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REPLICATION OF LONG BONE LENGTH QTL IN THE F₉ - F₁₀ LG,SM ADVANCED INTERCROSS

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Abstract

Quantitative trait locus (QTL) mapping techniques are frequently used to identify genomic regions associated with variation in phenotypes of interest. However, the F₂ intercross and congenic strain populations usually employed have limited genetic resolution resulting in relatively large confidence intervals that greatly inhibit functional confirmation of statistical results. Here, we use the increased resolution of the combined F₉ and F₁₀ generations (n=1,455) of the LG,SM advanced intercross to fine-map previously identified QTL associated with the lengths of the humerus, ulna, femur, and tibia. We detected 81 QTL affecting long bone lengths. Of these, 49 were previously identified in the combined F₂-F₃ population of this intercross while 32 represent novel contributors to trait variance. Pleiotropy analysis suggests that most QTL affect 3-4 long bones or serially homologous limb segments. We also identified 72 epistatic interactions involving 38 QTL and 88 novel regions. This analysis shows that using later generations of an advanced intercross greatly facilitates fine-mapping of confidence intervals, resolving 3 F₂-F₃ QTL into multiple linked loci and narrowing confidence intervals of other loci, as well as allowing identification of additional QTL. Further characterization of the biological bases of these QTL will help provide a better understanding of the genetics of small variations in long bone length.

Keywords

Quantitative trait loci; advanced intercross; genetic architecture; long bone lengths

INTRODUCTION

Endochondral ossification, the process through which many skeletal elements including the long bones grow, proceeds via known molecular pathways controlled by genes established using traditional Mendelian techniques involving mutations of large effect (Kronenberg 2003; Zelzer and Olsen 2003). However, many of the alleles associated with long bone length variation in populations have small effect sizes (Kenney-Hunt et al. 2006; Norgard et al. 2008) and cannot be analyzed using such approaches. Long bone length presents an ideal opportunity to use quantitative trait locus (QTL) mapping strategies to identify novel genomic elements and interactions involved in producing adult skeletal structures. After the establishment of the growth plate by embryonic day 17.5 (Kaufman and Bard 1999), all longitudinal growth in murine long bones occurs via endochondral ossification, offering the prospect of identifying genomic entities that specifically affect this complex process.

QTL mapping strategies have revealed many details of the genetic control of variation in adult long bone lengths using large, phenotypically normal populations of mice (Corva et al. 2001; Drake et al. 2001; Masinde et al. 2003; Shultz et al. 2003; Lang et al. 2005; Kenney-Hunt et al. 2006; Christians and Senger 2007; Norgard et al. 2008; Yu et al. 2009). Combining the numerous targeted genetic studies of genes of large effect with QTL mapping strategies that identify allele combinations associated with subtler variation allows the assembly of a network of genes or other genomic elements that underlie variation in long bone length. The greater resolution achieved by this combination of analyses is crucial for gaining a full understanding of how dynamic systems of transcription factors, morphogens, growth factors, body size regulators, hormones, and other genomic elements affecting bone growth contribute to produce phenotypes in adult animals.

Most murine long bone length QTL have been mapped in second generation intercross populations (Drake et al. 2001; Masinde et al. 2003; Shultz et al. 2003; Lang et al. 2005; Kenney-Hunt et al. 2006; Norgard et al. 2008) and several have been fine-mapped using congenic lines (Corva et al. 2001; Christians et al. 2003; Shultz et al. 2003; Christians and Senger 2007; Yu et al. 2009). Congenic strains, where a QTL from one donor genetic background is transferred to a second recipient genetic background using standard breeding procedures (Flaherty 1981), can be used to identify interactions between the known QTL and the recipient background. Second generation intercross populations, where the genome of each individual is a unique permutation of the initial contributing strains, can be used to detect QTL and their interactions both with other regions of the genome as well as various environmental factors. Both techniques are useful in different contexts but tend to be imprecise because they identify relatively large regions of sequence.

Alternatively, QTL mapping in the later generations of an intercross (Darvasi and Soller 1995; Darvasi 1998) can be used to build on information gained from congenic or second generation intercross populations by increasing the resolution of previously identified QTL and detecting new QTL or novel genetic interactions. These later generations, or advanced intercross (AI) lines, are generated by outbreeding the F_2 and all subsequent generations. This results in the accumulation of additional genetic recombination leading to a reduction in the average size of segregating linkage blocks (Haldane and Waddington 1931; Bartlett and Haldane 1935; Hanson 1959c, d, b, a; Darvasi and Soller 1995; Rockman and Kruglyak 2006). Thus, confidence intervals identified in later generations of AI lines are expected to be much reduced from those in F_2 studies. We previously identified 70 QTL for long bone length in the F_2 - F_3 generations of the LG,SM intercross (Kenney-Hunt et al. 2006; Norgard et al. 2008). In this study, the use of the combined F_9 - F_{10} populations results in a five-fold expansion of the F_2 - F_3 map, increasing QTL resolution and providing greater insight into the genetic architecture influencing murine long bone length.

MATERIALS AND METHODS

Mouse population and genotyping

The mice used in this study were the F₉ (n = 150) and F₁₀ (n = 1,305) generations of a previously initiated LG,SM advanced intercross (Cheverud et al. 1996; Kramer et al. 1998; Vaughn et al. 1999; Cheverud et al. 2001; Kenney-Hunt et al. 2006; Norgard et al. 2008). All animals were between 12 and 40 weeks of age at death (correction for age is described below). Animal husbandry and tissue processing details can be found in (Norgard et al. 2008). Each individual in the population (n = 1,455) was genotyped with a panel of 1470 polymorphic SNPs using the Illumina GoldenGate platform. Therefore, there is 1 marker for every 1.66 Mb of sequence in the F₉-F₁₀.

Long bone lengths

The F₉ long bones (right-side humerus, ulna, femur, and tibia) were measured to the nearest 0.01 mm using digital calipers and the F₁₀ long bones were photographed and measured to the nearest 0.01 mm in ImageJ (NIH). Broken or missing bones were either substituted with left-side bones or not included in the analysis. All individual bone lengths were density-plotted and determined to fall in a normal distribution. Femur lengths were plotted against adult body weight to identify outliers, which were removed from analysis. Similarly, the humerus, ulna, and tibia lengths were plotted against the femur lengths to identify and remove outliers. This resulted in n > 1,300 for all analyses. Long bone length measurement repeatabilities range from 96% to 99%.

Data correction, heritability, and imputation

Long bone lengths were corrected for sex, generation, age at necropsy, litter size at birth, and litter size at weaning; residual values from a linear regression including these factors as independent variables were used in all subsequent analyses. Heritabilities and genetic correlations were calculated from the F₁₀ population using the full sibship method (Falconer and Mackay 1996). Imputation and logarithmic transformation of probabilities to LOD-equivalent LPR scores proceeded as described in (Norgard et al. 2008). The X chromosome was not analyzed.

QTL fine-mapping

All statistical models were run in SYSTAT 12.0 (<http://www.systat.com>) or R (<http://www.r-project.org>). The genetic map was calculated using R/QTL treating the F₉-F₁₀ population as an F₂ because these later generations are an intercross population with accumulated recombination. Corrections for family structure were imposed on genome scan results by adjusting the significance thresholds. This map is related to the F₂ map by an order of 5X over short distances (see Appendix 1). QTL were fine-mapped using composite interval mapping (Jiang and Zeng 1995) with the equation:

$$y_{ijk} = \mu + a * X_{ai} + d * X_{dj} + e_{ijk} | X_{al} \quad X_{dl} \quad X_{am} \quad X_{dm},$$

where y is the vector of trait values for all individuals, μ is the constant, X_{ai} and X_{dj} are vectors of additive and dominance genotypic scores for all individuals, a and d are the associated regression coefficients representing additive and dominance genotypic values, and e is the residual error. The Haley and Knott method was used to calculate genotype scores (Haley and Knott 1992). This assumes no interference but does allow for double recombinations in the intermarker interval. The vertical bar indicates that the regression is performed while holding constant the effects of the additive and dominance genotypic scores to its right. The genotypic scores held constant were chosen to separate apparent QTL peaks in order to eliminate the

potential effects of other QTLs proximal (locus l) and distal (locus m) to the region of interest. Three previously identified peaks were resolved into multiple QTL on the basis of these composite interval maps, with additional evidence provided by differences in effect size and direction as well as non-overlapping confidence intervals. QTL positions are reported here on the F₁₀ mapping scale; over short distances, one F₁₀ cM is equivalent to a 0.2 F₂ cM distance. Thus, the F₁₀ generation has an average of 80% fewer nucleotides per cM than the F₂ generation.

Established QTL peaks were tested for sex-specificity using the model (Kenney-Hunt et al. 2008):

$$y_{ijk} = \mu + a_x * (\text{sex}_i * X_{aj}) + d_x * (\text{sex}_i * X_{dk}) | \text{sex}_i \quad X_{aj} \quad X_{dk},$$

where y is the vector of trait values for all individuals, μ is the constant, sex_i is the vector of sexes with a value of “1” if an individual is male and “0” if female, X_{aj} and X_{dk} are vectors of additive and dominance genotypic scores for all individuals, and a_x and d_x are the associated regression coefficients for sex interaction. The vertical bar indicates that the regression is performed while holding constant the effects of sex and the additive and dominance genotypic scores at the locus of interest. If a significant sex interaction was noted in this analysis ($p < 0.05$), the 1-QTL model was applied to each sex separately. Visual inspection was then used to determine whether established QTL peaks were sexually dimorphic (whether a QTL peak was higher in one sex than the other or present in one sex but not the other). Pleiotropy and genome-wide pair-wise epistasis were tested as described in (Knott and Haley 2000; Norgard et al. 2008).

Significance thresholds and confidence intervals

To determine significance thresholds, an algorithm based on the experimental protocol of the AI design was used to simulate 1,000 replicate populations. Each replicate population had individuals that corresponded to those in the phenotypic dataset. A large number (~1,000) of independent markers were simulated for each individual. Since there is no causal connection between the genotypes and the phenotypes in the simulation, the associations between the markers and the phenotypes in the simulation approximate the distribution of results expected by chance. Using properties of this distribution, the following formulae were developed:

$$\text{Pointwise LPR threshold} = 1.38 + 4.12 * h^2;$$

Chromosome LPR threshold = $-\text{LOG}_{10} (1 - (1 - \text{Pointwise probability})^{1/N(\text{eff})}) + 3.66 * h^2$ where the pointwise threshold is calculated using the heritability which accounts for family structure and based on the simulations described above (first formula) and where $N(\text{eff})$ is the effective number of markers on each chromosome (second formula). The $N(\text{eff})$ was calculated using the Li and Ji method on a chromosome-by-chromosome basis and the genome-wide $N(\text{eff})$ was equal to the sum of the $N(\text{eff})$ for each chromosome (Li and Ji 2005). The pointwise LPR significance thresholds for humerus, ulna, femur, and tibia were 3.34, 3.79, 3.16, and 3.78, respectively. Inflation of these pointwise thresholds relative to the canonical 1.30 (Probability = 0.05) threshold is due to familial autocorrelation for the traits analyzed. An alternative method for significance testing AI lines is presented in (Peirce et al. 2008).

Confidence intervals (CIs) for the map location of QTL are also subject to distortion by the effects of family structure. We used computer simulation to estimate CIs using the simulated genotypes generated for threshold estimation, simulated trait heritability levels, and simulated QTL effect strengths. For each iteration of the simulation, a QTL of a given effect size was

placed on a chromosome for several characteristics with differing heritability. The location of the maximum LPR score was recorded in cases where it fell within 20 cM of the true location on the F_{10} scale. This guards against false positives artificially inflating the variance in the location, which can occur frequently in the case of loci with small effects where there is low power to detect a QTL in its true location. The results of 1000 iterations were then summarized and used to estimate a numerical approximation of a confidence interval. These CIs are essentially 1-LPR drops that have been corrected for the inflated LPR scores due to familial autocorrelation. Confidence intervals (CIs) were defined using the equation:

$$CI \text{ cM} = \pm 1.96 * \exp(-0.416 - 0.438 * \ln[R^2/h^2]),$$

where CI is the 95% confidence interval encompassing the peak, R^2 is the multiple squared r calculated for a single-trait QTL fit at the locus, and h^2 is the single-trait narrow-sense heritability estimated using the sibship method (Table 1). The ratio R^2/h^2 represents the proportion of the additive genetic variation accounted for by the QTL in question.

RESULTS

Long bone lengths are controlled by numerous genetic factors

Long bone length heritabilities in the F_{10} population were lower than in previous populations (Norgard et al. 2008), ranging from 0.37 to 0.61 (Table 1), while genetic correlations remained high, ranging from 0.79 to 0.94.

We detected the presence of 81 single-trait QTL, listed in Table 2, spread over all 19 autosomes except chromosomes 5, 14, and 15. These QTL collectively accounted for 23% of the phenotypic variation in the humerus, 34% of the variation in ulna, 27% of the variation in femur, and 32% of the variation in tibia. Additional traits were significant at thirteen F_2 - F_3 QTL and thirteen entirely new pleiotropic loci were observed, including three F_2 - F_3 QTL, *Lbn1.1*, *Lbn3.2*, and *Lbn6.1*, that were resolved into multiple linked loci in this analysis: *Lbn1.1a* affecting ulna and tibia and *Lbn1.1b*, *Lbn3.2a*, *Lbn3.2b*, *Lbn6.1a*, and *Lbn6.1b* affecting all traits. Interestingly, while most F_2 - F_3 pleiotropic QTL (Norgard et al. 2008) were at least partly replicated (at least one trait significant in the F_2 - F_3 also significant in the F_9 - F_{10}) in this study, 27 single-trait QTL comprising parts of previously identified pleiotropic loci were not replicated, and loci *Lbn1.3*, *Lbn3.3*, *Lbn4.2*, *Lbn5.1_M*, *Lbn9.1*, *Lbn9.2*, *Lbn11.1*, *Lbn14.1*, *Lbn15.1_F*, and *Lbn15.2_M* were not replicated at all. This was most likely caused by a combination of our application of strict Bonferroni-corrected thresholds in the present study, to loci with decreased individual significance and the Beavis effect (Beavis 1994) altering the identified subset of QTL with lower LPR scores (see discussion).

Sex interaction analysis revealed the presence of fifteen sexually dimorphic single-trait QTL, including pleiotropic loci *Lbn3.2a* (all trait effects stronger in females than males), *Lbn3.2b* (humerus and femur effects female-specific and ulna and tibia effects greater in females than males), *Lbn4.1* (humerus effects greater in females than males), *Lbn7.1* (femur effects greater in males than females), *Lbn8.1* (tibia effects greater in males than females), *Lbn11.2* (tibia effects greater in males than females), *Lbn16.2* (humerus effects male-specific and ulna effects greater in males than females), and *Lbn17.1* (tibia effects greater in females than males).

Almost all the QTL (79 of 81) showed significant additive genotypic effects (a/SD in Table 2), with absolute values of standardized additive effects ranging from 0.084 to 0.436 SD units. These additive effects were distributed such that most were small in effect size (0.1-0.2 SD units) with fewer loci having large effect sizes (0.3-0.4 SD units). No single locus contributed more than 10% to the overall phenotypic variance. Generally, the LG/J allele led to longer bone

length. However, ten single-trait QTL comprising *Lbn3.3*, *Lbn6.1a*, *Lbn7.2*, *Lbn9.3*, and *Lbn16.2* had negative additive genotypic effects, indicating that the presence of the SM/J allele at those loci leads to longer bone lengths. Interestingly, *Lbn16.2* had opposite effects in males (negative effect) and females (positive effect). The average a/SD for significant QTL was 0.198, but when the sign of the effects was taken into account, this normalized average decreased to 0.145, indicating an overall positive influence of the LG/J allele at QTL with significant additive effects.

Almost half of the loci showed significant dominance effects, including seven cases of underdominance ($d/a < -1.5$), four cases of SM/J dominance ($-1.5 < d/a < -0.5$), fifteen cases of LG/J dominance ($0.5 < d/a < 1.5$), and eleven cases of overdominance ($1.5 < d/a$). The 44 remaining QTL were considered co-dominant ($-0.5 < d/a < 0.5$). The average normalized dominance effect size (d/SD) was 0.203, but with directionality factored in, this dropped to 0.072, suggesting that overall, dominance effects average to zero, with neither LG/J nor SM/J alleles most commonly dominant.

Body size, skeletal growth, and long bone growth modules can be detected pleiotropically

Pleiotropy analysis suggested that the 81 single-trait QTL could be categorized into 26 pleiotropic and five single-trait loci, as summarized in Table 2. Of the pleiotropic loci, 9 affected all four long bones, 5 affected three of the four long bones, and 12 affected only two of the four long bones. Interestingly, ten of these last twelve pleiotropic loci affect serially homologous limb elements, either humerus and femur length (*Lbn3.3* and *Lbn10.1*) or ulna and tibia length (*Lbn1.1a*, *Lbn2.3*, *Lbn8.1*, *Lbn8.2*, *Lbn9.2*, *Lbn10.2*, *Lbn11.2*, and *Lbn12.1*). Additionally, *Lbn11.4* and *Lbn16.2* affected only forelimb components (humerus and ulna), with no QTL affecting hindlimb only (femur and tibia).

Some difficulty in discriminating multiple linked loci was encountered during pleiotropy analysis, which is performed assuming a single peak. Although some linked loci can be distinguished in the F_9 - F_{10} generations, this was not always the case. *Lbn6.1*, identified in the F_2 - F_3 analysis, was observed in the F_9 - F_{10} to be composed of two linked loci with additive effects in opposite directions (*Lbn6.1a* and *Lbn6.1b*, Table 2). However, for *Lbn1.1*, *Lbn1.2*, *Lbn2.1*, *Lbn3.2*, *Lbn10.1*, and *Lbn17.1*, QTL peaks were broad with all affected traits showing the same peak shape but with the highest point of the peak varying in position by trait. When combined with narrow confidence intervals, which in some cases did not overlap for peaks reported as pleiotropic, this led to cases where the multivariate peak did not adequately explain the results and hindered efforts to identify specific candidates for pleiotropic loci. These regions may still carry multiple genes affecting the traits.

Epistatic interactions play a large role in long bone length variation

Each pair of epistatic loci can participate in one or all of the four canonical forms of epistasis (additive-by-additive (aa), additive-by-dominance (ad), dominance-by-additive (da), and dominance-by-dominance (dd)) interactions. Thus, while we detected 72 epistatic relationships (Table S1) in this analysis, we identified a total of 155 individual interactions. This is ~3X the number of interactions identified in the F_2 - F_3 analysis (Norgard et al. 2008). Most interactions involved associations among regions not previously known to contain QTL. All four long bones were subject to epistatic interactions among loci, with humerus having 16 significant interactions, ulna having 11, femur having 19, and tibia having 26. Epistasis accounted for a much larger proportion of the phenotypic variance in this population than in the F_2 - F_3 (in which epistasis contributed ~3% to trait variance) (Norgard et al. 2008), contributing 13.5% of the phenotypic variation in the humerus, 7.7% in ulna, 13.8% in femur, and 13.2% in tibia.

Of the 155 significant interactions, 39% exhibited significant *aa* interactions, with normalized interaction values ranging from 0.108 to 0.455 SD units. The average *aa* effect size was 0.300 SD units, but when the sign of the epistatic effects was taken into account, this decreased to -0.059 SD units, indicating a balance of positive and negative epistatic effects. Additionally, 46% were significant for *ad* or *da* interactions, with normalized interaction term values ranging from 0.073 to 0.605 SD units. The average normalized *ad* or *da* effect size was 0.278 SD units, but with signs, this dropped to 0.077 SD units. Finally, 15% of the epistatic interactions had significant *dd* interaction, with normalized interaction values ranging from 0.219 to 0.564 SD units. The average normalized *dd* effect size was 0.347 SD units, but with sign taken into account, this value again dropped to 0.012 SD units. These interaction values are similar in magnitude to the single-trait *a*/SD and *d*/SD values (Table 2), but are much higher than the epistatic interaction values observed in the F₂-F₃ population (Norgard et al. 2008).

DISCUSSION

The analysis of our F₉-F₁₀ population has given us the opportunity to replicate previously detected QTLs and provided new, more resolved insight into both the genetic architecture of long bone length and the genomic regions partially responsible for the observed effects. We found that using a very dense SNP marker map to analyze advanced intercross generations led to an increase in our ability to detect and resolve QTL. The large number of QTL suggests that many genomic elements contribute to long bone length in ways not yet understood. We replicated 36 of the original 70 F₂-F₃ single trait QTL (~50%) and identified 13 new single-trait QTL at F₂-F₃ positions that did not produce significant results in the F₂-F₃ analysis, in addition to resolving 3 F₂-F₃ QTL into multiple linked loci. The probability of QTL replication varied with the LPR scores in the F₂-F₃ analysis. If the LPR score in the F₂-F₃ was low (LPR < 7.0; scores are inflated by familial autocorrelation) in the original analysis, only 16% (2 of 12) of the QTL replicated while ~70% (41 of 58) of QTL with higher LPR scores (LPR > 7.0) were replicated.

There are several reasons for QTL to fail to replicate: 1) we expect that some small portion of the F₂-F₃ QTL are false positives; 2) the Beavis effect (Beavis 1994), operating randomly in the F₂-F₃ and F₉-F₁₀, may result in different subsets of true loci exceeding the significance threshold in different replicate populations—QTLs with small effects near the detection threshold will randomly exceed or fail to reach the significance threshold in different replicates by chance, leading to an apparent lack of replication in addition to an upward bias in effect sizes; 3) we used very stringent significance thresholds in the F₉-F₁₀ requiring relatively high LPRs to be included in the mapped set; and 4) QTL detected in the F₂-F₃ may actually be due to two or more linked QTL that map separately and hence display smaller effects in the F₉-F₁₀ and therefore fail to replicate. Despite these caveats, future studies on the genetic architecture of long bone length should focus on the replicated QTLs for higher success rates.

Mean trait size and genetic correlations (Table 1) were similar in the early and later AI populations, but heritabilities were depressed. One reason for this was a strong, significant increase (~3.3X) in environmental variance that was observed between the F₂-F₃ and F₉-F₁₀ populations. The F₂-F₃ population was born and raised within a short time interval while, due to practical issues of breeding and husbandry, the F₉-F₁₀ population was born and raised over a longer period of time. The additive genetic variance of the F₉-F₁₀ population was also smaller than in the F₂-F₃ (~0.5X) but this reduction was much smaller than the observed increase in environmental variance, leading to lower heritabilities. This highlights the importance of the contribution of environment to phenotypic variation, as seemingly small changes in animal facility conditions in which both the F₂-F₃ and the F₉-F₁₀ generations were raised would not necessarily be expected to have such a large effect on heritability.

As expected, average confidence interval sizes, which were 12.8 cM for single-trait QTL in the F₂-F₃ population, were narrowed to 8.26 F₁₀ cM in the F₉-F₁₀ generation (~1.7 F₂ cM). On average, this encompasses about 35 genes in a confidence interval, compared with 275 per confidence interval in the F₂-F₃. With a large number of QTLs, as in the LG/J by SM/J cross, the confidence regions of many QTLs can be narrowed simultaneously in a single experiment, much more efficiently than the production of congenic and micro-congenic lines that treat a single QTL at a time. Additive gene effects for the F₉-F₁₀ were higher in magnitude than in the F₂-F₃, while the d/a pattern was similar but with more loci involved in dominance in the F₉-F₁₀ than the F₂-F₃. These results may be caused by the improved resolution of linked loci, allowing more accurate detection and estimation of gene effect sizes. Further evidence of our increased power was the relative lack of sex-specific QTL—of the fifteen sexually dimorphic QTL identified here, all but three were significant in both sexes, but with larger effect sizes in one sex relative to the other. Additionally, previously identified sex-specific locus *Lbn19.1_F*, affecting the tibia in females, affects all four long bones in both sexes in the F₉-F₁₀ population.

The percentage of genetic variance jointly accounted for by the single locus QTLs was 62% for the humerus, 56% for the ulna, 59% for the femur, and 53% for the tibia (from Table 1; R^2_{Main} values divided by heritabilities). These percentages are perhaps biased upwards because the heritability based on full-sib analysis contains only 50% of the total dominance variance, while it is all included in the QTL-based estimate. Such a finding is not unusual in experimental QTL studies and suggests that there are many more small effect QTLs segregating in the cross than identified here.

We found 72 loci involved in 155 significant epistatic interactions. Epistatic interactions were counted as significant only if they surpassed the significance thresholds calculated for single-trait QTL. This significance testing involved pooling the sums of squares and degrees of freedom for all four interaction terms (*aa*, *ad*, *da*, and *dd*). Most locus pairs were significant for only one or two of these terms, leading to an underestimate of epistasis. Despite this, a ~3-fold increase in the number of epistatic locus pairs was detected in the F₉-F₁₀. As in the F₂-F₃, most interactions were *aa*, followed by *ad* or *da*, with the fewest interactions being *dd*. These epistatic interactions, especially the large proportion of *aa* interactions, have a tendency to mask single-locus QTL effects in a population with generally intermediate allele frequencies (Cheverud and Routman 1996), as in the AI line analyzed here.

Epistatic interactions are responsible for ~10-15% of the genetic variation in bone length observed in the F₉-F population, as shown by the increase in the R^2 values of models for main and epistatic QTL effects combined as compared with models of only main QTL effects (Table 1). The standardized interaction values were much higher than in the F₂-F₃, but averaged to zero when the sign of the effect was taken into account. This suggests that the epistatic interactions affecting these traits are not directional. However, standardized absolute values of more than double those of the additive genetic effects, which include epistatic components, underscore the importance of epistasis in modulating long bone length.

Eight F₉-F₁₀ QTL mapped near F₂-F₃ loci previously associated with body size (Fawcett et al. 2008). Of these, half affected 3 or 4 long bones, 3 affected a single trait, and only one affected a serially homologous pair of long bones (ulna and tibia, *Lbn8.1*). These eight QTL are associated with both skeletal growth and adiposity, indicating that the genomic elements underlying these traits contribute to total body size or that the genomic region contains multiple loci influencing skeletal growth and adiposity. Also, the presence of sexually dimorphic QTL indicates interaction of QTL with sex hormones and sex-specific genomic elements known to influence total body size. The presence of QTL with overlapping effects on skeletal growth and adiposity is expected of complex, integrated phenotypes such as body size (i.e., large body size requires both large skeletal structures and more soft tissue mass than small body size).

Nine F₉-F₁₀ QTL mapped near F₂ loci associated with general skeletal growth including growth of the skull, mandible, forelimb, hindlimb, vertebrae, and sacrum (Kenney-Hunt et al. 2008). Of these nine, three influence 3 or more long bones, while the remaining six QTL affect serially homologous long bones (5 loci affecting ulna and tibia; 1 locus affecting humerus and femur) or limb-specific pairs of long bones (1 locus affecting humerus and ulna). The genomic elements underlying these QTL are expected to affect the processes of endochondral and intramembranous ossification, as both of these mechanisms contribute to general skeletal growth. The remaining nine F₉-F₁₀ QTL, which do not overlap with body size or general skeletal growth QTL, are expected to be composed of genomic elements specific for long bone growth. Overall, this analysis indicates that multiple levels of regulation (total body size vs. general skeletal growth vs. long bone-specific growth) interact to modulate long bone length.

One-third of the pleiotropic F₉-F₁₀ QTL mapped here affect serially homologous traits, the stylopod (humerus and femur) or zeugopod (ulna and tibia). This would be expected if genomic elements specific to proximal and distal limb segments were being detected. Such elements may be regulated by responses of mesenchyme to signals from the apical ectodermal ridge (AER), acting downstream of signals of proximal and distal identity in the limbs. Removal of the AER during later stages of development leads to truncation of the distal limbs (reviewed in (Mariani and Martin 2003)). Indeed, a *HoxD* gene cluster is proximal to *Lbn2.1*; the differential roles of the *HoxA* and *HoxD* gene clusters on the development of the stylopodia versus the zeugopodia have been well-established and are reviewed in (Zakany and Duboule 2007). Many other genes affecting proximal-distal patterning have also been identified (reviewed in (Mariani and Martin 2003; Tickle 2003; Robert and Lallemand 2006)). The common finding of effects on serially homologous limb segments in our population suggests that some of these QTL may interact with known proximal-distal patterning genes. Additionally, different growth plates have been observed to display different rates of growth (Wilsman et al. 1996; Wilsman et al. 2008) either different local paracrine effects or differential response of specific growth plate chondrocytes to whole body growth signals. The presence of skeletal modules could provide insight into the mechanism underlying this phenomenon. The two forelimb-specific QTL could harbor genomic elements expressed early during development, as the forelimbs bud before the hindlimbs (Mariani and Martin 2003) and/or are responsive to genes specifying forelimb identity.

Overall, the results of this and previous mapping studies of skeletal traits in this intercross (Kenney-Hunt et al. 2006; Kenney-Hunt et al. 2008; Norgard et al. 2008) suggest that the discrimination of multiple, linked QTL for long bone lengths and other skeletal traits will lead to pleiotropic patterns of potential physiological relevance. In the case of long bone lengths, it appears that many QTL affect serially homologous structures, as discussed above. This information, combined with detailed analysis of other aspects of the genetic architecture, may provide clues as to how variation in bone length arises and will guide future work to identify the biological mechanisms responsible for these QTL.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Appendix

APPENDIX 1 SNP NAMES, PHYSICAL POSITIONS, AND MAPPINGS DISTANCES

The chromosome, official name, physical position in bp, mapping distance in cM, and distance between adjacent markers in cM is given for each SNP marker in the study.

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
1	rs3683945	3187481	0.00	0.00
1	rs3658242	4133260	0.00	0.00
1	rs3677817	5176060	0.07	0.07
1	rs13475709	6646045	0.24	0.17
1	rs6321307	7664255	2.40	2.16
1	rs13475717	8812450	2.47	0.07
1	rs3698285	10014245	2.51	0.03
1	rs3697012	10886542	6.01	3.50
1	rs3681537	11919371	6.53	0.52
1	rs13475748	18906895	29.77	23.24
1	rs6334092	20149054	30.43	0.66
1	rs13475757	21272108	33.48	3.05
1	rs6361963	22619335	42.51	9.02
1	rs13475765	23769510	46.44	3.93
1	rs13475769	24846397	46.92	0.48
1	rs13475774	25989464	50.97	4.05
1	mCV25266528	27738474	51.00	0.03
1	rs3713281	28897117	51.04	0.03
1	rs13475788	29695684	51.07	0.03
1	rs4137502	30775319	52.94	1.87
1	rs3707642	32456046	53.50	0.55
1	rs13475816	37502485	80.94	27.45
1	rs3685569	38494949	82.38	1.44
1	rs3680400	39801417	87.58	5.20
1	gnf01.037.906	41039173	94.13	6.56
1	rs3663706	41958034	98.46	4.33
1	rs13475837	43055810	110.02	11.56
1	rs13475863	50661113	119.23	9.20
1	rs6217547	51878212	124.17	4.94
1	rs13475874	54390664	129.56	5.38
1	rs3653534	56753998	134.74	5.18
1	rs8238898	57999346	137.16	2.42
1	petAF067836-350A-1	58771471	139.91	2.75
1	rs6353774	59667724	149.69	9.78

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
1	rs13475894	63512708	151.27	1.58
1	rs3163007	63975386	155.20	3.93
1	rs6293581	64677041	158.51	3.32
1	rs13475896	64999299	158.51	0.00
1	rs13475902	66348120	162.98	4.46
1	rs13475903	66669378	163.08	0.10
1	rs13475906	67504991	163.08	0.00
1	rs6288543	68443591	167.93	4.85
1	rs6323094	70661423	171.06	3.12
1	rs6191076	71887420	174.93	3.88
1	rs3716722	72248019	175.77	0.83
1	rs4222426	72327598	175.77	0.00
1	rs13475919	72907188	180.04	4.27
1	mCV23057534	73531902	180.21	0.17
1	rs13475922	73672586	180.48	0.28
1	rs13475927	74835399	183.76	3.27
1	rs6405821	75170020	183.96	0.21
1	rs13475931	76258164	187.58	3.62
1	rs13475932	76444119	187.61	0.03
1	rs3715800	76774218	187.65	0.03
1	rs3703285	77452449	188.10	0.45
1	gnf01.075.385	77787777	188.20	0.10
1	rs3667200	78050737	188.24	0.03
1	rs6182343	78199098	192.27	4.04
1	rs13475939	78566739	192.27	0.00
1	rs3692514	78611654	192.27	0.00
1	rs8253473	79314371	192.31	0.03
1	rs3692549	79643707	193.00	0.69
1	mCV23431007	80204878	198.38	5.37
1	rs13475945	80469115	198.38	0.00
1	mCV23433457	80859015	200.43	2.05
1	rs6290463	81254975	200.91	0.48
1	rs13475950	81689002	202.03	1.12
1	rs13475951	81905694	202.06	0.03
1	rs6288514	83407501	206.33	4.27
1	rs4222486	84182818	207.63	1.29
1	rs3694406	88251290	210.64	3.01
1	rs13475970	90180941	213.39	2.75
1	rs13475973	91326182	216.22	2.83
1	UT-1-92.862916	92780957	221.25	5.03

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
1	rs3664800	93657926	222.79	1.55
1	rs6268443	95212994	227.74	4.95
1	rs3675505	96969374	228.75	1.01
1	rs13475997	97657605	228.78	0.03
1	rs13475999	97985866	228.82	0.03
1	rs6342650	98352409	228.82	0.00
1	rs3695980	101403319	228.92	0.10
1	rs3692731	107809343	233.04	4.12
1	rs13476036	108686329	233.21	0.17
1	rs3664301	108911373	233.21	0.00
1	rs13476044	110509119	234.05	0.83
1	rs13476045	110891823	234.08	0.03
1	rs3685919	111459291	234.74	0.66
1	rs6382744	111689041	234.74	0.00
1	rs6319405	112294079	235.19	0.45
1	CEL-1-111503693	113308942	235.23	0.03
1	rs6168275	113574021	235.23	0.00
1	mCV22824651	114148833	235.64	0.41
1	rs13476060	115417164	235.64	0.00
1	rs3725808	115976329	237.29	1.65
1	rs13476064	116419473	237.29	0.00
1	rs13476067	117088911	237.60	0.31
1	mCV24201027	117557750	237.60	0.00
1	rs13476069	117863776	237.67	0.07
1	rs3694226	118950072	241.53	3.85
1	CEL-1-117526378	119326291	241.53	0.00
1	gnf01.117.970	120137156	241.53	0.00
1	rs3695581	120568031	241.53	0.00
1	rs3719973	120901154	241.98	0.45
1	rs13476079	121208303	242.57	0.59
1	rs3686671	123756187	249.52	6.95
1	rs13476086	124051659	249.52	0.00
1	rs13476089	124494709	249.52	0.00
1	rs3717360	124828212	249.55	0.03
1	rs3694822	125672652	249.62	0.07
1	rs6189020	126447468	251.28	1.65
1	rs3687720	126839287	251.38	0.10
1	rs13476094	127123367	251.38	0.00
1	rs13476095	127412738	251.41	0.03
1	rs3090765	127692008	251.45	0.03

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
1	rs3716165	127766212	251.48	0.03
1	rs6228473	128454808	252.21	0.73
1	rs3691374	128761074	254.97	2.75
1	rs13476100	128773786	254.97	0.00
1	rs6308228	133120148	263.85	8.89
1	rs3678662	134309461	266.46	2.61
1	gnf01.132.831	135046333	269.86	3.40
1	rs13476122	136686564	271.66	1.80
1	rs13476125	137934031	276.41	4.75
1	rs6250257	139456817	278.14	1.73
1	rs13476136	140643589	280.64	2.50
1	rs6382880	144337911	285.75	5.11
1	rs6186115	146475325	287.01	1.26
1	rs13476158	147551268	288.16	1.15
1	rs3711440	149011592	288.54	0.38
1	CEL-1-148141836	149970161	289.03	0.48
1	rs3023658	151578693	290.90	1.87
1	rs6393307	152787183	291.45	0.55
1	rs3688042	153018031	291.90	0.45
1	rs6267646	154311055	294.28	2.38
1	rs3674280	154995564	294.63	0.35
1	gnf01.157.188	159616227	309.20	14.57
1	rs3709285	160871634	314.62	5.42
1	rs13476207	162943480	316.60	1.98
1	rs3685643	164086738	317.16	0.55
1	rs13476211	164897411	320.36	3.20
1	rs8256589	165903497	328.89	8.52
1	rs8242852	172887366	375.52	46.63
1	rs13476237	173538070	380.41	4.90
1	rs13476241	174698879	385.80	5.38
1	rs13476248	175988348	388.33	2.53
1	rs6213386	177168916	388.43	0.10
1	rs3723788	178021381	391.48	3.05
1	rs13476258	178819283	393.28	1.80
1	mCV23509126	182575681	403.85	10.57
1	CEL-1-182091301	183842640	407.21	3.36
1	rs6157620	185263110	411.49	4.28
1	mCV24555989	186504053	416.68	5.19
1	rs13476286	187587911	427.14	10.46
1	rs3694793	188622087	427.83	0.69

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
1	rs13476293	189964007	439.23	11.40
1	rs3654705	191036148	447.62	8.39
1	mCV23990401	191859659	455.56	7.94
1	rs13476308	193487329	462.26	6.70
1	rs13493060	194316272	462.99	0.73
1	rs13476312	195667981	464.94	1.94
2	rs13476319	3379629	0.00	0.00
2	rs6308296	4671229	3.35	3.35
2	rs3699393	5887011	3.73	0.38
2	rs6359983	6664321	4.89	1.15
2	rs13476339	8237601	14.12	9.23
2	rs13476343	9063247	14.43	0.31
2	gnf02.007.482	10474680	21.98	7.55
2	rs3688854	20199460	64.02	42.03
2	mCV23209429	31102003	113.29	49.27
2	rs13459063	32055709	113.36	0.07
2	rs13476425	34445470	113.77	0.41
2	rs6313371	39418018	125.83	12.06
2	rs13476457	41946679	126.10	0.28
2	rs13476462	43089645	126.17	0.07
2	rs3680197	44030901	127.33	1.15
2	rs13476472	45515236	133.89	6.56
2	rs13476473	45893126	133.89	0.00
2	rs13476476	46815322	134.79	0.90
2	rs3718711	56351202	155.95	21.16
2	rs6247544	57130582	156.26	0.31
2	rs13476523	58311050	162.30	6.04
2	rs3708975	59401287	169.38	7.08
2	rs3022886	62446173	179.43	10.05
2	rs8263587	69048086	205.52	26.09
2	rs13476563	69932834	209.88	4.36
2	rs6295014	71575179	215.07	5.19
2	rs6345126	72414169	220.30	5.23
2	rs3710094	74160110	225.16	4.87
2	rs3713848	75819513	231.32	6.15
2	rs6360325	77280105	235.32	4.00
2	CEL-2-79237503	79144282	237.85	2.53
2	rs13476598	80824240	242.17	4.32
2	mCV23002990	82350941	247.83	5.67
2	gnf02.082.243	83404108	247.87	0.03

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
2	rs8273639	84573173	247.90	0.03
2	mCV24333820	87411316	249.13	1.22
2	rs6314788	88147138	249.13	0.00
2	rs3715323	89381357	249.75	0.62
2	rs13476631	90279980	249.75	0.00
2	rs13476637	91746329	250.44	0.69
2	rs13476640	92774981	250.69	0.24
2	rs6252400	94050785	252.20	1.51
2	rs13476647	95399411	254.65	2.46
2	rs6220079	97286584	254.96	0.31
2	rs13476660	99017841	259.16	4.19
2	rs6406705	100160818	260.67	1.51
2	rs13476667	101384787	261.64	0.98
2	rs6275228	102143201	261.68	0.03
2	rs13469470	103251340	265.18	3.50
2	rs3674721	104502169	266.98	1.80
2	rs3715478	105989630	268.20	1.22
2	rs6208879	109583535	272.98	4.78
2	rs3658023	110615020	273.01	0.03
2	rs3681694	112085690	274.20	1.19
2	CEL-2-113459249	113369113	276.87	2.68
2	rs3701250	114572438	283.14	6.27
2	rs3708146	115697820	286.95	3.81
2	rs13476723	116984238	293.31	6.36
2	rs3725853	117950419	294.18	0.87
2	rs3661254	119200614	294.35	0.17
2	rs3718386	120453485	294.38	0.03
2	rs6317255	121597502	295.82	1.44
2	rs13476746	122602507	295.86	0.03
2	rs13476750	123346917	295.93	0.07
2	rs6401493	124989214	299.17	3.24
2	rs13476761	127158432	300.39	1.22
2	rs6411422	128064932	300.56	0.17
2	rs6318992	128955495	303.47	2.90
2	rs3661596	129836256	305.19	1.73
2	rs13476774	131106484	306.99	1.80
2	rs13476787	134831202	316.29	9.30
2	rs13476790	135335424	319.53	3.24
2	rs13476794	136433405	321.84	2.31
2	rs6249968	137483864	328.88	7.04

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
2	rs6200333	138760978	331.37	2.49
2	rs6303304	141134756	337.37	6.00
2	rs13476811	142406167	338.34	0.98
2	rs6195594	143286177	338.38	0.03
2	mCV23169908	145578041	344.54	6.17
2	rs3701696	147120170	347.45	2.91
2	rs3676033	149136720	358.84	11.39
2	rs13476846	152722877	372.60	13.76
2	rs6209403	153731653	391.24	18.64
2	rs13476860	155958918	417.75	26.51
2	UT-2-158.095429	157161264	418.40	0.66
2	gnf02.161.674	158432220	419.45	1.05
2	rs6204920	161431812	435.09	15.64
2	rs3673613	162543107	439.49	4.40
2	rs3697980	163703933	441.65	2.16
2	rs6185704	164644730	447.98	6.33
2	rs13476894	165742632	456.31	8.33
2	rs6160839	168657891	462.76	6.45
2	rs3689258	169179105	464.38	1.62
2	rs13476925	172917631	502.18	37.79
2	rs8238755	174061449	505.30	3.13
2	rs13476936	179137491	515.24	9.94
2	rs13476944	180856846	523.45	8.20
2	rs6402916	181736931	524.21	0.76
3	rs13476950	3771070	0.00	0.00
3	rs13476954	4769220	0.00	0.00
3	rs13476958	5887356	0.10	0.10
3	rs6274760	6996087	0.14	0.03
3	rs13476964	7905200	1.40	1.26
3	rs3668064	9252892	2.02	0.62
3	rs13476970	10001205	2.68	0.66
3	rs13476974	11101846	4.26	1.58
3	rs3694133	12484309	4.26	0.00
3	rs6172421	13625765	6.42	2.16
3	rs13476985	14864639	9.32	2.90
3	rs13476992	17111202	14.73	5.41
3	rs3689046	18302686	15.25	0.52
3	rs13477007	20649337	22.54	7.29
3	rs6235984	21722530	27.43	4.89
3	rs13477017	22799153	28.87	1.44

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
3	rs3677132	28111276	35.52	6.65
3	CEL-3-31146697	31559021	45.90	10.38
3	rs6351323	32655781	47.62	1.73
3	rs4223864	33135377	49.24	1.62
3	rs3720738	36179337	63.41	14.17
3	rs13477066	38590402	78.37	14.96
3	gnf03.036.164	39508386	78.99	0.62
3	rs13477072	40651105	84.27	5.27
3	CEL-3-46558020	46650247	85.67	1.40
3	rs3671459	50220254	97.32	11.64
3	rs3719360	51351249	99.70	2.38
3	rs6335414	53105788	109.56	9.86
3	gnf03.051.000	54365744	110.25	0.69
3	rs13477123	56116839	118.09	7.84
3	rs13477127	57043340	122.40	4.31
3	rs6363066	57911222	125.90	3.50
3	rs13477144	61356178	133.77	7.86
3	rs6176848	62162621	134.36	0.59
3	rs13477154	63727868	134.98	0.62
3	rs3674810	68230731	143.84	8.86
3	rs13477178	69832783	145.45	1.62
3	rs3659688	70943247	147.84	2.38
3	rs3715136	72478400	147.84	0.00
3	rs4137345	73309724	148.32	0.48
3	gnf03.073.308	76319796	154.70	6.37
3	rs3726567	77543251	156.10	1.40
3	rs13477217	78785784	156.44	0.35
3	rs3659866	80978466	160.26	3.81
3	rs3685286	81581113	167.85	7.59
3	rs13477230	82887966	170.27	2.42
3	rs3708227	84111778	170.79	0.52
3	rs6243021	85230294	175.66	4.87
3	rs13477242	86169224	175.76	0.10
3	rs13475064	88995879	179.08	3.32
3	rs13477254	90176699	183.88	4.80
3	UT-2-93.461287	90846829	186.30	2.42
3	rs13477261	922048^1	188.47	2.17
3	rs13459185	96031920	198.38	9.91
3	rs13477276	97017412	201.70	3.32
3	rs13477279	98070220	204.16	2.46

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
3	UT-3-102.173433	99481704	206.10	1.94
3	rs3162061	100848755	206.66	0.55
3	rs3671622	102510897	209.56	2.91
3	rs3701653	103763188	210.22	0.66
3	rs13477307	104697802	212.98	2.76
3	rs13477309	105598460	214.45	1.48
3	rs13477313	106612799	215.39	0.94
3	rs3684333	107598757	215.43	0.03
3	rs8256683	110107608	223.68	8.25
3	rs3676545	110384367	224.23	0.55
3	rs3711702	111440782	225.71	1.48
3	rs13477355	116103024	233.30	7.59
3	rs13477364	118579161	257.04	23.74
3	rs13477379	122829730	271.17	14.14
3	rs3707706	124007345	277.36	6.19
3	rs13477384	124800689	277.71	0.35
3	rs8255228	125906837	277.77	0.07
3	rs13477391	127151056	285.36	7.59
3	rs3670168	128284556	287.46	2.09
3	rs13477400	129378766	291.66	4.20
3	rs3658914	130817194	302.73	11.07
3	rs134774101320	132004220	307.44	4.71
3	rs13477421	134179590	323.71	16.27
3	gnf03.138.849	135371859	324.16	0.45
3	CEL-3-137067761	136454912	331.49	7.33
3	rs13477438	137745404	333.69	2.20
3	rs13477448	139891637	338.67	4.98
3	rs6189225	141334190	339.78	1.12
3	rs4224277	142510122	343.63	3.85
3	CEL-3-145329096	144699660	354.89	11.26
3	rs13477529	146019141	358.90	4.01
3	rs13477477	147263250	364.18	5.28
3	rs3722447	148883059	369.77	5.60
3	rs13477488	150333553	376.94	7.16
3	rs13477494	151501707	382.04	5.11
3	rs3695139	152299755	384.50	2.46
3	rs3695386	155718002	395.39	10.89
4	rs13477541	6320883	0.00	0.00
4	rs13477546	7682681	1.98	1.98
4	rs13477550	8920439	3.96	1.98

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
4	rs6324271	10242308	7.93	3.97
4	rs13477558	10825524	7.93	0.00
4	rs13477569	13886135	20.61	12.68
4	rs13477576	15649659	24.31	3.70
4	rs13477595	20609933	39.35	15.03
4	gnf04.018.158	21507449	39.62	0.28
4	rs13477608	24075914	42.04	2.42
4	rs4224426	25340958	43.09	1.05
4	rs3681849	26554443	44.82	1.73
4	rs13477621	28107054	46.94	2.13
4	rs13477623	29747076	57.24	10.30
4	rs13477625	30201791	57.80	0.55
4	CEL-4-30832818	30770256	58.53	0.73
4	gnf04.029.494	33074980	59.64	1.12
4	CEL-4-34055416	34152669	65.28	5.63
4	rs3719299	36318399	73.61	8.34
4	rs13477649	37079405	76.25	2.64
4	rs3684104	38511591	79.76	3.51
4	rs13477659	39400829	80.21	0.45
4	CEL-4-40541402	40638655	81.26	1.05
4	rs4138630	41845694	85.49	4.24
4	rs6321462	43671949	86.51	1.01
4	rs13477678	45510532	94.18	7.67
4	rs3707178	47057244	95.83	1.65
4	rs3663355	48134434	99.19	3.36
4	rs13477694	49609693	103.39	4.20
4	CEL-4-51636888	52412942	113.83	10.44
4	rs134777115392358611	53923586	114.81	0.98
4	rs3677770	54740583	119.00	4.20
4	rs13477725	57707764	132.27	13.26
4	UT-4-58.126445	58468079	135.85	3.58
4	rs3671277	59538592	136.33	0.48
4	rs13477738	62515930	140.93	4.59
4	rs13477741	63715217	140.93	0.00
4	gnf04.062.327	66202605	144.66	3.74
4	rs6370644	70029285	153.53	8.87
4	rs13477769	72022109	153.67	0.14
4	rs13477773	72841912	153.67	0.00
4	rs6292114	74453443	154.26	0.59
4	rs3708471	76341959	156.06	1.80

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
4	rs3669136	78110189	157.53	1.47
4	CEL-4-78089985	79286970	159.51	1.98
4	rs2020477	80567883	160.28	0.76
4	rs6323325	81878165	163.71	3.43
4	rs3700579	83410542	164.44	0.73
4	rs13477816	84795527	170.56	6.12
4	rs3707373	86404414	171.43	0.87
4	CEL-4-86185890	87382670	173.89	2.46
4	rs13477831	88422961	178.91	5.03
4	rs13477849	94100559	188.05	9.14
4	rs13477854	95311468	189.88	1.84
4	CEL-4-95976899	97138641	196.17	6.29
4	rs6255772	98365517	200.49	4.32
4	rs13477868	99462176	202.66	2.16
4	rs13477873	100928177	203.45	0.80
4	rs13477876	101891210	203.49	0.03
4	rs13477882	103146992	207.00	3.51
4	rs13477886	104205257	209.53	2.53
4	rs13477893	105797445	214.61	5.08
4	rs3709496	107329290	216.73	2.13
4	rs3670382	110339061	222.09	5.35
4	mCV22668736	112158476	222.09	0.00
4	rs3687391	113862670	224.81	2.72
4	rs3022993	114984900	226.86	2.05
4	mCV24303778	115750410	227.27	0.41
4	rs6173859	117070664	234.08	6.80
4	rs3678308	120241930	243.18	9.10
4	CEL-4-120039566	121191835	244.22	1.05
4	rs13477952	122454188	244.26	0.03
4	rs3677161	124342657	252.16	7.90
4	rs13474356	124570462	252.16	0.00
4	rs13477968	126899605	256.80	4.64
4	rs4138996	128379877	259.29	2.50
4	rs3698956	129600819	262.24	2.94
4	rs3673061	130629841	263.93	1.69
4	rs4224808	132272311	265.30	1.37
4	rs13477991	133151575	267.06	1.76
4	rs3663950	135001608	282.99	15.93
4	rs3023025	142449103	343.07	60.08
4	rs4136314	144312174	347.93	4.85

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
4	UT-4-146.099338	146830181	353.46	5.53
4	UT-4-147.232882	147963725	355.07	1.62
4	rs3720325	148605726	355.84	0.76
4	rs13478051	149791893	356.60	0.76
4	rs6378384	152404852	366.90	10.30
4	rs3696703	154069473	377.05	10.15
4	rs3720634	154751394	380.56	3.51
5	rs13478093	3974781	0.00	0.00
5	rs6190354	4864920	1.08	1.08
5	rs3709946	6795772	1.67	0.59
5	rs13478104	7981730	2.19	0.52
5	rs6410022	8922546	2.22	0.03
5	rs3676096	10677084	3.99	1.76
5	rs3714258	12377163	5.75	1.76
5	mCV25284008	13097986	6.27	0.52
5	rs13478133	21126070	45.03	38.76
5	rs4225096	23919594	51.82	6.79
5	rs13478148	24864581	54.53	2.72
5	rs3718492	32333638	77.59	23.05
5	rs13478175	33905036	79.57	1.98
5	rs13459085	35225633	79.67	0.10
5	rs13478184	36367399	81.47	1.80
5	rs13478204	40964302	89.54	8.07
5	rs13478217	44452843	98.14	8.60
5	rs13478223	45644545	102.15	4.01
5	CEL-5-45872918	47536005	104.31	2.16
5	rs6248036	53097028	119.84	15.53
5	rs3711950	64291534	142.15	22.31
5	rs6267669	66781760	152.21	10.05
5	rs3684754	67639329	156.02	3.82
5	rs3691938	68545648	156.96	0.94
5	rs6409508	73407447	167.14	10.18
5	gnf05.069.163	75160364	171.41	4.27
5	rs6221589	75984771	174.35	2.94
5	rs6257272	77961975	183.45	9.11
5	rs3662055	79468514	185.07	1.62
5	rs3658150	80866440	185.10	0.03
5	rs13478352	82205070	188.49	3.38
5	rs13478355	83234453	190.07	1.58
5	rs13478361	84456375	190.07	0.00

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
5	rs3678577	85710555	190.10	0.03
5	rs13478370	86535759	191.97	1.87
5	rs13459087	88166641	193.51	1.54
5	rs3667067	89312201	193.51	0.00
5	rs13478383	90456154	195.82	2.30
5	rs3716445	91725791	200.35	4.53
5	rs13478392	92825965	205.64	5.29
5	UT-5-94.545323	94250929	206.12	0.48
5	rs13478400	96076599	206.16	0.03
5	rs3661241	98077658	212.38	6.22
5	rs6350578	106535278	230.91	18.53
5	rs13478447	107644645	232.49	1.58
5	rs13478451	108895064	233.65	1.15
5	rs3658755	113008644	240.30	6.65
5	rs13478473	114471987	242.24	1.94
5	UT-5-114.525467	115715070	247.54	5.30
5	gnf05.110.207	116367455	247.54	0.00
5	mCV22554962	117828709	253.71	6.17
5	rs3662655	118521108	259.93	6.22
5	rs13478487	119569248	263.21	3.28
5	rs8239888	121828493	274.77	11.56
5	CEL-5-120064766	122811451	278.27	3.51
5	rs13478501	124051672	280.14	1.87
5	rs13478509	125804739	280.91	0.76
5	rs3701266	126973082	284.53	3.62
5	rs13478522	128787589	292.63	8.10
5	rs6377710	132660907	316.47	23.84
5	rs13478539	133347411	318.41	1.94
5	rs13478540	134329694	323.04	4.63
5	rs3023058	136114083	332.76	9.72
5	rs3711751	137202743	338.97	6.21
5	rs6393330	139131517	351.77	12.80
5	rs3023061	144184811	384.26	32.49
5	mCV25009162	144789685	385.70	1.44
5	rs4225575	145435430	390.33	4.63
5	mCV22895274	146892805	391.56	1.22
5	rs13478589	148511763	418.66	27.11
5	rs3718776	149859031	420.68	2.02
5	rs13478595	150614341	420.68	0.00
6	rs13478602	3797193	0.00	0.00

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
6	rs13478608	5219016	2.06	2.06
6	rs13478612	6508473	2.78	0.73
6	rs13478615	7222703	2.85	0.07
6	CEL-6-9421791	9639647	7.41	4.56
6	CEL-6-10519419	10733840	7.72	0.31
6	rs13478631	11226305	8.56	0.83
6	rs3655979	13135398	12.22	3.66
6	rs3678711	14239843	14.46	2.24
6	rs13478641	16011005	18.32	3.86
6	UT-6-18.199327	18272206	20.15	1.84
6	gnf06.016.989	19886053	22.95	2.79
6	rs3710004	23153568	31.09	8.14
6	rs3684494	24365688	33.58	2.50
6	rs13478667	25547631	36.30	2.72
6	rs13478671	26419444	37.42	1.12
6	rs13478676	27605718	38.47	1.05
6	rs13478681	28755006	40.26	1.80
6	rs13478693	31993167	41.77	1.51
6	rs6303641	33443594	43.79	2.02
6	rs6297560	34583476	48.85	5.06
6	gnf06.032.524	35461927	51.13	2.27
6	gnf06.033.454	36415492	53.92	2.79
6	rs13478717	37619186	56.75	2.83
6	rs13478719	38474947	58.66	1.91
6	gnf06.037.785	40728903	62.39	3.74
6	rs13478726	42331878	70.17	7.78
6	rs13478727	43756420	71.11	0.94
6	rs13478730	44956026	72.84	1.73
6	rs3684860	48915623	88.54	15.70
6	rs3023069	52172725	102.92	14.38
6	rs13478759	53309941	103.37	0.45
6	rs13478762	54155255	112.53	9.16
6	gnf06.058.959	59736319	118.74	6.20
6	rs6378343	63752662	121.49	2.76
6	rs8270116	65047471	122.43	0.94
6	rs13478818	73032676	134.24	11.80
6	rs6411497	75444437	137.67	3.43
6	rs13478833	76560177	139.18	1.51
6	rs13478839	77741032	147.83	8.65
6	rs13478845	78926735	150.77	2.94

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
6	rs13478853	80505315	154.13	3.36
6	rs4226024	81923883	156.59	2.46
6	CEL-6-83434907	83163032	157.67	1.08
6	rs13459097	84855960	161.14	3.47
6	CEL-6-86437630	86074562	162.19	1.05
6	rs3677567	87237718	162.92	0.73
6	rs13478880	88552728	165.45	2.53
6	rs13478882	89630674	167.21	1.76
6	rs6156752	90739207	170.00	2.79
6	rs6223362	92585998	181.85	11.85
6	gnf06.092.758	93829424	185.36	3.51
6	gnf06.093.201	94270950	187.78	2.42
6	rs13478949	105099432	232.96	45.18
6	rs13478952	106271276	233.52	0.55
6	gnf06.105.887	107031044	233.62	0.10
6	gnf06.107.451	108615463	237.13	3.51
6	rs13478965	109423023	237.20	0.07
6	rs13478969	110721818	241.05	3.85
6	rs13478974	111946505	244.75	3.70
6	rs6393943	114372840	251.45	6.70
6	rs6204829	115881154	254.66	3.20
6	mCV23042866	116722348	254.66	0.00
6	rs13478999	118767628	261.73	7.07
6	rs3722157	122383727	269.96	8.23
6	gnf06.122.747	124022113	271.50	1.55
6	UT-6-127.071239	125109990	276.25	4.74
6	CEL-6-127435117	126769948	285.36	9.12
6	rs13479024	127557206	286.41	1.05
6	rs3662241	129575852	289.72	3.32
6	rs3654483	130451567	289.76	0.03
6	rs3721822	131273852	289.79	0.03
6	rs3704289	131956146	289.93	0.14
6	CEL-6-132620146	132514422	289.96	0.03
6	mCV22521691	132829073	289.96	0.00
6	rs3655878	133597942	290.00	0.03
6	rs13479051	133820643	295.67	5.67
6	rs6339546	133933426	296.26	0.59
6	rs13479053	134216927	298.13	1.87
6	rs13479055	134587480	298.27	0.14
6	rs3671932	134823803	298.27	0.00

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
6	rs13479058	135287793	301.18	2.91
6	rs13479059	135625864	301.18	0.00
6	rs3711652	135943958	301.91	0.73
6	rs3704502	136223652	302.42	0.52
6	rs13479064	136576443	302.46	0.03
6	rs13479066	136905048	302.80	0.35
6	rs13479070	137944102	306.05	3.24
6	rs13479071	138219207	306.05	0.00
6	rs6261913	138613864	306.08	0.03
6	rs6255954	139025943	308.32	2.24
6	gnf06.139.257	139141854	309.02	0.69
6	rs6288584	139483929	309.40	0.38
6	rs3664540	140080496	309.67	0.28
6	rs6199136	140401643	310.09	0.41
6	rs8268650	141494615	310.15	0.07
6	rs6329892	142377540	312.32	2.16
6	rs6235887	142681574	312.98	0.66
6	rs6391555	142960186	313.29	0.31
6	rs4226359	143254941	313.29	0.00
6	rs6152631	144011272	320.33	7.04
6	rs6386657	144271273	320.33	0.00
6	rs13479084	144462102	323.34	3.01
6	rs4140069	144823129	328.16	4.82
6	rs13459098	145131829	328.65	0.48
6	rs13479086	145252975	328.68	0.03
6	rs6387265	145702488	329.27	0.59
6	rs3023105	146433967	335.31	6.04
6	rs3712253	146700209	335.34	0.03
6	rs13479099	147156396	335.34	0.00
6	rs6265387	147212027	335.34	0.00
7	CEL-7-6502564	12748874	0.00	0.00
7	rs6295100	15619858	6.05	6.05
7	UT-7-14.584506	16839985	9.55	3.50
7	UT-7-16.347574	18515217	9.55	0.00
7	CEL-7-12787527	23760916	11.10	1.54
7	rs13479154	25000014	15.80	4.70
7	rs13479163	26776607	32.29	16.50
7	CEL-7-16849862	27602326	38.70	6.41
7	rs13479171	28858955	39.12	0.41
7	rs13479174	29731663	51.73	12.62

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
7	CEL-7-20534424	31218721	58.88	7.14
7	CEL-7-21610843	33237086	58.88	0.00
7	rs3694031	34623640	64.45	5.58
7	rs6217275	36135464	74.05	9.60
7	gnf07.032.360	40170634	85.76	11.71
7	rs4232449	41099523	90.94	5.18
7	rs6316536	43372300	91.98	1.05
7	rs3719256	44406689	93.96	1.98
7	rs3689409	44873964	98.63	4.66
7	rs3717293	55844999	126.46	27.83
7	rs3696018	56975004	129.18	2.72
7	rs13479276	58330022	129.21	0.03
7	rs3693478	59914044	135.09	5.88
7	gnf07.056.997	62429428	135.12	0.03
7	rs3679779	64279234	135.26	0.14
7	rs6160140	66160238	136.81	1.55
7	rs3667441	67507017	139.19	2.38
7	rs6296859	68855004	142.06	2.87
7	rs3723790	70038472	150.59	8.52
7	rs13479325	71171778	157.09	6.50
7	rs3676254	72559778	159.81	2.72
7	mCV25303361	73482627	163.86	4.05
7	rs13479342	74842909	167.90	4.05
7	rs13479347	76161186	170.47	2.57
7	rs13479351	77371729	170.47	0.00
7	rs3686423	79456771	176.23	5.76
7	rs8248433	80376099	177.78	1.55
7	rs3663343	81412766	178.93	1.15
7	rs6213614	82158286	182.18	3.24
7	rs13479376	84324548	183.01	0.83
7	CEL-7-73288107	86002592	183.01	0.00
7	rs13479385	87009942	183.01	0.00
7	rs3663323	88187474	184.31	1.30
7	rs13479393	89283087	186.77	2.46
7	CEL-7-77948585	90591215	188.42	1.65
7	rs3663374	91328843	191.07	2.64
7	rs3683030	92968513	197.20	6.14
7	rs6224196	95042288	204.91	7.70
7	UT-7-90.803899	99210626	214.91	10.01
7	rs13479427	99902832	216.07	1.15

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
7	rs13479429	101045112	217.22	1.15
7	rs3713052	101643497	220.34	3.13
7	rs13479437	103060554	221.75	1.40
7	rs3662937	104106798	221.78	0.03
7	rs13459173	105510122	222.68	0.90
7	rs3711721	107017200	224.12	1.44
7	rs6315049	108844312	224.43	0.31
7	rs13479457	110222539	225.66	1.22
7	rs13479461	111739733	227.89	2.24
7	rs3726290	113143517	228.41	0.52
7	rs13479470	114490155	228.96	0.55
7	rs3656074	115925415	233.21	4.24
7	gnf07.120.460	123365567	260.99	27.79
7	rs13479507	124682503	268.40	7.41
7	rs6403908	125889384	271.24	2.83
7	rs6177803	127116226	274.49	3.25
7	CEL-7-116160192	128473185	280.26	5.78
7	rs8236684	130822289	286.07	5.81
7	rs3719258	134524389	318.77	32.69
7	CEL-7-126301023	138501575	343.89	25.13
7	rs6299045	140005209	349.79	5.89
7	rs3702894	142161252	353.80	4.02
7	rs6176332	143287287	355.71	1.91
7	rs6216320	144991090	360.36	4.64
8	rs6273176	7850079	0.00	0.00
8	rs13479601	9055795	1.40	1.40
8	rs6288205	12246821	17.12	15.72
8	rs6287472	13314046	17.74	0.62
8	rs6410533	14301441	18.58	0.83
8	rs13479624	16859124	33.90	15.33
8	rs13479628	18316424	40.87	6.96
8	CEL-8-25677705	28357852	62.06	21.19
8	rs13479769	56099587	128.57	66.51
8	rs13479776	59270814	136.09	7.51
8	UT-8-57.168981	60348175	143.77	7.68
8	rs13479784	61653365	147.77	4.00
8	rs6398181	63107823	147.94	0.17
8	rs3672639	64113928	148.01	0.07
8	rs6394046	65395936	152.44	4.43
8	rs13479799	66453039	153.45	1.01

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
8	gnf08.064.413	67774204	154.46	1.01
8	rs3694940	68800962	154.46	0.00
8	rs13479811	69982295	155.90	1.44
8	rs13479814	71250525	159.41	3.51
8	rs3698093	80921407	179.13	19.72
8	rs6296891	82880019	183.88	4.76
8	rs3696786	83897536	186.19	2.31
8	rs13479860	85157384	186.75	0.55
8	rs4227283	86162738	187.58	0.83
8	UT-8-84.8318	86859920	189.09	1.51
8	rs13479873	88120817	193.41	4.32
8	rs13479879	89399073	194.17	0.76
8	rs3682243	90223661	194.52	0.35
8	rs3705695	98245251	215.50	20.98
8	rs6374927	114518266	290.04	74.54
8	rs6347490	119458949	316.20	26.15
8	rs3675125	125136019	344.64	28.45
8	rs13480022	125341117	351.01	6.37
8	rs13480023	125648980	351.46	0.45
8	rs13480024	125780328	351.49	0.03
8	rs3693295	125833783	351.49	0.00
8	rs4227429	126154807	351.49	0.00
8	rs8249856	126856145	351.94	0.45
8	rs8238636	127443134	352.32	0.38
8	rs6300613	128333199	352.81	0.48
8	UT-8-130.396331	131389274	359.97	7.16
9	rs13480065	9252350	0.00	0.00
9	mCV25073238	10534851	1.94	1.94
9	rs13480073	13179717	7.03	5.09
9	gnf09.009.970	15442495	9.52	2.49
9	rs13480112	26355793	31.64	22.11
9	rs6182405	27593903	34.17	2.53
9	petM-05537-1	28872451	46.46	12.29
9	CEL-9-29909656	29690406	49.62	3.16
9	rs13480130	33041069	64.17	14.55
9	rs3711756	34208409	65.86	1.69
9	rs13480138	35265783	73.49	7.63
9	mCV25302097	36184291	73.53	0.03
9	rs3719607	36949517	73.70	0.17
9	rs3694949	38206132	74.39	0.69

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
9	rs3675289	39460687	75.47	1.08
9	rs13480153	40426603	78.37	2.90
9	rs3676086	42592846	88.43	10.06
9	rs13480166	43822743	93.86	5.42
9	rs13480172	45988349	97.32	3.47
9	rs3673816	46982807	98.16	0.83
9	rs13480180	48172738	102.55	4.39
9	gnf09.044.276	49729098	104.35	1.80
9	rs13480191	50908883	116.54	12.20
9	rs13480194	52065162	122.37	5.83
9	rs13480198	53044520	123.85	1.47
9	rs8259443	53963733	126.64	2.79
9	rs3660104	54782339	128.00	1.37
9	rs6334600	56337386	129.76	1.76
9	rs13480218	57786985	137.21	7.45
9	rs6154433	58988608	137.32	0.10
9	rs13480227	60848809	145.48	8.17
9	rs13480232	61964183	150.94	5.46
9	rs13480236	63005996	156.35	5.42
9	rs3664300	64251169	156.56	0.21
9	rs13480247	65344248	162.22	5.66
9	rs3670579	66705910	163.91	1.69
9	rs3716689	67912998	167.18	3.27
9	rs13480258	68691173	177.31	10.13
9	rs3703045	70112134	179.80	2.49
9	rs13459110	71281792	182.15	2.34
9	rs3711813	72161148	183.02	0.87
9	rs13480273	73069886	189.38	6.36
9	rs3724833	74674675	199.95	10.57
9	mCV25328470	75830214	200.26	0.31
9	rs13480288	77185425	201.06	0.80
9	rs3658458	80089158	203.81	2.75
9	rs3670195	81062720	205.50	1.69
9	rs13480312	83590729	212.89	7.38
9	rs13480315	84770251	212.95	0.07
9	rs13480318	86104312	214.21	1.26
9	rs6182207	87235216	217.49	3.28
9	gnf09.087.298	90481092	220.32	2.83
9	rs6202847	91495575	221.80	1.47
9	CEL-9-92503233	92463575	224.74	2.94

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
9	rs13480351	94088160	228.13	3.40
9	rs3690580	95160132	234.25	6.12
9	rs13480367	98732369	234.98	0.73
9	gnf09.096.289	99563108	235.02	0.03
9	rs6190068	101474936	237.51	2.49
9	rs3657346	103029321	238.27	0.76
9	rs13480387	103783418	238.90	0.62
9	rs3711089	105349763	244.33	5.43
9	rs3723953	110881584	264.78	20.45
9	rs6320810	115004672	295.89	31.11
9	rs3669563	117767462	302.17	6.28
9	rs6316481	118823143	309.94	7.76
9	rs13480454	120546536	316.10	6.16
9	rs6299531	122773921	322.34	6.25
9	rs8241505	123639001	327.34	4.99
10	rs13480510	15772078	0.00	0.00
10	rs13480516	17202854	2.64	2.64
10	rs3703211	18226351	3.16	0.52
10	rs13480527	19305720	6.63	3.47
10	rs13480531	20462900	12.12	5.49
10	rs13480536	21623321	15.28	3.16
10	rs3679120	22610695	21.90	6.62
10	rs13480547	24176978	30.17	8.27
10	rs3672342	25383512	30.65	0.48
10	rs13459121	26487123	36.46	5.81
10	rs3023233	28285463	52.68	16.22
10	rs13459120	35728463	73.25	20.56
10	rs13480601	43994834	101.01	27.77
10	rs6212358	45807465	102.38	1.37
10	rs3676667	46640996	103.71	1.33
10	rs3715820	48252306	103.85	0.14
10	rs6164020	49436630	105.00	1.15
10	rs6186864	52416044	106.87	1.87
10	rs6243167	54472874	110.53	3.66
10	rs6374078	60500677	129.42	18.89
10	rs6312070	62470059	133.23	3.82
10	rs6335027	64756252	138.99	5.75
10	rs13480630	67216450	140.46	1.47
10	rs13480638	68840024	147.44	6.98
10	rs6295890	72043098	153.66	6.23

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
10	rs13480652	74056142	159.60	5.94
10	rs13480678	84115180	173.63	14.03
10	rs13480684	85302383	174.82	1.19
10	rs13480687	86526277	183.43	8.61
10	gnf1 0.087.008	87455489	183.84	0.41
10	rs3701829	88763846	198.09	14.25
10	mCV25373751	90138990	198.19	0.10
10	rs13480703	90847609	200.83	2.64
10	rs3661495	92087950	209.19	8.36
10	rs13480712	92946034	215.25	6.06
10	rs3704401	98672238	229.21	13.96
10	rs6390581	99258280	229.28	0.07
10	rs3710293	99544486	229.62	0.35
10	rs6185093	100172778	232.19	2.57
10	rs13480734	101805079	235.35	3.16
10	rs13480739	103152390	238.62	3.28
10	rs13480740	103482886	238.62	0.00
10	rs3688351	103920166	239.53	0.90
10	rs3716899	104373161	239.53	0.00
10	rs13480745	104588949	239.53	0.00
10	rs3716443	104916467	239.81	0.28
10	rs13480749	105404705	240.15	0.35
10	rs13480752	106234197	241.55	1.40
10	rs3654717	106608140	242.00	0.45
10	rs13480754	106888238	242.56	0.55
10	rs6174062	108931790	246.18	3.62
10	rs6293699	109544937	248.12	1.94
10	rs4228452	110698362	249.24	1.12
10	rs6353445	111098211	250.64	1.40
10	rs13480766	111287511	253.96	3.32
10	CEL-10-113177617	112803963	257.20	3.24
10	rs13480773	114146219	264.73	7.53
10	rs6201222	114277985	264.87	0.14
10	rs4228477	114482945	264.90	0.03
10	rs6363315	116258586	271.10	6.19
10	CZECH-10-116791624	116400103	271.10	0.00
10	rs6335076	116549811	271.10	0.00
10	rs3670118	116797981	273.00	1.91
10	rs6256918	116955805	273.25	0.24
10	rs6284081	117526565	273.87	0.62

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
10	rs6317716	118880363	277.95	4.08
10	rs3659572	119469405	282.65	4.70
10	rs13480792	119810882	282.85	0.21
10	rs6197175	120097023	285.49	2.64
10	rs13480793	120431114	285.60	0.10
10	rs6197961	121264519	289.83	4.23
10	rs13480797	121330793	289.83	0.00
10	rs13480808	123799692	301.55	11.72
10	rs4140243	124240424	302.21	0.66
10	rs13480811	124510365	302.21	0.00
10	gnf10.124.898	124894140	304.85	2.64
10	rs6281696	124990091	304.95	0.10
10	rs3697243	126215960	305.89	0.94
10	rs13480821	126900861	308.72	2.82
10	rs6290842	128518968	313.69	4.97
11	rs13480835	3234216	0.00	0.00
11	rs3682937	4580335	1.51	1.51
11	rs6393401	5771105	2.63	1.12
11	rs13480853	7315081	5.34	2.72
11	rs3661631	9234548	8.47	3.13
11	rs13480869	10903789	12.12	3.66
11	rs13480880	13332444	16.40	4.27
11	rs3724116	14612721	18.05	1.65
11	rs3689494	16181190	24.73	6.68
11	rs3658216	19463110	49.79	25.06
11	rs6393028	20753810	55.14	5.36
11	rs3154937	21470891	56.40	1.26
11	rs3661074	22652480	57.52	1.12
11	rs13480913	23633252	57.55	0.03
11	rs13480918	25018970	65.32	7.77
11	rs3719024	26370846	67.30	1.98
11	rs6276300	27148057	69.39	2.09
11	UT-11-29.443258	29445002	78.64	9.25
11	rs3707274	31821624	86.53	7.88
11	rs3710499	33611128	88.62	2.09
11	rs3690160	36858486	108.40	19.78
11	rs13480993	42760802	119.69	11.29
11	gnf1 1.045.072	43286588	121.96	2.27
11	rs3660692	46059444	138.77	16.81
11	rs6250130	47319541	146.21	7.44

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
11	rs6326787	48554234	150.41	4.20
11	rs6199956	50588690	154.37	3.97
11	rs13481023	51854721	155.35	0.98
11	rs6398148	52932157	157.08	1.73
11	rs13481031	54262014	157.63	0.55
11	rs3684076	56254330	167.73	10.10
11	rs3023260	57090732	172.47	4.74
11	rs3697686	58383745	175.93	3.46
11	rs13481050	60570259	180.40	4.46
11	rs3675335	62294912	182.93	2.53
11	rs3714311	64087574	195.15	12.22
11	rs13481068	64598818	196.51	1.37
11	rs13481075	66318908	201.86	5.35
11	rs6262977	67708611	202.07	0.21
11	rs3658906	68925261	202.55	0.48
11	UT-11-70.128831	70373860	208.59	6.04
11	rs13481090	71224856	211.35	2.75
11	rs13481093	72366706	215.05	3.70
11	CEL-11-73459270	73662909	218.14	3.09
11	rs13481102	74875871	218.28	0.14
11	UT-11-75.985289	76230318	218.86	0.59
11	rs6384104	77608935	219.24	0.38
11	rs6381209	78672763	220.26	1.01
11	rs6379880	79610777	220.88	0.62
11	rs6178421	80822413	224.92	4.04
11	rs13481123	82073679	229.91	4.98
11	rs13481127	83228724	233.03	3.13
11	rs3661657	84548563	234.76	1.73
11	rs13481135	85663384	235.84	1.08
11	rs3719581	86775076	238.26	2.42
11	gnf1 1.093.966	87179927	238.71	0.45
11	rs3688955	90352625	249.29	10.58
11	rs13481161	92277348	260.55	11.25
11	rs3656982	93471841	265.46	4.91
11	rs3710148	96341521	268.93	3.47
11	rs3686162	97959851	274.65	5.72
11	rs13474433	98868195	276.45	1.80
11	rs3695865	101495082	287.00	10.56
11	rs6180460	102770175	290.25	3.25
11	rs6407687	105082152	314.79	24.54

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
11	rs13481210	106128972	315.59	0.80
11	rs6376890	107413027	323.60	8.01
11	rs13481220	108336005	326.39	2.79
11	rs3683086	109149017	328.19	1.80
11	rs13481228	110411467	331.93	3.74
11	rs13481233	111617886	339.03	7.10
11	gnf1 1.121.400	112459408	353.08	14.05
11	rs3662930	115338133	361.51	8.43
11	gnf1 1.125.992	117062953	370.79	9.28
11	CEL-11-118234030	118378990	377.41	6.62
12	rs3699421	4057363	0.00	0.00
12	rs6278204	6074541	1.33	1.33
12	rs13481288	7813147	2.63	1.29
12	rs3089046	8995881	3.04	0.41
12	rs6209157	10599344	6.54	3.50
12	rs3718992	12020026	6.61	0.07
12	rs13481308	13352935	10.27	3.66
12	rs6403731	14954124	12.00	1.73
12	rs13481322	16983902	14.83	2.83
12	rs3717860	25318059	16.70	1.87
12	rs6328018	26719624	21.06	4.36
12	rs13481361	28151550	21.13	0.07
12	UT-12-24.561109	30506674	37.00	15.87
12	rs13481375	31704286	39.38	2.39
12	rs6390855	32060490	41.08	1.69
12	rs6223000	34767992	46.15	5.08
12	gnf12.033.545	35706447	51.42	5.27
12	rs3695382	36834922	54.78	3.36
12	rs3088766	38299037	60.30	5.51
12	rs13481408	40966872	64.27	3.97
12	rs13481412	42491959	65.96	1.69
12	CEL-12-38970880	44767263	66.86	0.91
12	rs6317361	48226582	74.45	7.59
12	rs6170134	49406312	74.83	0.38
12	rs13481450	52311976	75.60	0.76
12	rs3670749	53880894	75.84	0.24
12	rs3700857	54841525	76.43	0.59
12	gnf12.053.286	55909868	83.25	6.82
12	rs3688680	57554123	86.53	3.28
12	rs3719306	58590291	89.25	2.72

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
12	rs3662939	59797785	93.49	4.24
12	rs6287262	61085187	95.72	2.24
12	rs3660822	62524421	96.87	1.15
12	mCV24690992	63873470	97.01	0.14
12	rs13481499	65306422	98.85	1.83
12	rs3686891	66399194	99.30	0.45
12	rs3691763	67583406	104.78	5.48
12	rs13481511	68942686	111.04	6.27
12	rs13481514	70522404	112.05	1.01
12	rs6335879	72838200	125.82	13.76
12	rs3687032	74417262	128.76	2.95
12	rs3709008	75600391	135.03	6.27
12	rs13481538	76811508	136.76	1.73
12	rs3682382	77217942	137.81	1.05
12	rs3696769	80658704	143.42	5.61
12	rs3654718	81893563	148.97	5.55
12	rs13481561	83085377	155.79	6.83
12	rs6263380	83729205	156.70	0.91
12	rs13481571	86832954	162.78	6.08
12	rs13481575	88168813	165.57	2.79
12	rs3711162	89664380	171.11	5.55
12	rs6288403	91376150	175.74	4.62
12	rs13481592	93362235	183.31	7.57
12	rs6207869	94763235	183.55	0.24
12	rs3679514	98363615	194.70	11.14
12	rs13481609	99664303	199.14	4.44
12	rs6184745	101246919	202.30	3.17
12	rs3700012	102160718	202.72	0.41
12	rs13481618	102929552	205.40	2.68
12	rs3724260	105120126	220.48	15.08
12	rs13481632	106797354	225.46	4.98
12	rs13481636	108001267	230.24	4.78
12	rs13481641	108819488	237.39	7.15
12	CEL-12-104545022	110244655	242.41	5.02
12	rs13481651	111768903	244.72	2.31
12	rs4229612	113706439	250.54	5.83
12	rs3709829	114788390	250.58	0.03
12	rs3654706	117523479	252.48	1.91
12	rs3711281	118632677	254.35	1.87
12	rs3679276	120329034	255.33	0.98

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
13	rs6215262	3783665	0.00	0.00
13	rs3695486	4160601	0.03	0.03
13	rs13481669	4598037	0.07	0.03
13	rs3686663	4915955	0.07	0.00
13	rs6298246	5337650	0.07	0.00
13	rs6318987	5977104	0.83	0.76
13	rs6243819	7110520	1.39	0.55
13	rs6343634	7287713	1.42	0.03
13	rs6301008	7702925	2.01	0.59
13	rs6239339	7998546	2.01	0.00
13	rs6250327	8305114	2.01	0.00
13	rs6396465	8777091	2.29	0.28
13	rs6178370	9016560	2.35	0.07
13	rs6329684	10065064	2.49	0.14
13	rs13481689	10839186	5.88	3.39
13	rs13481702	14548227	11.63	5.75
13	rs134817061613170416	16131704	16.10	4.47
13	rs3678616	17074230	16.10	0.00
13	gnf13.016.175	18871595	17.00	0.90
13	rs6314295	20128655	21.64	4.63
13	gnf13.018.407	21149230	22.33	0.69
13	rs13481727	22171547	24.46	2.13
13	gnf13.020.621	23395716	28.66	4.20
13	rs6297873	25672696	32.83	4.16
13	rs4229685	35881157	59.80	26.97
13	rs6200652	36979566	61.74	1.94
13	rs3724709	38245266	65.25	3.51
13	gnf13.038.133	40049739	78.28	13.03
13	rs13481777	40652761	79.65	1.37
13	rs6271232	42466710	83.46	3.81
13	rs13481789	43836016	88.68	5.22
13	gnf13.042.658	44593553	88.68	0.00
13	rs3688207	45370260	93.26	4.59
13	rs6244558	47827575	95.24	1.98
13	rs3699522	53003023	105.33	10.08
13	rs8273881	55408572	119.60	14.28
13	rs13481823	57047377	123.06	3.46
13	gnf13.057.762	59713868	126.60	3.54
13	rs6410679	61246715	128.40	1.80
13	rs13481849	63717707	129.06	0.66

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
13	rs3720797	64767706	130.86	1.80
13	rs4229817	67316285	132.26	1.40
13	rs3718727	69796522	136.57	4.32
13	rs6381045	70757677	141.88	5.31
13	rs3658685	72165953	146.47	4.59
13	rs3688781	73319304	150.93	4.47
13	rs3721965	74453958	155.88	4.95
13	rs8274592	75559141	156.09	0.21
13	rs13481886	76596223	156.96	0.87
13	rs13481892	77861907	158.61	1.65
13	rs13481897	78959507	159.52	0.90
13	rs3705043	79860769	159.65	0.14
13	rs3693887	81073783	159.72	0.07
13	rs13481905	81570691	163.42	3.70
13	mCV24625340	85174631	173.14	9.72
13	rs13481919	86156394	174.94	1.80
13	rs6296621	87436552	175.98	1.05
13	gnf13.092.499	92346249	188.13	12.15
13	rs13481947	94774232	194.64	6.51
13	rs3697202	94899974	194.64	0.00
13	rs13481958	97617278	201.78	7.14
13	rs13481964	98881378	205.25	3.47
13	gnf13.099.677	100124182	207.38	2.13
13	rs3088752	101062457	210.51	3.13
13	rs3688959	104229756	227.66	17.14
13	rs6389588	104955006	228.35	0.69
13	rs13481990	106155126	231.45	3.10
13	rs13482000	108692123	243.24	11.79
13	mCV24886326	111716695	254.28	11.05
13	rs6247696	116287920	272.87	18.59
13	rs13482028	117370793	275.04	2.17
13	rs13482032	118459784	276.55	1.51
14	rs3687889	18479914	0.00	0.00
14	rs6397486	19725405	4.19	4.19
14	rs3690631	20540804	6.43	2.23
14	rs3658866	21747331	12.78	6.35
14	rs13482143	38477139	59.48	46.70
14	rs6314716	39525916	61.07	1.58
14	rs13482160	44832603	64.65	3.58
14	gnf14.040.022	45769390	69.46	4.82

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
14	rs4230315	47178395	70.94	1.47
14	rs13482174	48505666	74.82	3.88
14	rs4197422	49504894	75.76	0.94
14	rs3680568	51058791	76.14	0.38
14	rs3140262	52754754	76.21	0.07
14	rs13482191	53600552	76.27	0.07
14	rs8244195	54925203	80.43	4.15
14	mCV23128760	58064416	96.67	16.24
14	rs13482206	58292218	96.74	0.07
14	rs3701623	71931676	150.78	54.04
14	rs13482254	73250217	151.34	0.55
14	rs13482256	73955530	151.34	0.00
14	rs13482262	76692934	159.04	7.70
14	rs3706792	77724884	160.87	1.83
14	rs6352085	78415693	162.31	1.44
14	rs13482269	79639201	162.62	0.31
14	rs13482272	81045435	162.72	0.10
14	rs13482276	82448660	166.23	3.51
14	rs13482281	84118633	167.27	1.05
14	rs3663148	85666288	171.39	4.12
14	rs13482290	86543121	171.43	0.03
14	rs13482296	87763571	171.46	0.03
14	rs3667933	88933708	173.48	2.02
14	rs6407863	90181473	173.55	0.07
14	rs4139735	91491323	176.08	2.53
14	rs3718262	92413488	176.15	0.07
14	rs6211694	107576665	230.96	54.82
14	rs13482366	108770838	231.94	0.98
14	rs13482372	109997097	234.25	2.31
14	rs3683221	111443102	236.34	2.09
14	rs13482386	114892329	244.58	8.24
14	CEL-14-110783830	117346142	253.79	9.22
14	rs3707842	118774157	262.57	8.78
14	rs3682013	119812313	267.85	5.27
14	gnf14.117.278	120853077	269.87	2.02
14	CEL-14-115300803	122104641	274.19	4.32
14	rs13482416	123897764	274.36	0.17
15	rs13459176	3229130	0.00	0.00
15	rs13482431	11256189	14.79	14.79
15	rs13482434	12108959	16.30	1.51

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
15	rs13482446	14490207	25.20	8.90
15	CEL-15-15919629	15955158	27.00	1.80
15	CEL-15-17259939	17198542	27.10	0.10
15	rs13482461	18874335	29.22	2.12
15	rs13482464	19583331	30.55	1.33
15	rs13482467	20409291	30.55	0.00
15	rs13482473	21956761	34.05	3.50
15	rs6367927	23622445	36.55	2.49
15	rs13482486	25676812	39.15	2.60
15	rs3670581	27015386	45.47	6.32
15	rs13482498	28442967	47.16	1.69
15	rs3088525	29576963	49.32	2.16
15	rs4230683	30911604	56.24	6.92
15	rs6333696	32062623	57.61	1.37
15	rs3091174	32640776	59.91	2.31
15	rs6188239	34275822	61.46	1.54
15	rs3089995	35560763	63.07	1.62
15	rs3695416	38428986	70.54	7.46
15	rs3677296	39939920	70.78	0.24
15	rs13482536	41699356	76.68	5.90
15	rs13482541	43371772	77.90	1.22
15	CEL-15-44698021	44505552	80.62	2.71
15	rs4138760	46185124	87.34	6.72
15	rs13482558	46996734	87.37	0.03
15	CEL-15-48446430	48254828	87.82	0.45
15	rs3660290	50687278	96.24	8.42
15	rs3692040	50905622	96.27	0.03
15	rs6165881	51647721	97.57	1.29
15	rs13482580	52852649	99.00	1.44
15	rs13482589	54731450	101.98	2.97
15	rs6400804	56636515	112.60	10.62
15	rs13482595	58446606	119.73	7.13
15	rs3654559	59792151	124.24	4.52
15	rs3683495	61032184	124.62	0.38
15	rs13482612	63932108	129.42	4.79
15	rs13482618	65688261	132.36	2.94
15	rs6197332	66836172	136.42	4.05
15	rs13482628	67706809	136.59	0.17
15	rs13482635	69275895	141.39	4.80
15	rs13482637	70330795	144.94	3.55

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
15	rs6204870	71347000	145.08	0.14
15	rs13482642	72040910	146.67	1.58
15	rs13482654	76521561	163.24	16.57
15	rs3660192	77651846	168.15	4.91
15	rs3721372	80232884	171.47	3.32
15	rs4230908	82954168	180.01	8.54
15	rs3660367	84529873	182.17	2.16
15	rs4230930	85686239	183.18	1.01
15	rs13482691	86800469	189.33	6.16
15	rs13482693	87905479	197.69	8.36
15	rs3720931	89326233	205.91	8.22
15	rs6287697	90594294	213.75	7.83
15	rs13482711	91887069	218.73	4.98
15	CEL-15-93579770	92989871	222.13	3.39
15	rs13482719	93935165	225.90	3.78
15	rs13482726	95777710	236.70	10.80
15	rs13482729	96939504	243.64	6.94
15	rs13482732	97958852	248.69	5.05
15	rs3708604	98953494	251.26	2.56
15	CEL-15-100463048	99829642	252.34	1.08
15	rs13482741	100947347	254.31	1.98
16	rs4152386	3902246	0.00	0.00
16	rs4152838	4944771	0.76	0.76
16	rs4165119	20412379	39.42	38.66
16	rs4165287	21944099	43.08	3.66
16	rs4165425	23712565	50.87	7.79
16	rs6294027	25624287	56.73	5.86
16	rs4165602	27351549	67.82	11.08
16	rs4166607	28479533	74.93	7.12
16	rs4167574	29589786	78.33	3.39
16	rs4167955	30213805	84.24	5.92
16	rs4168890	31162488	86.77	2.53
16	rs4170074	32114527	87.86	1.08
16	rs4171440	33400923	91.44	3.58
16	rs4172338	34643179	96.95	5.51
16	rs4173709	36434699	99.63	2.68
16	rs4174469	38089980	103.79	4.17
16	rs4175608	39101821	108.75	4.95
16	rs4177203	40155116	111.35	2.61
16	rs4178513	41620197	113.85	2.49

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
16	rs4179117	42652205	116.12	2.27
16	rs4179233	43530097	116.16	0.03
16	rs4180126	44581329	116.85	0.69
16	rs4182243	45971994	122.49	5.64
16	rs4183448	47116785	122.49	0.00
16	rs4184315	48585928	122.73	0.24
16	rs4185176	49811478	126.93	4.20
16	rs4185639	50217963	127.52	0.59
16	rs3696661	51596050	137.13	9.61
16	rs6164817	52950060	137.76	0.62
16	rs3687272	54581203	140.70	2.94
16	rs6271301	55949034	142.65	1.94
16	rs4189277	57213842	143.59	0.94
16	rs4190414	58481691	144.42	0.83
16	rs4192132	59586860	146.92	2.50
16	rs4192837	60271395	147.86	0.94
16	rs4197416	66324367	160.64	12.78
16	rs4197725	67300263	164.38	3.74
16	rs4198737	68894101	169.21	4.83
16	rs4202372	72792320	179.94	10.74
16	rs4203891	73967387	184.77	4.83
16	rs4205524	75179218	189.09	4.32
16	rs4206648	76540190	190.78	1.69
16	rs4207452	77311776	190.84	0.07
16	rs4211515	82276082	199.46	8.62
16	rs4212102	84980634	203.59	4.12
16	rs4219239	91559023	247.29	43.70
16	rs4219897	92678867	252.23	4.95
16	rs4220529	94551647	259.65	7.42
16	rs4220927	95114092	260.59	0.94
16	rs3164088	96420993	262.53	1.94
17	rs6310831	3184302	0.00	0.00
17	rs3686875	4323325	3.50	3.50
17	rs13482854	6986634	16.83	13.32
17	rs3090641	8895768	20.72	3.89
17	rs3702484	9531709	28.00	7.28
17	rs13482870	10567907	31.47	3.47
17	rs13482875	11647255	34.26	2.79
17	rs3723317	13454553	37.09	2.83
17	rs13482887	14331468	37.16	0.07

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
17	rs3675740	15964322	37.43	0.28
17	rs3721884	17277701	38.41	0.98
17	mCV25045820	18645790	44.94	6.53
17	rs6341891	19931203	44.94	0.00
17	rs6185197	20993698	44.94	0.00
17	CEL-17-21229557	22220914	46.09	1.15
17	rs4231344	23402584	49.25	3.16
17	rs3090500	25070890	50.02	0.76
17	rs4136360	25913582	51.96	1.94
17	rs6358703	28506799	58.52	6.56
17	rs6308773	28909195	58.59	0.07
17	gnf1 7.027.979	30172992	59.96	1.37
17	rs13482947	31361561	73.34	13.38
17	rs3705058	32756815	76.50	3.16
17	gnf17.035.152	34663289	78.48	1.98
17	rs3682923	35442186	78.83	0.35
17	rs13482968	36739736	79.03	0.21
17	rs13482973	37790219	79.55	0.52
17	rs6395893	38785974	79.55	0.00
17	rs3690398	40306887	79.93	0.38
17	CEL-17-400737194139	41391073	81.26	1.33
17	rs4231494	42552590	84.09	2.83
17	rs13482997	43287692	84.79	0.69
17	rs3090988	46219223	87.54	2.76
17	rs13483011	47875738	96.11	8.56
17	mCV22888090	63284167	149.01	52.91
17	rs13483075	65621900	157.61	8.60
17	rs13483078	66667135	162.57	4.96
17	gnf1 7.069.331	67934113	168.54	5.97
17	rs3657117	68954404	173.61	5.07
17	rs6210797	69606295	180.36	6.75
17	rs6176494	70657083	182.27	1.91
17	rs6322076	72154381	187.39	5.12
17	rs13483101	73245412	187.39	0.00
17	rs13465627	74293273	190.11	2.72
17	rs3710559	75179830	193.40	3.28
17	rs13483110	76067016	196.72	3.32
17	rs6386440	78260450	207.27	10.56
17	rs3684732	82916140	247.16	39.89
17	rs3701338	83915245	253.32	6.16

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
17	rs13483144	85794298	265.20	11.89
17	rs3723150	88460884	272.03	6.83
17	rs13483159	89629145	278.36	6.32
18	rs13483183	3516539	0.00	0.00
18	CEL-18-4270744	4100246	0.03	0.03
18	gnf1 8.002.818	5772955	2.16	2.12
18	rs3680906	6681133	2.16	0.00
18	rs3689558	8042686	3.34	1.19
18	rs13483200	9902166	8.42	5.08
18	rs13483210	11926038	10.87	2.45
18	rs13483215	13213816	12.20	1.33
18	mCV23617245	14673570	17.04	4.85
18	rs13483223	15584838	18.98	1.94
18	rs13483226	16210547	26.18	7.20
18	rs13483228	16929356	26.35	0.17
18	rs13483235	18836315	29.96	3.61
18	rs6303064	19743302	29.96	0.00
18	rs13483244	20967270	33.01	3.05
18	rs6194744	22002448	33.29	0.28
18	rs6368237	23583518	34.58	1.29
18	rs13483256	24774410	35.17	0.59
18	rs13483262	26279499	38.97	3.80
18	rs3722205	27823848	40.98	2.01
18	rs13483277	30505594	44.68	3.69
18	CEL-18-32158369	31844292	45.79	1.12
18	rs6385006	32672795	45.93	0.14
18	UT-18-33.980716	33920757	49.02	3.09
18	rs3675531	35170734	55.92	6.90
18	gnf1 8.033.953	36629378	58.12	2.20
18	rs6230993	39588412	63.75	5.63
18	rs13483319	41034026	65.51	1.76
18	rs6313313	41787428	65.82	0.31
18	rs3676196	43049783	73.07	7.25
18	rs13483331	43977152	76.62	3.55
18	rs4138936	45054522	78.60	1.98
18	rs13483340	46181189	81.50	2.90
18	rs6184541	47564489	85.63	4.12
18	rs3684561	48788342	85.70	0.07
18	rs13483356	50432771	94.16	8.46
18	CEL-18-52103795	51749036	95.31	1.15

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
18	gnf18.051.412	53228356	97.29	1.98
18	CEL-18-55824525	55451981	102.84	5.54
18	rs3654438	56422910	106.50	3.66
18	rs13483378	57419259	112.60	6.11
18	rs13483382	58520491	120.22	7.61
18	CEL-18-60214752	59824531	125.20	4.98
18	rs13483390	60999097	126.03	0.83
18	rs13483394	62078532	130.03	4.00
18	rs13483398	63212405	131.32	1.29
18	rs3688789	64639716	141.25	9.93
18	rs13483409	66005313	150.29	9.04
18	rs3716803	67123418	153.53	3.24
18	rs13483417	68006694	155.76	2.24
18	rs13483423	69655712	164.82	9.05
18	rs3675825	70820019	165.83	1.01
18	gnf1 8.069.928	71769983	169.98	4.16
18	CEL-18-73439948	73035787	170.82	0.83
18	rs6302629	75081888	181.38	10.56
18	rs13483444	76262954	182.28	0.90
18	rs3705890	77074534	189.12	6.84
18	rs3671707	80968369	203.95	14.83
18	rs13483466	82375034	219.08	15.13
19	rs3713033	5029791	0.00	0.00
19	CEL-19-8529644	9497607	5.39	5.39
19	rs13483526	10663263	11.07	5.67
19	rs6316813	11389269	14.19	3.13
19	rs13483541	15836265	26.32	12.13
19	rs8267392	17742452	37.15	10.82
19	UT-19-18.800709	18705581	40.54	3.39
19	rs6245242	21545835	56.86	16.32
19	rs6342493	22700137	70.74	13.87
19	rs13483569	23838724	71.61	0.87
19	rs3720897	25189044	78.46	6.85
19	rs13483577	26422375	81.10	2.65
19	rs6291559	27640321	86.63	5.52
19	rs3714482	29003386	100.21	13.59
19	UT-19-29.979736	30305221	103.31	3.09
19	mCV24505422	30731440	103.31	0.00
19	CEL-19-32349880	33103279	116.19	12.89
19	rs13483599	34461413	116.19	0.00

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
19	rs13483601	35015786	116.96	0.76
19	rs13483606	36121746	121.47	4.51
19	mCV23121032	41033158	143.10	21.62
19	rs4232174	41819857	143.51	0.41
19	rs13483650	47426719	179.65	36.14
19	CEL-19-48242857	48951703	189.62	9.97
19	rs6194426	50182341	190.21	0.59
19	rs3718102	52317419	201.55	11.34
19	rs13483677	53912816	206.82	5.27
19	rs3654713	55072167	216.69	9.87
19	rs3686750	56401399	227.57	10.88
19	rs6211533	57045660	228.33	0.76
19	rs3711945	58764614	236.35	8.02
X	rs13483712	8709313	0.00	0.00
X	rs13483716	9602109	0.75	0.75
X	rs13483724	32439530	54.18	53.43
X	rs13483756	49195646	69.91	15.74
X	rs13483777	57436012	79.52	9.60
X	rs13483781	58636499	82.35	2.83
X	rs13483783	59905100	83.45	1.10
X	rs13483786	60876307	83.50	0.04
X	gnfX.049.002	61879384	84.18	0.69
X	gnfX.049.915	62823723	84.84	0.65
X	petM-05810-1	65923304	88.23	3.39
X	gnfX.076.619	88928219	106.66	18.43
X	rs13483884	90157590	106.75	0.09
X	rs13483887	91254297	107.78	1.03
X	rs13483890	91850154	109.06	1.28
X	rs13483899	94735133	112.69	3.63
X	gnfX.084.751	97034762	118.74	6.06
X	gnfX.086.039	98329375	125.91	7.16
X	gnfX.089.712	102060354	134.90	9.00
X	CEL-X-100299803	105098165	137.45	2.55
X	rs13483935	105855859	138.56	1.10
X	rs13483937	106808631	138.56	0.00
X	CEL-X-104298527	109088019	139.48	0.93
X	rs13483951	110443774	141.16	1.68
X	CEL-X-106858553	111640689	141.16	0.00
X	CEL-X-108186660	112968795	141.16	0.00
X	rs13483962	113826940	141.16	0.00

Chr	SNP Name	Physical Position (bp)	Mapping Distance (cM)	Distance between 5' marker and current marker (cM)
X	CEL-X-110179980	114962115	141.26	0.10
X	rs13483971	115921675	141.67	0.42
X	gnfX. 104.523	117085412	141.67	0.00
X	CEL-X-113373391	118159308	141.67	0.00
X	CEL-X-114268662	119054579	141.67	0.00
X	CZECH-X-116527625	121926222	141.67	0.00
X	rs13483986	123217915	141.72	0.05
X	rs6205221	125642051	149.56	7.84
X	rs13484003	128950267	154.67	5.11
X	CEL-X-124532966	129872168	157.22	2.54
X	rs3702256	130295583	158.86	1.64
X	CEL-X-125736335	131075537	160.68	1.82
X	gnfX. 118.600	133671728	163.59	2.91
X	rs13484030	134698943	164.08	0.50
X	rs13484031	135187074	164.45	0.37
X	rs13484032	135489376	164.54	0.09
X	rs13484034	136024796	166.59	2.05
X	rs13484038	136722215	173.99	7.40
X	gnfX.124.190	138461556	179.88	5.89
X	rs3667513	138731844	179.95	0.07
X	CEL-X-133525088	138880333	181.14	1.18
X	rs13484050	139781932	184.34	3.20
X	rs13484060	142212603	186.14	1.80
X	rs13484070	146048985	186.19	0.05
X	gnfX. 129.308	147463249	186.19	0.00
X	rs13484093	152428352	192.27	6.08
X	rs13484094	152648875	192.39	0.12
X	rs6286296	154576953	195.60	3.21
X	rs6365259	155523124	196.63	1.04
X	gnfX.141.820	156929727	201.27	4.64

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SKELETAL HERITABILITIES AND GENETIC CORRELATIONS

Mean values and SDs are listed in millimeters for each long bone trait (H, humerus; U, ulna; F, femur; T, tibia). Heritabilities (diagonal) and genetic correlations (off-diagonal) were calculated from the F₁₀ population using the full sibship method (Falconer and Mackay 1996). The R² values for a model of the main effects of all individual-trait QTL (R²_{Main}) and the R² values for a model of the main effects of individual-trait QTL combined with the epistatic effects for each trait (R²_{Main + Epistatic}) are also given.

TRAIT	MEAN ± SD	H	U	F	T	R ² _{Main}	R ² _{Main + Epistatic}
H	12.26 ± 0.322	0.37				0.229	0.383
U	14.13 ± 0.339	0.84	0.60			0.336	0.445
F	15.40 ± 0.466	0.94	0.80	0.46		0.272	0.434
T	17.16 ± 0.444	0.79	0.93	0.82	0.61	0.323	0.490

F9-F10 LONG BONE LENGTH

QTL are listed by pleiotropic QTL name, chromosome, and trait affected (H, humerus; U, ulna; F, femur; T, tibia), with the F₉-F₁₀ QTL peak given in cM. Next, LPR scores, confidence intervals (CI), the genotyped SNP closest to the peak, and mapping intervals used for composite interval mapping (MI) are given. Gene effects (a/SD, d/a, and R², followed by standard errors (SE) as appropriate) for each QTL are given, with sexually dimorphic gene effects listed separately beneath affected QTL. Bold values indicate significance at the p < 0.05 level. Finally, multivariate (MV) peaks are listed with their associated LPR scores and mapping intervals in cM.

QTL	C	TRAIT	PEAK (cM)	LPR	CI (cM)	CLOSEST SNP	MI (cM)	a/SD	SE	d/SD	SE	d/a	R ²	MV PEAK (cM)	LPR	MI (cM)
Lbn1.2	1	H	15	3.94	8.27	rs3681537	0-77	0.17	0.01	0.04	0.02	0.24	0.03	22	7.96	0-100
	1	F	15	6.38	8.86	rs3681537	0-100	0.19	0.02	-0.09	0.03	-0.49	0.03			
	1	T	30.4	3.74	5.50	rs6334092	0-84	0.11	0.02	-0.11	0.02	-1.08	0.11			
Lbn1.1a	1	U	187.6	15.07	6.40	rs3715800	88-241	0.25	0.01	0.06	0.02	0.23	0.08	187.6	8.1	100-222
	1	T	187.6	20.38	5.50	rs3715800	84-251	0.29	0.02	0.04	0.02	0.13	0.11			
Lbn1.1b	1	H	222	4.98	8.27	rs3664800	77-251	0.13	0.01	-0.11	0.02	-0.87	0.03	212	11.95	188-250
	1	T	222	19.69	5.50	rs3664800	84-251	0.19	0.02	-0.19	0.02	-1.02	0.11			
	1	U	222.8	14.2	6.40	rs3664800	88-241	0.15	0.01	-0.18	0.02	-1.21	0.08			
Lbn2.1	1	F	222.8	6.3	8.86	rs3664800	100-250	0.08	0.02	-0.15	0.02	-1.81	0.03	294.3	5.85	150-300
	2	F	273.0	3.87	8.12	rs3658023	134-322	0.12	0.02	0.09	0.02	0.74	0.03			
	2	T	294.2	4.35	8.06	rs3725853	243-392	0.11	0.02	-0.06	0.02	-0.51	0.05			
Lbn2.3	2	H	298	7.36	7.23	rs13476761	161-306	0.18	0.01	0.03	0.02	0.19	0.04			
	2	U	347	13.79	10.37	rs3701696	251-447	0.21	0.01	0.11	0.02	0.49	0.03	347	3.65	300-400
	2	T	347	17.41	8.06	rs3701696	251-447	0.14	0.02	0.06	0.02	0.43	0.05			
Lbn2.2	2	F	411	5.43	8.12	rs13476860	325-524	0.20	0.02	-0.09	0.03	-0.43	0.03	428	6.59	306-524
	2	T	438	4.1	8.06	rs3673613	392-524	0.14	0.02	-0.06	0.02	-0.39	0.05			
	2	H	439.5	4.46	7.23	rs3673613	325-524	0.16	0.01	0.06	0.02	0.39	0.04			
Lbn3.1	3	F	134	5.95	6.38	rs13477144	0-144	0.11	0.02	0.07	0.03	0.65	0.06		No pleiotropy	
Lbn3.2a	3	H	201	7.85	6.15	rs13477276	180-278	0.16	0.02	0.05	0.02	0.29	0.05	201.7	10.27	175-300
				Females super-significant			females	0.16	0.02	0.07	0.03	0.42	0.07			
							males	0.12	0.02	0.06	0.03	0.48	0.02			
3	F		205	6.71	6.38	rs13477279	144-275	0.13	0.02	-0.10	0.03	-0.75	0.06			
							females	0.20	0.03	-0.06	0.04	-0.30	0.05			
							males	0.14	0.06	-0.12	0.04	-0.85	0.02			
3	U		208	6.9	8.33	rs3162061	180-300	0.07	0.02	-0.27	0.02	-4.09	0.04			
							females	0.15	0.03	-0.25	0.03	-1.70	0.06			

QTL	C	TRAIT	PEAK (cM)	LPR	CI (cM)	CLOSEST SNP	MI (cM)	a/SD	SE	d/SD	SE	d/a	R ²	MV PEAK (cM)	LPR	MI (cM)
Lbn3.2b	3	T	208	4.15	10.11	rs3162061	males	-0.05	0.02	-0.22	0.03	4.62	0.02			
							175-300	0.03	0.02	-0.23	0.03	-7.28	0.03			
							females	0.10	0.03	-0.15	0.04	-1.56	0.04			
							males	-0.04	0.03	-0.23	0.04	6.12	0.02			
Lbn3.2b	3	H	224.2	7.02	6.15	rs3676545	180-278	0.18	0.02	0.04	0.02	0.25	0.05	224.2	5.43	175-300
							females	0.29	0.02	0.01	0.03	0.05	0.07			
							males	0.08	0.02	0.06	0.03	0.77	0.02			
							180-300	0.24	0.02	0.20	0.02	0.83	0.04			
Lbn3.2b	3	U	224.2	7.82	8.33	rs3676545	females	0.24	0.03	0.13	0.03	0.52	0.06			
							males	0.21	0.02	0.20	0.03	0.94	0.02			
							144-275	0.14	0.02	0.09	0.03	0.62	0.06			
							females	0.18	0.03	0.08	0.04	0.43	0.05			
Lbn3.2b	3	F	224.2	6.14	6.38	rs3676545	males	0.06	0.03	0.11	0.04	1.98	0.02			
							175-300	0.21	0.02	0.18	0.03	0.86	0.03			
							females	0.09	0.03	0.03	0.04	0.34	0.04			
							males	0.15	0.03	0.26	0.04	1.75	0.02			
Lbn3.3	3	H	364.2	4.78	6.15	rs13477477	278-394	-0.14	0.01	-0.07	0.02	0.53	0.05	364.2	4.92	300-395.3
							275-394	-0.21	0.02	-0.06	0.03	0.30	0.06			
							118-223	0.11	0.02	0.32	0.02	2.84	0.03			
							114-205	0.11	0.02	0.30	0.03	2.77	0.02			
Lbn4.1	4	T	175	7.4	10.17	rs13477831	118-223	0.14	0.01	0.19	0.02	1.40	0.02			
							114-205	0.11	0.02	0.30	0.03	2.77	0.02			
							118-223	0.14	0.01	0.19	0.02	1.40	0.02			
							females	0.16	0.02	0.34	0.03	2.04	0.03			
Lbn6.1a	4	U	187	10.28	8.49	rs13477849	males	0.11	0.02	0.04	0.03	0.37	0.01			
							118-238	0.25	0.01	0.18	0.02	0.72	0.04			
							0-50	-0.16	0.02	0.01	0.02	-0.04	0.05	32	12.74	0-50
							0-67	-0.29	0.01	0.06	0.02	-0.20	0.07			
Lbn6.1b	6	T	32	12.68	6.83	rs3710004	0-65	-0.37	0.02	0.07	0.02	-0.18	0.06			
							0-50	-0.17	0.01	0.01	0.02	-0.09	0.02			
							50-200	0.21	0.02	0.10	0.02	0.48	0.06			
							50-200	0.20	0.01	0.03	0.02	0.13	0.02	103.4	8.54	50-200
Lbn6.1b	6	H	88.5	5.12	8.43	rs3684860	50-200	0.20	0.01	0.03	0.02	0.13	0.02			
							50-200	0.24	0.01	0.06	0.02	0.24	0.07			
							50-200	0.24	0.01	0.06	0.02	0.24	0.07			
							50-200	0.24	0.01	0.06	0.02	0.24	0.07			

QTL	C	TRAIT	PEAK (cM)	LPR	CI (cM)	CLOSEST SNP	MI (cM)	a/SD	SE	d/SD	SE	d/a	R ²	MV PEAK (cM)	LPR	MI (cM)
Lbn6.2	6	F	95	9	6.77	rs3684860	46-200	0.27	0.02	0.05	0.03	0.18	0.05			
	6	U	328.2	4.14	6.83	rs4140069	200-334	0.16	0.01	0.14	0.02	0.91	0.07	328.2	3.21	200-335.3
	6	F	328.2	3.45	6.77	rs4140069	200-334	0.17	0.02	0.07	0.03	0.38	0.05			
Lbn7.2	6	T	328.2	4.07	6.96	rs4140069	200-334	0.13	0.02	0.15	0.02	1.18	0.06			
	7	U	51.7	8.52	9.96	rs13479174	0-144	-0.13	0.01	0.28	0.02	-2.14	0.03		No pleiotropy	
	7	F	176	6.02	10.08	rs3686423	85-204	0.18	0.02	0.15	0.02	0.83	0.02		No pleiotropy	
Lbn8.2	Males super-significant															
	8	U	17.7	4.67	8.53	rs6287472	0-61	0.13	0.01	0.20	0.02	1.51	0.04	17.8	4.14	0-100
	8	T	18	5.16	8.90	rs6287472	0-61	0.14	0.02	0.20	0.02	1.42	0.04			
Lbn8.1	8	T	157	4.9	8.90	rs13479811	61-201	0.17	0.02	0.020	0.02	-0.01	0.04	172	3.08	100-200
	Males super-significant															
	8	U	169	6.41	8.53	rs13479814	61-229	0.17	0.02	-0.07	0.04	0.45	0.03			
Lbn9.2	9	U	205	7.52	13.43	rs3670195	0-250	0.21	0.01	0.06	0.02	0.26	0.04			0-250
	9	T	205.5	3.88	18.20	rs3670195	0-250	0.17	0.01	-0.01	0.02	-0.05	0.01	203.8	6.5	
	9	H	284	5.45	9.53	rs3723953	199-327	0.12	0.02	0.00	0.02	0.00	0.01			
Lbn10.1	10	H	178	8.22	8.34	rs13480684	101-232	-0.18	0.02	0.06	0.02	-0.32	0.02		No pleiotropy	
	10	F	190	5.34	15.55	rs13480687	101-232	0.18	0.01	0.18	0.02	1.01	0.03	178	7.1	100-232
	10	U	312	13.16	8.45	rs6290842	232-313	0.10	0.02	0.10	0.03	0.97	0.01			
Lbn10.2	10	T	313.7	9	9.81	rs6290842	232-313	0.27	0.01	0.04	0.02	0.15	0.04	312	11.58	225-313.7
	11	U	148	9.47	8.11	rs6326787	0-175	0.23	0.02	0.02	0.02	0.11	0.03			
	11	T	155.3	7.19	8.93	rs13481023	0-180	0.12	0.01	0.27	0.02	2.25	0.04	149	8.39	0-175
Lbn11.3	Males super-significant															
	11	T	206	8.15	8.93	rs3658906	males	0.06	0.02	0.19	0.02	3.11	0.04			
	11	H	359	7.96	8.49	rs3662930	females	0.11	0.02	0.22	0.03	1.92	0.05			
Lbn11.4	11	U	365	5.39	8.11	rs3662930	females	0.01	0.03	0.18	0.03	28.60	0.04		No pleiotropy	
	12	U	71	6.32	11.65	rs6317361	180-377	0.18	0.02	0.04	0.03	0.24	0.04			
	12	T	71	9.38	12.21	rs6317361	238-377	0.23	0.01	0.03	0.02	0.13	0.02	360	6.17	238-377
Lbn12.1	11	U	365	5.39	8.11	rs3662930	238-377	0.21	0.01	0.04	0.02	0.18	0.04			
	12	U	71	6.32	11.65	rs6317361	0-100	0.16	0.01	-0.24	0.02	-1.51	0.02	70	5.57	0-155
	12	T	71	9.38	12.21	rs6317361	0-100	0.14	0.02	-0.23	0.03	-1.63	0.02			
Lbn13.1	13	H	235	11.66	6.49	rs13481990	175-276	0.33	0.01	0.06	0.02	0.17	0.05	236	15.9	175-276.5

QTL	C	TRAIT	PEAK (cM)	LPR	CI (cM)	CLOSEST SNP	MI (cM)	a/SD	SE	d/SD	SE	d/a	R ²	MV PEAK (cM)	LPR	MI (cM)
Lbn16.2	13	F	235	9.72	7.99	rs13481990	175-276	0.29	0.02	0.06	0.03	0.21	0.04			
	13	T	235	13.06	7.56	rs13481990	175-276	0.36	0.02	0.03	0.03	0.07	0.05			
	13	U	236	19.5	6.41	rs13481990	175-276	0.44	0.01	0.05	0.02	0.11	0.08			
	16	H	226	6.48	13.18	rs4219239	200-end	-0.14	0.02	-0.17	0.03	1.19	0.01	229	8.34	200-262.5
Lbn17.2	16	U	239	7.44	10.81	rs4219239	127-262	-0.25	0.01	0.05	0.02	-0.21	0.02			
Lbn17.1	17	T	87	20.77	6.14	rs3090988	0-158	0.30	0.02	-0.04	0.02	-0.13	0.08		18.37	0-150
Lbn18.1	17	U	87.5	21.5	5.52	rs3090988	0-158	0.42	0.02	-0.12	0.03	-0.28	0.09			
Lbn19.1	18	F	81.5	6.37	10.04	rs13483340	0-150	0.21	0.02	0.00	0.02	0.01	0.02		No pleiotropy	
Lbn19.1	19	F	3	9.69	8.39	rs3713033	0-71	0.24	0.02	0.09	0.03	0.36	0.03	5	10.17	0-75
Lbn19.1	19	T	3	10.48	9.38	rs3713033	0-71	0.21	0.02	0.17	0.03	0.79	0.03			
Lbn19.1	19	H	4	12.18	6.64	rs3713033	0-71	0.27	0.01	0.14	0.02	0.54	0.04			
Lbn19.1	19	U	4	11.47	9.19	rs3713033	0-71	0.24	0.01	0.11	0.02	0.45	0.03			