genotype class in the analysis, as suggested earlier (Rowe *et al.*, 2012).

462 (ii) Utilisation: Optimal usage in a purebred situation is different from that in a
463 crossbred and it is important to consider if the aim is to exploit the muscling
464 effects or the growth effects of TM-QTL. In a pure-bred scenario, in terms of
465 muscling, one wants to take the QTL to a frequency of ca. 0.5 (although for
466 live weight it should go higher). But for maximum benefit in crossbred progeny
467 (assuming that the dam breed does not carry the QTL) one simply wants all
468 sires to be homozygous, so that their progeny benefit in terms of both
469 liveweight and muscling effects. This implies that for the optimum utilisation
470 strategy for the muscling effects in crossbred lambs, the performance in the
471 purebred population is not at its optimum. In contrast to the muscling effects,
472 the growth effects of TM-QTL seem to show an additive effect, with animals
473 inheriting two copies of TM-QTL showing an increase of 1.5 kg or 9% in
474 carcass weight when slaughtered at a fixed age, and an increase in live
475 weight across a range of ages from birth to slaughter (+4 to +15%), compared
476 to wildtype animals (Macfarlane *et al.*, 2012). Such differences have
477 implications for exploitation within the stratified industry structure typical of the
478 UK. To benefit fully from the effects on growth and carcass weight, the TM-
479 QTL will need to be introgressed into the dam line as well as fixed within
480 terminal sires; however this will lose the benefits for muscling. Exploitation of
481 the effects on loin muscling will require TM-QTL to be absent in the dam line
482 and fixed in a homozygous state within terminal sire breeds to derive
483 maximum commercial benefit.

484

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497

- 500 Bunger L, Macfarlane JM, Lambe NR, Conington J, McLean KA, Moore K, Glasbey CA and
501 Simm G 2011. Use of X-ray computed tomography (CT) in UK sheep production and
502 breeding. In CT Scanning - Techniques and Applications (ed S Karuppasamy), pp. 329-348.
503 INTECH Open access Publisher, Rijeka, Croatia.
- 504 Charlier C, Segers K, Wagenaar D, Karim L, Berghams S, Jaillon O, Shay T, Weissenbach
505 J, Cockett N, Gyapay G and Georges M 2001a. Human-ovine comparative sequencing of a
506 250-kb imprinted domain encompassing the callipyge (*clpg*) locus and identification of six
507 imprinted transcripts: *DLK1*, *DAT*, *GTL2*, *PEG11*, *antiPEG11*, and *MEG8*. *Genome*
508 *Research* 11, 850-862.
- 509 Charlier C, Segers K, Wagenaar D, Karim L, Berghmans S, Jaillon O, Shay T, Weissenbach
510 J, Cockett N, Gyapay G and Georges M 1-5-2001b. Human-Ovine Comparative Sequencing
511 of a 250-kb Imprinted Domain Encompassing the Callipyge (*clpg*) Locus and Identification of
512 Six Imprinted Transcripts: *DLK1*, *DAT*, *GTL2*, *PEG11*, *antiPEG11*, and *MEG8*. *Genome*
513 *Research* 11, 850-862.
- 514 Churchill GA and Doerge RW 1994. Empirical threshold values for quantitative trait mapping.
515 *Genetics* 138, 963-971.
- 516 Cockett NE, Jackson SP, Shay TL, Nielsen D, Moore SS, Steel MR, Barendse W, Green RD
517 and Georges M 1994a. Chromosomal localization of the callipyge gene in sheep (*Ovis aries*)
518 using bovine DNA markers. *Proceedings of the National Academy of Sciences of the United*
519 *States of America* 91, 3019-3023.
- 520 Cockett NE, Jackson SP, Snower GD, Shay TL, Berghmans S, Beever JE, Carpenter C and
521 Georges M 1996a. Polar overdominance at the ovine *callipyge* locus. *Journal of Animal*
522 *Science* 77 (Suppl 2), 221-227.
- 523 Cockett NE, Jackson SP, Shay TL, Farnir F, Berghmans S, Snower GD, Nielsen DM and
524 Georges M 1996b. Polar overdominance at the Ovine callipyge locus. *Science* 273, 236-238.
- 525 Cockett NE, Jackson SP, Shay TL, Nielsen D and Moore SS 1994b. Chromosomal
526 localization of the callipyge gene in sheep (*Ovis aries*) using bovine DNA markers. [ABA 62,
527 5543]. *Proceedings of the National Academy of Sciences of the United States of America* 91,
528 3019-3023.
- 529 Freking BA, Keele JW, Beattie CW, Kappes SM, Smith TP, Sonstegard TS, Nielsen MK and
530 Leymaster KA 1998. Evaluation of the ovine callipyge locus: I. Relative chromosomal
531 position and gene action. *Journal of Animal Science* 76, 2062-2071.
- 532 Freking BA, Keele JW, Shackelford SD, Wheeler TL, Koohmaraie M, Nielsen MK and
533 Leymaster KA 1999. Evaluation of the ovine callipyge locus: III. Genotypic effects on meat
534 quality traits. *Journal of Animal Science* 77, 2336-2344.
- 535 Freking BA, Murphy SK, Wylie AA, Rhodes SJ, Keele JW, Leymaster KA, Jirtle RL and
536 Smith TP 2002. Identification of the single base change causing the callipyge muscle
537 hypertrophy phenotype, the only known example of polar overdominance in mammals.
538 *Genome Res* 12, 1496-1506.

- 539 Garg P, Borel C and Sharp AJ 2012. Detection of parent-of-origin specific expression
540 quantitative trait loci by cis-association analysis of gene expression in trios. Plos One 7,
541 e41695.
- 542 GenStat 11 Committee 2008. GenStat. Lawes Agricultural Trust, Rothamstead Experimental
543 Station, Harpenden, UK.
- 544 Georges M and Cockett N 1996. The ovine callipyge locus: A paradigm illustrating the
545 importance of non-Mendelian genetics in livestock. Reproduction Nutrition Development 36,
546 651-657.
- 547 Jones HE, Lewis RM, Young MJ and Wolf BT 2002. The use of X-ray computer tomography
548 for measuring the muscularity of live sheep. Animal Science 75, 387-399.
- 549 Jopson NB, Nicoll GB, Stevenson-Barry JM, Duncan S, Greer GJ, Bain WE, Gerard EM,
550 Glass BC, Broad TE and Mcewan JC 2001. Mode of inheritance and effects on meat quality
551 of the rib-eye muscling (REM) QTL in Sheep. Proceedings of the Association for the
552 Advancement of Animal Breeding and Genetics 14, 111-114.
- 553 Knott SA, Elsen JM and Haley CS 1996. Methods for multiple-marker mapping of
554 quantitative trait loci in half-sib populations. Theoretical And Applied Genetics 93, 71-80.
- 555 Lambe NR, Richardson RI, Macfarlane JM, Nevison I, Haresign W, Matika O and Bunger L
556 2011. Genotypic effects of the Texel Muscling QTL (TM-QTL) on meat quality in purebred
557 Texel lambs. Meat Science 89, 125-132.
- 558 Macfarlane JM, Lambe NR, Bishop SC, Matika O, Rius-Vilarrasa E, McLean KA, Haresign
559 W, Wolf BT, McLaren RJ and Bunger L 2009. Effects of the Texel muscling quantitative trait
560 locus on carcass traits in crossbred lambs. Animal 3, 189-199.
- 561 Macfarlane JM, Lambe NR, Haresign W and Bunger L 2012. The effect of the Texel
562 Muscling QTL (TM-QTL) on live and carcass weight in Texel lambs. Small Ruminant
563 Research 85, 715-720.
- 564 Macfarlane JM, Lambe NR, Matika O, McLean KA, Masri AY, Johnson PL, Wolf BT,
565 Haresign W, Bishop SC and Bunger L 2010. Texel loin muscling QTL (TM-QTL) located on
566 ovine chromosome 18 appears to exhibit imprinting and polar overdominance. Proceedings
567 of the 9th World Congress on Genetics Applied to Livestock Production, Leipzig abstract
568 199.
- 569 Mann AD, Young MJ, Glasbey CA and McLean KA 2003. *STAR: Sheep Tomogram Analysis*
570 *Routines* (V.3.4). BioSS - Biomathematics and Statistics Scotland, Edinburgh, UK.
- 571 Masri AY, Macfarlane JM, Lambe NR, Haresign W, Brotherstone S and Bunger L 2011.
572 Evaluating the effects of the c.*1232G > A mutation and TM-QTL in Texel x Welsh Mountain
573 lambs using ultrasound and video image analyses. Small Ruminant Research 99, 99-109.
- 574 Matika O, Sechi S, Pong-Wong R, Houston RD, Clop A, Wooliams JA and Bishop SC 2011.
575 Characterization of OAR1 and OAR18 QTL associated with muscle depth in British
576 commercial terminal sire sheep. Animal Genetics 42, 172-180.
- 577 McLaren RJ, Mcewan JC, For R, Glass BC, Broad TE, Greer GJ and Nicoll GB 2003.
578 Recombination breakpoint mapping of the Carwell locus for Rib-eye muscling in sheep.
579 Proceedings of the International Congress of Genetics XIX, Melbourne, Australia, July 6-11,
580 2003, Abstract 01064 .

- 581 Navajas EA, Glasbey CA, McLean KA, Fisher AV, Charteris AJL, Lambe NR, Bunger L and
582 Simm G 2006. *In vivo* measurements of muscle volume by automatic image analysis of
583 spiral computed tomography scans. *Animal Science* 82, 545-553.
- 584 Navajas EA, Lambe NR, McLean KA, Glasbey CA, Fisher AV, Charteris AJL, Bunger L and
585 Simm G 2007. Accuracy of *in vivo* muscularity indices measured by computed tomography
586 and their association with carcass quality in lambs. *Meat Science* 75, 533-542.
- 587 Nicoll GB 2007. The Landcorp Carwell Experience. Proceedings of the Sheep Breeders'
588 Roundtable 2007; Nottingham, 9-11 November, 2007;
589 <http://www.nationalsheep.org.uk/SBRT>.
- 590 Rowe S, Bishop S and Koning DJd 2012. Imprinting in Genome Analysis: Modeling Parent-
591 of-Origin Effects in QTL Studies. In ed H Khatib), pp. 113-129. John Wiley & Sons, Inc.,
- 592 Seaton G, Haley CS, Knott SA, Kearsey M and Visscher PM 2002. QTL Express: mapping
593 quantitative trait loci in of simple and complex pedigrees. *Bioinformatics* 18, 339-340.
- 594 Walling GA, Visscher PM, Wilson AD, McTeir BL, Simm G and Bishop SC 2004. Mapping of
595 quantitative trait loci for growth and carcass traits in commercial sheep populations. *Journal*
596 *of Animal Science* 82, 2234-2245.
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603 **Tables**

604

605 Table 1. Distribution of TM-QTL genotype status of lambs across the seven different sires

606 used

TM-QTL	Sire							Total
Genotype	1 *	2	3	4	5	6	7	
+/+		1	2	11	3	14	9	40
+/TM		3			7		7	17
TM/+	21	1	2	5	4	14	6	53
TM/TM	22	1			5		6	34
Unknown	11	4	7	2	4	11	28	67

607 *Note: Sire 1 was homozygous and sires 2 to 7 all heterozygous

608 The sires in bold have been used on both farms

609

610 Table 2. Least squares means[†] for live weight at 20 weeks (US LW) and ultrasound muscle
 611 depth and fat depth, both adjusted (UMD_LW, UFD_LW) for live weight and unadjusted for
 612 live weight (UMD, UFD) for the four TM-QTL genotype groups and the p-values for the tests
 613 of different modes of action for the QTL

Genotype	US LW ¹	UMD ²	UMD_LW ³	UFD ⁴	UFD_LW ⁵
+/+ [§]	35.8 ^b	23.5 ^b	22.5 ^b	3.04 ^b	2.87 ^{ab}
+ /TM	34.4 ^b	23.7 ^{ab}	23.5 ^{ab}	2.91 ^b	2.88 ^{ab}
TM/+	36.9 ^{ab}	25.5 ^a	23.9 ^a	3.08 ^b	2.81 ^b
TM/TM	38.4 ^a	25.4 ^a	23.3 ^{ab}	3.46 ^a	3.10 ^a
average s.e.d.	1.43	0.940	0.593	0.182	0.155
minimum s.e.d.	1.13	0.71	0.480	0.145	0.122
maximum s.e.d.	1.67	1.12	0.700	0.213	0.182
P values for:					
Additive effect	0.08	0.05	0.32	0.03	0.19
Dominance effect	0.56	0.41	0.10	0.20	0.23
Reciprocal heterozygote effect	0.70	0.38	0.40	0.80	0.51
Maternal dominance effect	0.55	0.92	0.50	0.46	0.64
Paternal polar overdominance	0.99	0.14	0.045	0.25	0.13

614 [†] LS means with common letters in their superscripts, within column, are not significantly
 615 different ($P > 0.05$), where differences were significant, p-values are shown in the numbered
 616 footnote corresponding to that trait. Average, minimum and maximum s.e.d. are shown for
 617 information.

618 [§]TM-QTL genetic groups: +/+ homozygous for the wild-type allele; TM/+ and +/TM
 619 heterozygote carriers of paternal and maternal origin of allele, respectively and TM/TM
 620 homozygous for the TM-QTL allele

621 1 US LW: TM/TM vs. +/+ = 0.049, TM/TM vs. +/TM = 0.017

622 2 UMD: TM/TM vs. +/+ = 0.020, TM/TM vs. +/+ = 0.050

623 3 UMD_LW: TM/+ vs. +/+ = 0.004

624 4 UFD: TM/TM vs. +/+ = 0.018, TM/TM vs. +/TM = 0.010, TM/TM vs. TM/+ = 0.013

625 5 UFD_LW: TM/+ vs. TM/TM = 0.025

626 Table 3. Least squares means[†] for live weight adjusted CT measured loin muscle area, depth and width (MLLA; mm², MLLD; mm, MLLW; mm),
 627 loin muscularity index (LRMI), loin muscle volume (LRMV; cm³) and lumbar spine length (LSL; cm) and dissected loin muscle weight (MLL wt;
 628 g) for the four TM-QTL genotype groups and the p-values for the tests of different modes of action of the QTL on these traits

	MLLA ¹	MLLD ²	MLLW ³	LRMI	LRMV ⁴	LSL ⁵	MLL wt ⁶
+/+	1739 ^{bc}	29.13 ^b	67.74 ^b	2.953	548.5 ^{bc}	18.3 ^{ab}	806 ^b
+ / TM	1699 ^c	29.12 ^b	68.61 ^{ab}	2.966	519.4 ^c	17.8 ^b	801 ^{ab}
TM/+	1877 ^a	31.13 ^a	69.71 ^a	2.99	577.9 ^a	18.7 ^a	837 ^a
TM/TM	1838 ^{ab}	30.35 ^{ab}	69.17 ^{ab}	3.041	567.4 ^{ab}	18.2 ^b	817 ^{ab}
ave s.e.d.	57.45	0.858	0.853	0.085	18.6	0.338	20.9
min s.e.d.	45.6	0.68	0.69	0.069	14.9	0.260	16.5
max s.e.d.	66.9	1.00	1.00	0.099	21.8	0.430	24.4
P values for							
Additive effect	0.08	0.091	0.031	0.35	0.62	0.73	0.83
Dominance effect	0.91	0.26	0.58	0.52	0.39	0.69	0.78
Reciprocal Heterozygote effect	0.004	0.09	0.022	0.66	0.01	0.08	0.02
Maternal dominance effect	0.15	0.90	0.41	0.51	0.06	0.24	0.32
Paternal polar overdominance	0.002	0.01	0.01	0.99	0.04	0.12	0.01

629 [†] LS means with common letters in their superscripts, within column, are not significantly different (P > 0.05), where differences were
 630 significant, p-values are shown in the numbered footnote corresponding to that trait. Average, minimum and maximum s.e.d. are shown for
 631 information.

632 ¹MLL_A: +/+ vs. TM/+ = 0.003, +/TM vs. TM/+ = 0.005, +/TM vs. TM/TM = 0.039

633 ²MLL_D: +/+ vs. TM/+ = 0.004, +/TM vs. TM/+ = 0.034; ³MLL_W: +/+ vs. TM/+ = 0.005

634 ⁴LRMV: +/+ vs. TM/+ = 0.049, +/TM vs. TM/+ = 0.004, +/TM vs. TM/TM = 0.029

635 ⁵ LSL: TM/+ vs. +/TM = 0.035, TM/+ vs. TM/TM = 0.047; ⁶ MLL wt: +/+ vs. TM/+ = 0.047

636
 637 Table 4. Least squares means[†] for cold carcass weight (kg) and carcass fat, muscle and bone weights (all adjusted for carcass weight)
 638 measured using post-slaughter carcass CT scanning for the four TM-QTL genotype groups and the p-values for the tests of different modes of
 639 action for the QTL on these traits

	Carcass wt (kg) ¹	Fat wt (g)	Muscle wt (g) ²	Bone wt (g)
+/+	14.6 ^b	2037	9390 ^b	2138
+/TM	14.5 ^b	2025	9428 ^{ab}	2103
TM/+	15.2 ^{ab}	1922	9518 ^a	2141
TM/TM	16.2 ^a	1980	9488 ^{ab}	2096
ave s.e.d.	0.715	80.9	72.6	39.2
min s.e.d.	0.567	65.0	58.2	31.2
max s.e.d.	0.836	95.5	85.8	46.3
P values for:				
Additive effect	0.03	0.22	0.06	0.46
Dominance effect	0.69	0.12	0.27	0.22
Reciprocal heterozygote effect	0.93	0.64	0.30	0.41
Maternal dominance effect	0.75	0.42	0.84	0.21
Paternal polar overdominance	0.85	0.12	0.07	0.99

640 [†] LS means with common letters in their superscripts, within column, are not significantly different ($P > 0.05$), where differences were
 641 significant, p-values are shown in the numbered footnote corresponding to that trait. Average, minimum and maximum s.e.d. are shown for
 642 information.

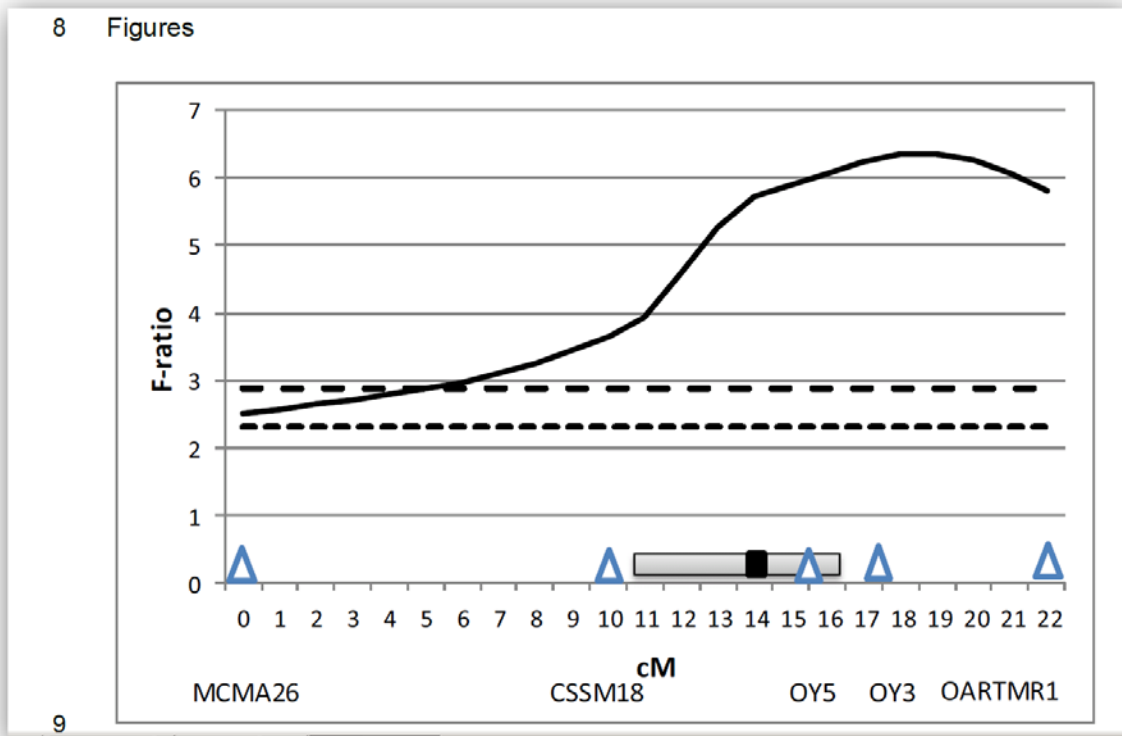
643 ¹ Carcass weight: TM/TM vs. +/+ $P = 0.021$, TM/TM vs. +/TM $P = 0.040$

644 ² Muscle weight: TM/+ vs. +/+ $P = 0.029$

645 **Caption for the Figure**

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647

648 Figure 1. Statistical evidence for a QTL affecting ultrasound muscle depth (shown
649 as solid line), expressed as an F ratio, at each cM along a segment of ovine
650 chromosome 18 between MCMA26 and OARTMR1, using an interval mapping
651 approach. Significance thresholds are shown by horizontal lines ($P = 0.01$ - - - ; $P =$
652 0.05 - - - -). Also included are the position of the Callipyge mutation (■; Freking *et al.*,
653 2002) and the approximate region thought to be associated with the Carwell QTL
654 (▨; McLaren *et al.*, 2003).



655