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BREEDING AND GENETICS

Addition of 455 Microsatellite Marker Loci to the High-Density *Gossypium hirsutum* TM-1 x *G. barbadense* 3-79 Genetic Map

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ABSTRACT

Four hundred fifty-five new microsatellite, also known as simple sequence repeat (SSR) marker loci, were added to the previously published 2072-locus genetic map that was constructed using 186 recombinant inbred lines (RILs) from an interspecific cross between *Gossypium hirsutum* TM-1 and *G. barbadense* 3-79. The augmented high-density map contained 2527 loci (2280 SSRs and 247 single nucleotide polymorphisms) and covered 3430 centiMorgans (cM) with an average marker locus interval of 1.36 cM. An addition of 455 new marker loci (a net increase 21.96%) resulted in only 50 cM or 1.48% net increase of total genetic distance, but reduced the number of large gaps (> 10 cM) from 21 to 14. Approximately 400 pairs of duplicate SSR loci were present in this augmented map. Most duplicate loci were mapped between homeologous chromosomes. Duplicate loci within a chromosome were observed in at least nine chromosomes. The telomeric regions are hot spots for intrachromosomal locus duplication. This augmented map is a saturated genetic map of tetraploid cotton genome whose total genetic distance is estimated at approximately 3500 cM.

A high-density genetic map plays important roles in understanding the genome structure, dissecting economically important traits, identifying molecular markers associated with agronomic traits, and cloning a gene of interest through map-based cloning strategy. In cotton, researchers have been constructing genetic maps with multiple types of DNA markers using different populations since the 1990s (Guo et al., 2007, 2008a; Lacape et al., 2003, 2009; Nguyen et al., 2004; Reinisch et al., 1994; Rong et al., 2004; Yu et al., 2011; Zhang et al., 2008). Reinisch et al. (1994) reported the first detailed restriction fragment length polymorphism (RFLP) genetic map in cotton using 57 F_2 plants derived from an interspecific cross between *Gossypium hirsutum* L. race palmeri and *G. barbadense* L. acc. K101. This map contained 705 RFLP loci. Using the same population, Rong et al. (2004) expanded the map to 2584 loci with average marker interval of 1.72 centiMorgans (cM). A majority were RFLP marker loci. This map provided one of the first insights into the allotetraploid cotton genome structure and evolution although the RFLP markers have proven to have limited portability and utility for marker assisted breeding (Ulloa et al., 2005). Guo et al. (2007, 2008a) constructed the first comprehensive microsatellite, also called a simple sequence repeat (SSR) map using 138 BC_1 plants derived from an interspecific cross of (*G. hirsutum* TM-1 x *G. barbadense* Hai 7124) x *G. hirsutum* TM-1. The majority of SSR markers in this map were derived from cotton expressed sequence tag (EST) sequences. Nguyen et al. (2004) constructed a 1160 loci [amplified fragment length polymorphism (AFLP), RFLP, and SSR] map using 75 BC_1 plants from a cross of (*G. hirsutum* Guazuncho 2 x *G. barbadense* VH8-4602) x *G. hirsutum* Guazuncho 2. Lacape et al. (2009) reported a genetic linkage map that consisted of a total of 800 (AFLP, RFLP, and SSR) marker loci using 140 recombinant inbred lines (RILs) derived from an interspecific cross between *G. hirsutum* Guazuncho 2 and *G. barbadense* VH8-4602. Yu et al. (2011) used 141 BC_1 plants derived from an interspecific cross of (*G. hirsutum* Emian 22 x *G. barbadense* 3-79) x *G. hirsutum* Emain 22 to construct a map. As with Guo et al. (2007, 2008a), this map exclusively contained SSR markers, the majority of which were derived from ESTs. In addition, a whole-genome radiation hybrid population of 93 plants derived from an interspecific cross of *G. barbadense* 3-79 x *G. hirsutum* TM-1 was also explored for mapping the cotton genome (Gao et al., 2004). Though

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less comprehensive in genome coverage, other maps have been constructed from *G. hirsutum* intraspecific populations (Lin et al., 2009; Shappley et al., 1998; Ulloa et al., 2002; Zhang et al., 2012). Recently, Yu et al. (2012b) reported a high-density SSR and single nucleotide polymorphism (SNP) genetic map of tetraploid cotton genome using 186 RILs derived from a cross between *G. hirsutum* TM-1 and *G. barbadense* 3-79. This high-density map consisted of 2072 loci (1825 SSRs and 247 SNPs) and covered 3380 cM with an average marker interval of 1.63 cM. A core set of 105 SSR markers were developed from this map for molecular germplasm characterization and other cotton genetic studies (Yu et al., 2012a).

In 2009, Monsanto Company released 2937 pairs of SSR primers to the public (Xiao et al., 2009). Of them, primers prefixed with CER or CGR were developed at Monsanto Company, St. Louis, MO. The primers prefixed with C2, COT, DC, DPL, or SHIN were developed at Delta and Pine Land Company (D&PL), Scott, MS. D&PL was sold to Monsanto Company in 2007. A portion of CER- or CGR-prefixed SSR markers were mapped using 94 F_2 plants derived from a cross between *G. hirsutum* DP33B and *G. barbadense* GB679. Independently, a portion of C2-, COT-, DC-, DPL- or SHIN-prefixed SSR markers were mapped using the 186 RILs derived from a cross between *G. hirsutum* TM-1 and *G. barbadense* 3-79 provided by John Yu at USDA-ARS, College Station, TX. A consensus map was generated by combining these two maps. In order not to jeopardize the publication of *G. hirsutum* TM-1 x *G. barbadense* 3-79 genetic map, Xiao et al. (2009) only reported the 20-cM bins for the mapped SSR marker loci without giving the actual mapping positions. However, a map with actual marker positions will be much more useful in genetic research and breeding. The genetic map developed by Yu et al. (2012b) was a coordinated community effort that involved nine organizations from both public institutions and private companies in the US. Researchers from each organization agreed to provide a set of SSR or SNP markers that would be included in the map construction. D&PL contributed 200 SSR markers prefixed with DPL to this map. Markers prefixed with C2, COT, DC, and SHIN that were developed by D&PL were not part of this coordinated community effort. In this paper, we report the addition of 455 C2-, COT-, DC-, DPL-, or SHIN-prefixed SSR marker loci to the published high density *G. hirsutum* TM-1 and *G. barbadense* 3-79 genetic map, and present an augmented 2527 loci map (2280 SSRs and 247 SNPs). To our knowledge, this augmented map is so far the highest density genetic map of tetraploid cotton genome constructed using a single population from the average marker interval distance point of view. This map will facilitate the advancement of many basic and applied genomic studies in cotton.

MATERIALS AND METHODS

Plant Materials and DNA Extraction. An immortal mapping population composed of 186 RILs at, on average, F_7 generation when genomic DNA was used in this mapping study. These lines derived from selfing, via single seed descent, original individual F_2 plants from a cross between *G. hirsutum* TM-1 and *G. barbadense* 3-79, two highly homozygous parents (Yu et al.; 2012b) .

Genomic DNA was extracted from fresh young leaf tissue of individual cotton plants grown in the greenhouse following the modified CTAB buffer DNA extraction procedure as described by Kohel et al. (2001) and modified by Yu et al. (2012a).

SSR Primers and Polymerase Chain Reaction (PCR) Assays. The primer pairs used in this study are those prefixed with C2, COT, DC, DPL, or SHIN. Development of these markers and their primer sequences were described by Xiao et al. (2009). Primer and clone sequences are also available at Cotton Marker Database (*http://www.cottonmarker.org/*).

PCR assay for amplifying SSR was performed according to Fang et al. (2010). Forward primers were fluorescent-labeled at 5′ end with 6-FAM (6-carboxyfluorescein), HEX (4, 7, 2′, 4′, 5, 7-hexachloro-carboxyfluorescein) or NED (7′, 8′-benzo-5-fluoro 2′, 4, 7,-trichloro-5-carboxy-fluorescein). SSR primer oligos were purchased from Sigma Genosys (Woodlands, TX) or Applied Biosystems Inc. (Foster City, CA). All markers were analyzed using non-multiplex PCR. Amplified PCR products were separated and measured on an automated capillary electrophoresis system ABI 3730 XL (Applied Biosystems Inc.). GeneScan-400 ROX® (Applied Biosystems Inc.) was used as an internal DNA size standard. The output was analyzed with GeneMapper 3.7 software (Applied Biosystems Inc.).

Marker Data Acquisition and Linkage Map Construction. Genotyping of the RIL population

for SSR was performed as previously described (Yu et al., 2012b). Duplicate marker loci were designated by adding a lower-case letter in alphabetical order after the primer name. Maps were constructed by using the JoinMap 4.0 program (Van Ooijen, 2006). The Kosambi mapping function (Kosambi, 1944) was used to convert a recombination frequency to a genetic distance in cM. Linkage groups and marker orders were determined on the basis of likelihood ratio statistic (or LOD) 10 or higher (up to LOD 15). Chromosome assignment was based on the common markers that were located in prior publications (Guo et al., 2007, 2008a; Gutiérrez et al., 2009; Lacape et al., 2003, 2009; Liu et al., 2000; Yu et al., 2011) and our recent publication (Yu et al., 2012b). SSR loci localized to one of chromosomes (Chr.) 1 to 13 were assigned to the A-subgenome (At), whereas loci localized to chromosomes 14 to 26 were assigned to the D-subgenome (Dt). The orientation of each chromosome is according to Gutiérrez et al. (2009) with long arm at the bottom and short arm on the top. Orientation of the chromosomes relied on the common markers whose chromosomal locations were characterized by deficiency analysis (Guo et al., 2008b; Gutiérrez et al., 2009; Liu et al., 2000; Yu et al., 2012b).

RESULTS

Marker Segregation Within the Mapping Population. Three hundred five pairs of SSR primers revealed 455 segregating loci within the mapping population (Table 1). Of them, 168 primer pairs amplified one locus, 125 revealed two loci, 11 amplified three loci and one generated four dominant loci. In general, more SSR primer pairs revealed one segregating locus than those revealing two or more segregating loci within the population. This was true in the present study except for the primers prefixed with DPL. It is worth mentioning that Yu et al. (2012b) previously mapped 213 DPL SSR marker loci generated by 200 primer pairs. These 200 DPL primer pairs were intentionally selected for their single-locus feature. If taking into consideration of all 372 DPL primer pairs analyzed before and in this study, 259 revealed one segregating locus, whereas 113 revealed two or more loci. Among the 455 new SSR marker loci, 366 were codominant, 53 were dominant loci that received alleles from TM-1, and 36 were dominant loci that received alleles from 3-79.

Table 1. New SSR markers added to the *G. hirsutum* TM-1 x *G. barbadense* 3-79 genetic map (Yu et al., 2012b).

SSR markers	No. primer pairs	No. primer pairs revealing one segregating locus	No. primer pairs revealing more than one segregating locus	No. loci mapped
C2	21	17	4	26
COT	29	23	6	36
DC	54	38	16	71
DPL	172	72	100	281
SHIN	29	18	11	41
Total	305	168	137	455

Among the 366 new codominant SSR loci, the average residual heterozygosity for individual markers was 4.3%, ranging from 0% to 31.7% with SSR marker DPL0604 showing the highest heterozygosity.

Distribution of 455 New SSR Marker Loci Among the Chromosomes. The 455 new SSR marker loci were mapped on all 26 chromosomes with almost equal distribution between two subgenomes (Table 2). Of them, 231 were mapped on At subgenome chromosomes, and 224 on Dt subgenome chromosomes. As for the individual chromosomes, Chr. 26 received 31 loci, the most, and Chr. 04 received 6, the least.

Augmented 2527-Locus Genetic Maps of the Allotetraploid Cotton. The augmented genetic linkage map comprised 2527 SSR and SNP loci mapped to the 26 chromosomes of allotetraploid cotton, for a total genetic distance of 3430 cM (Table 2 and Fig. 1). The average marker locus interval in this map was 1.36 cM, the smallest among all tetraploid cotton genetic maps reported so far. The At subgenome consisted of 1369 marker loci with a total genetic distance of 1769.4 cM and an average marker locus interval of 1.29 cM. The largest chromosome in terms of recombination frequency was Chr. 05, which spanned 200.1 cM with 165 marker loci. The shortest was Chr. 13, which spanned 104.1 cM with 85 loci (Table 2 and Fig. 1). In the At subgenome, there were five gaps greater than 10 cM, and the largest gap between two loci was 16.62 cM on Chr. 08.

The Dt subgenome consisted of 1158 marker loci with a total genetic distance of 1660.9 cM and an average marker locus interval of 1.43 cM. The

largest chromosome with respect to recombination frequency was Chr. 19, which spanned 182.3 cM with 143 loci, and the shortest chromosome was Chr. 17, which spanned 98.4 cM with 54 loci (Table 2 and Fig. 1). There were nine gaps greater than 10 cM, and the largest gap between two loci was 16.42 cM on Chr. 17.

Table 2. Distribution of 455 new SSR marker loci among the 26 allotetraploid cotton chromosomes.

Chromosome	New Loci	No. loci	Size (cM)	Average Marker Interval (cM)	No. Gaps >10cM (largest)
A-subgenome					
Chr.01(A01)	16	82	145.2	1.77	1 (14.46)
Chr.02(A02)	15	75	124.8	1.66	1 (10.09)
Chr.03(A03)	18	105	116.4	1.11	0 (6.33)
Chr.04(A04)	6	62	106.3	1.72	2 (15.57)
Chr.05(A05)	26	165	200.1	1.21	0 (9.42)
Chr.06(A06)	15	104	133.8	1.29	0 (8.35)
Chr.07(A07)	20	107	140.0	1.31	0 (9.34)
Chr.08(A08)	26	118	149.9	1.27	1 (16.62)
Chr.09(A09)	17	116	141.2	1.22	0 (8.86)
Chr.10(A10)	16	91	114.8	1.26	0 (8.16)
Chr.11(A11)	12	152	170.1	1.12	0 (7.32)
Chr.12(A12)	23	107	122.8	1.15	0 (8.79)
Chr.13(A13)	21	85	104.1	1.22	0 (6.71)
Totat-At	231	1369	1769.4	1.29	5 (16.62)
D-subgenome					
Chr.15(D01)	21	114	119.9	1.05	1 (10.05)
Chr.17(D02)	12	54	98.4	1.82	2 (16.42)
Chr.14(D03)	17	96	126.4	1.32	1 (14.00)
Chr.22(D04)	8	69	110.9	1.61	0 (6.27)
Chr.19(D05)	27	143	182.3	1.27	1 (16.30)
Chr.25(D06)	15	85	125.4	1.48	0 (8.59)
Chr.16(D07)	21	79	126.3	1.60	1 (13.62)
Chr.24(D08)	20	82	124.8	1.52	1 (10.62)
Chr.23(D09)	15	98	143.1	1.46	0 (8.47)
Chr.20(D10)	11	87	124.8	1.43	0 (9.19)
Chr.21(D11)	13	93	149.0	1.60	0 (9.31)
Chr.26(D12)	31	84	120.2	1.43	1 (10.99)
Chr.18(D13)	13	74	109.3	1.48	1 (11.35)
Total-Dt	224	1158	1660.9	1.43	9 (16.42)
Total	455	2527	3430	1.36	14 (16.62)

Addition of 455 SSR marker loci increased the total genetic distance from 3380 cM (Yu et al., 2012b) to 3430 cM with a net 50 cM or 1.48% increase. Three chromosomes, Chr. 07, Chr. 21, and Chr. 22, had the greatest net increase, i.e., 11.1, 12.2, 33.0 cM, respectively. Two chromosomes, Chr. 17 and Chr. 19, had notable net decrease, i.e., 16.4 and 44.9 cM, respectively. The remaining 21 chromosomes had little change.

Addition of 455 new loci to the published genetic map (Yu et al., 2012b) caused little change in marker orders. One notable change was observed on Chr. 24 (D08). The marker JESPR291a was previously mapped at 52.7 cM position, but its duplicate locus, JESPR291b, was mapped at the telomere region of the short arm on Chr. 08 (A08) (Yu et al., 2012b). In the present study, the marker JESPR291a was mapped at the telomere region of the short arm on Chr. 24 (D04), which was comparable to the position of its duplicate locus JESPR291b on Chr. 08 (A08). Remapping with additional 455 loci also identified a mapping error that involved Chr. 19 and Chr. 22. A group of 16 loci that were previously mapped at the telomeric region of Chr. 19 were mapped as part of Chr. 22 in the present study.

Inter- and Intrachromosomal Marker Loci Duplication of Allotetraploid Cotton. As mentioned above, 137 SSR primer pairs amplified two or more loci. Excluding dominant loci amplified by DPL0687, there were 275 codominant loci that were duplicated resulting in 142 pairs (Table 3). Most of the duplicate loci were mapped on the homeologous chromosome pairs (Table 3 and Fig. 1). The relative orders of most duplicate loci on the homeologous chromosomes were similar.

A few duplicate loci were also present between non-homeologous chromosomes and/or within the same chromosome, indicating likely genome rearrangements (Table 3 and Fig. 1). Intrachromosome duplications from all mapped SSR marker loci were observed in Chr. 01, Chr. 05, Chr. 09, Chr. 11, Chr. 12, Chr. 20, Chr. 21, Chr. 23, and Chr. 26. On Chr. 05, markers SHIN-0289, NAU1042, and NAU1221 were duplicated in tandem (Fig. 1). The duplications on Chr. 09, Chr. 11 and Chr. 21 were also in tandem. On Chr. 12 (A12), two duplicate DPL0208 loci were found at the lower end of the chromosome. Similarly, there were two duplicate DPL0404 loci at the lower end of Chr. 26 (D12).

Seven new pairs of duplicate loci (Table 3) suggested a post-polyploidization reciprocal transloca-

tion of Chr. 02 (A02) and Chr. 03 (A03). Three pairs were between Chr. 02 (A02) and Chr. 14 (D03), and 4 pairs between Chr. 03 (A03) and Chr. 17 (D02).

DISCUSSION

Due to differences ranging from mapping population sizes and structures, numbers of mapped marker loci to the software programs used in mapping analysis, the map distances between various maps from the same species can be different (Lacape et al., 2009). The reported total genetic distance of tetraploid cotton genome ranged from 3380 cM (Yu et al., 2012b) to 5454 cM (Zhang et al., 2008). However, the map reported by Zhang et al. (2008) did not reduce to 26 linkage groups (chromosomes), thus the total distance might be overestimated. An updated map from the same group (Yu et al., 2011) reduced the total genetic distance to 4419 cM. This distance might still be overestimated because this map had 35 gaps that were larger than 10 cM, and five of them larger than 20 cM. Rong et al. (2004) reported a 4448 cM map constructed using MapMaker 3.0 software. MapMaker and JoinMap use different algorithms and, as a consequence, they are known to generate differences in distance, typically shorter distance with JoinMap software as compared with MapMaker (Lacape et al., 2009). Lacape et al. (2009) reported that the total map distance generated by JoinMap was 28% smaller than the MapMaker map when analyzing the same cotton marker dataset. The maps reported by Guo et al. (2008a) and Lacape et al. (2009) were 3540 cM and 3637 cM, respectively. Our previously reported map (Yu et al., 2012b) covered 3380 cM. An addition of 455 SSR marker loci (an increase of 21.96%) increased the total genetic distance to 3430 cM with a net 1.48% increase. Three chromosomes had net increase of more than 10 cM, and two chromosomes had net decrease of 10 cM or more. We believe that the augmented high-density map reported herein is a saturated one for the allotetraploid cotton. Further increase in the number of marker loci might not significantly change the total genetic length of this map but will decrease the number of large gaps, and might provide better marker orders. Taking into consideration of all the maps published so far, we suggest that the total genetic distance of tetraploid cotton genome is around 3500 cM. A further integrated map will be needed to confirm this suggestion.

Previously, Yu et al. (2012b) reported that the average residual heterozygosity for individual markers was 4.2% ranging between 0% and 66.7%. In the present study, an average of 4.3% residual heterozygosity was observed for these 455 new loci. Although all 26 chromosomes contained marker loci with high (5%) residual heterozygosity (Fig. 1), the distribution was clearly not even. More than 35% of the loci mapped in these 15 chromosomes (2, 17, 4, 22, 5, 19, 8, 24, 10, 20, 11, 21, 12, 26 and 15) had residual heterozygosity higher than 5%. It is worth mentioning that except Chr. 15, the remaining 14 chromosomes are seven pairs of homeologs. It remains unclear what caused this, and how it will impact the introgression of a *G. barbadense* trait/gene into *G. hirsutum*.

Duplicated marker loci at homeologous chromosomes are common in tetraploid cotton (Reinisch et al., 1994; Rong et al., 2004). Both RFLP and SSR markers revealed abundance of duplicate loci (Guo et al., 2008a; Lacape et al., 2009; Rong et al., 2004; Yu et al., 2011). Genes controlling fiberless traits, reniform nematode resistance, and cellulose synthesis were reported to have duplicates (An et al., 2010; Fang and Stetina, 2011; Kim et al., 2012). Previously, Yu et al. (2012b) reported 204 duplicated loci between homeologous chromosomes. In the current research, we identified an additional 110 pairs between homeologous chromosomes (Table 3). All together, 314 pairs of duplicate loci are identified, which account for approximately 27.5% of total mapped SSR loci (Fig. 1). Guo et al. (2008a) reported 182 pairs of duplicated loci that account for 19% of the mapped SSR marker loci. The difference might be due to the population structures, and more importantly the methods for detecting PCR products. We used ABI genetic analyzers to separate fluorescent-labeled PCR products. This method has resolution to separate 2-bp difference. Guo et al. (2007, 2008a) used polyacrylamide gel electrophoresis that has lower resolution, and consequently might have missed some fragments. For example, for markers BNL1030, BNL1034, BNL1122, BNL1161, and BNL1227, we revealed two loci for all of them, but Guo et al. (2007, 2008a) reveled only one locus for each primer pair.

Though less common, duplications between non-homeologous chromosomes are present in cotton genome. Yu et al. (2012b) identified 43 pairs in their report, and we revealed an additional 27 pairs in the present research. Guo et al. (2008a) reported 67 pairs. Non-homeologous duplications could be vestiges of

ancient polyploidization, i.e., remnants of ancient octaploid origins (Gutiérrez et al., 2009; Rong et al., 2004). They also could be the products of genomic re-arrangements, such as segmental translocations, transposition, or duplication (Endrizzi et al., 1985).

Intrachromosomal marker locus duplication has been observed in at least nine chromosomes. They are either in tandem (Chr. 05, Chr. 09, Chr. 11, Chr. 21) or disperse (Chr. 01, Chr. 12, Chr. 23, Chr. 20, Chr. 26). On Chr. 05, duplicate loci of three markers, SHIN-0289, NAU1042, and NAU1221, were mapped about 10 cM apart. Guo et al. (2008a) also observed intrachromosomal duplication for NAU1042. However, they mapped the duplicate loci on Chr. 19 with 14 cM apart. Duplication of COT003 loci on Chr. 11 validated our previous finding demonstrated by TMB0426 marker loci (Yu et al., 2012b). For the homeologous chromosome pair Chr. 12 and Chr. 26, one pair of duplicate loci was observed for each chromosome, mapped about 20 cM apart at the lower end of each chromosome (Fig. 1). Similarly, Guo et al. (2008a) reported duplicate loci of NAU3862, mapped 26 cM apart at the telomeric region of Chr. 26. Although telomeric regions of plant chromosomes are primarily heterochromatic, they are important not only in maintaining the integrity of chromosome structure but also in harboring the genes of interest. In cotton, the rootknot nematode resistance genes (Wang et al., 2006; Ynturi et al., 2006), blue disease resistance gene (Fang et al., 2010), bacterial blight resistance gene (Xiao et al., 2010), and Ligon-lintless 2 gene (Hinchliffe et al., 2011) are known to reside at or near telomeric regions. It is of much interest in studying the biological impact resulted from locus duplication.

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Table 3. One hundred forty-two pairs of duplicate SSR loci and their chromosome locations.

#	Marker loci	Homeologous relationship	Chromosomes	Position (cM)
1	DPL0003a	Chr.01--Chr.15	Chr.01(A01)	70.2
2	DPL0003b	Chr.01--Chr.15	Chr.15(D01)	50.3
3	DPL0029a	Chr.01--Chr.15	Chr.15(D01)	58.6
4	DPL0029b	Chr.01--Chr.15	Chr.01(A01)	84.8
5	DPL0052a	Chr.01--Chr.15	Chr.15(D01)	62.6
6	DPL0052b	Chr.01--Chr.15	Chr.01(A01)	88.9
7	DPL0053a	Chr.01--Chr.15	Chr.01(A01)	97.2
8	DPL0053b	Chr.01--Chr.15	Chr.15(D01)	68.3
9	DPL0090a	Chr.01--Chr.15	Chr.01(A01)	145.2
10	DPL0090b	Chr.01--Chr.15	Chr.15(D01)	119.0
11	DPL0109a	Chr.01--Chr.15	Chr.15(D01)	63.6
12	DPL0109b	Chr.01--Chr.15	Chr.01(A01)	90.5
13	DPL0187a	Chr.01--Chr.15	Chr.01(A01)	71.0
14	DPL0187b	Chr.01--Chr.15	Chr.15(D01)	47.7
15	SHIN-1397b	Chr.01--Chr.15	Chr.01(A01)	35.5
16	SHIN-1397c	Chr.01--Chr.15	Chr.15(D01)	30.6
17	COT064a	Chr.02--Chr.17	Chr.02(A02)	53.8
18	COT064b	Chr.02--Chr.17	Chr.17(D02)	44.8
19	DPL0041a	Chr.02--Chr.17	Chr.17(D02)	53.1
20	DPL0041b	Chr.02--Chr.17	Chr.02(A02)	58.1
21	DPL0200a	Chr.02--Chr.17	Chr.02(A02)	58.1
22	DPL0200b	Chr.02--Chr.17	Chr.17(D02)	53.3

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#	Marker loci	Homeologous relationship	Chromosomes	Position (cM)
23	DPL0883a	Chr.02--Chr.17	Chr.02(A02)	54.3
24	DPL0883b	Chr.02--Chr.17	Chr.17(D02)	45.5
25	C2-0037a	Chr.03--Chr.14	Chr.03(A03)	87.6
26	C2-0037b	Chr.03--Chr.14	Chr.14(D03)	94.6
27	DPL0195a	Chr.03--Chr.14	Chr.14(D03)	83.2
28	DPL0195b	Chr.03--Chr.14	Chr.03(A03)	82.2
29	DPL0268a	Chr.03--Chr.14	Chr.14(D03)	79.7
30	DPL0268b	Chr.03--Chr.14	Chr.03(A03)	78.6
31	DPL0756a	Chr.03--Chr.14	Chr.03(A03)	50.9
32	DPL0756c	Chr.03--Chr.14	Chr.14(D03)	48.9
33	SHIN-0659a	Chr.03--Chr.14	Chr.14(D03)	78.2
34	SHIN-0659b	Chr.03--Chr.14	Chr.03(A03)	76.5
35	DC40049a	Chr.04--Chr.22	Chr.04(A04)	80.0
36	DC40049b	Chr.04--Chr.22	Chr.22(D04)	84.1
37	DPL0107a	Chr.04--Chr.22	Chr.04(A04)	52.1
38	DPL0107b	Chr.04--Chr.22	Chr.22(D04)	60.7
39	DPL0126a	Chr.04--Chr.22	Chr.04(A04)	56.8
40	DPL0126b	Chr.04--Chr.22	Chr.22(D04)	68.5
41	DPL0562a	Chr.04--Chr.22	Chr.04(A04)	64.5
42	DPL0562b	Chr.04--Chr.22	Chr.22(D04)	78.2
43	COT010a	Chr.05--Chr.19	Chr.05(A05)	73.7
44	COT010b	Chr.05--Chr.19	Chr.19(D05)	60.0
45	COT089a	Chr.05--Chr.19	Chr.05(A05)	141.2
46	COT089b	Chr.05--Chr.19	Chr.19(D05)	117.6
47	DC20067b	Chr.05--Chr.19	Chr.05(A05)	187.5
48	DC20067c	Chr.05--Chr.19	Chr.19(D05)	167.6
49	DPL0001a	Chr.05--Chr.19	Chr.19(D05)	87.7
50	DPL0001b	Chr.05--Chr.19	Chr.05(A05)	112.3
51	DPL0064a	Chr.05--Chr.19	Chr.05(A05)	132.2
52	DPL0064b	Chr.05--Chr.19	Chr.19(D05)	104.6
53	DPL0138a	Chr.05--Chr.19	Chr.19(D05)	140.3
54	DPL0138b	Chr.05--Chr.19	Chr.05(A05)	158.0
55	DPL0145a	Chr.05--Chr.19	Chr.19(D05)	123.8
56	DPL0145b	Chr.05--Chr.19	Chr.05(A05)	142.6
57	DPL0155a	Chr.05--Chr.19	Chr.05(A05)	109.0
58	DPL0155c	Chr.05--Chr.19	Chr.19(D05)	91.2
59	DPL0174a	Chr.05--Chr.19	Chr.19(D05)	87.8
60	DPL0174b	Chr.05--Chr.19	Chr.05(A05)	98.4
61	DPL0297a	Chr.05--Chr.19	Chr.19(D05)	119.7
62	DPL0297b	Chr.05--Chr.19	Chr.05(A05)	141.0
63	DPL0305a	Chr.05--Chr.19	Chr.05(A05)	143.4
64	DPL0305b	Chr.05--Chr.19	Chr.19(D05)	115.5

Continued next page

#	Marker loci	Homeologous relationship	Chromosomes	Position (cM)
65	DPL0397a	Chr.05--Chr.19	Chr.05(A05)	187.9
66	DPL0397c	Chr.05--Chr.19	Chr.19(D05)	168.3
67	DPL0556a	Chr.05--Chr.19	Chr.19(D05)	141.8
68	DPL0556b	Chr.05--Chr.19	Chr.05(A05)	155.3
69	DPL0908a	Chr.05--Chr.19	Chr.05(A05)	72.8
70	DPL0908b	Chr.05--Chr.19	Chr.19(D05)	59.6
71	SHIN-0289a	Chr.05--Chr.19	Chr.05(A05)	148.9
72	SHIN-0289b	Chr.05--Chr.19	Chr.19(D05)	121.1
73	DPL0059a	Chr.06--Chr.25	Chr.06(A06)	133.8
74	DPL0059b	Chr.06--Chr.25	Chr.25(D06)	118.3
75	DPL0124a	Chr.06--Chr.25	Chr.06(A06)	75.1
76	DPL0124c	Chr.06--Chr.25	Chr.25(D06)	69.1
77	DPL0244a	Chr.06--Chr.25	Chr.06(A06)	56.1
78	DPL0244b	Chr.06--Chr.25	Chr.25(D06)	50.0
79	DPL0257a	Chr.06--Chr.25	Chr.25(D06)	31.2
80	DPL0257b	Chr.06--Chr.25	Chr.06(A06)	34.1
81	DPL0375a	Chr.06--Chr.25	Chr.25(D06)	76.9
82	DPL0375b	Chr.06--Chr.25	Chr.06(A06)	82.0
83	DPL0702a	Chr.06--Chr.25	Chr.25(D06)	86.1
84	DPL0702b	Chr.06--Chr.25	Chr.06(A06)	86.9
85	C2-0011Ba	Chr.07--Chr.16	Chr.07(A07)	87.8
86	C2-0011Bb	Chr.07--Chr.16	Chr.16(D07)	81.5
87	COT104a	Chr.07--Chr.16	Chr.07(A07)	30.3
88	COT104b	Chr.07--Chr.16	Chr.16(D07)	17.0
89	DC20124a	Chr.07--Chr.16	Chr.07(A07)	89.0
90	DC20124c	Chr.07--Chr.16	Chr.16(D07)	82.9
91	DPL0013c	Chr.07--Chr.16	Chr.16(D07)	43.6
92	DPL0013d	Chr.07--Chr.16	Chr.07(A07)	52.7
93	DPL0167a	Chr.07--Chr.16	Chr.16(D07)	73.0
94	DPL0167b	Chr.07--Chr.16	Chr.07(A07)	79.9
95	DPL0364a	Chr.07--Chr.16	Chr.16(D07)	125.1
96	DPL0364b	Chr.07--Chr.16	Chr.07(A07)	134.8
97	DPL0492a	Chr.07--Chr.16	Chr.16(D07)	2.9
98	DPL0492b	Chr.07--Chr.16	Chr.07(A07)	3.0
99	SHIN-0376a	Chr.07--Chr.16	Chr.07(A07)	105.1
100	SHIN-0376b	Chr.07--Chr.16	Chr.16(D07)	99.2
101	SHIN-1405a	Chr.07--Chr.16	Chr.07(A07)	108.3
102	SHIN-1405b	Chr.07--Chr.16	Chr.16(D07)	102.0
103	DC40127a	Chr.08--Chr.24	Chr.24(D08)	28.8
104	DC40127b	Chr.08--Chr.24	Chr.08(A08)	67.5
105	DC40404a	Chr.08--Chr.24	Chr.24(D08)	96.3
106	DC40404b	Chr.08--Chr.24	Chr.08(A08)	116.5

Continued next page

#	Marker loci	Homeologous relationship	Chromosomes	Position (cM)
107	DPL0031a	Chr.08--Chr.24	Chr.08(A08)	85.0
108	DPL0031b	Chr.08--Chr.24	Chr.24(D08)	60.0
109	DPL0111a	Chr.08--Chr.24	Chr.24(D08)	22.9
110	DPL0111b	Chr.08--Chr.24	Chr.08(A08)	59.3
111	DPL0133a	Chr.08--Chr.24	Chr.08(A08)	71.7
112	DPL0133b	Chr.08--Chr.24	Chr.24(D08)	43.3
113	DPL0152a	Chr.08--Chr.24	Chr.24(D08)	118.4
114	DPL0152b	Chr.08--Chr.24	Chr.08(A08)	146.2
115	DPL0154a	Chr.08--Chr.24	Chr.24(D08)	30.7
116	DPL0154b	Chr.08--Chr.24	Chr.08(A08)	59.1
117	DPL0214a	Chr.08--Chr.24	Chr.08(A08)	89.8
118	DPL0214b	Chr.08--Chr.24	Chr.24(D08)	59.9
119	DPL0488a	Chr.08--Chr.24	Chr.08(A08)	114.1
120	DPL0488b	Chr.08--Chr.24	Chr.24(D08)	68.2
121	DPL0862a	Chr.08--Chr.24	Chr.24(D08)	26.5
122	DPL0862b	Chr.08--Chr.24	Chr.08(A08)	61.2
123	DPL0877a	Chr.08--Chr.24	Chr.24(D08)	28.8
124	DPL0877b	Chr.08--Chr.24	Chr.08(A08)	65.5
125	SHIN-0352a	Chr.08--Chr.24	Chr.08(A08)	87.1
126	SHIN-0352b	Chr.08--Chr.24	Chr.24(D08)	59.7
127	SHIN-0426a	Chr.08--Chr.24	Chr.24(D08)	72.7
128	SHIN-0426b	Chr.08--Chr.24	Chr.08(A08)	93.4
129	SHIN-1435a	Chr.08--Chr.24	Chr.08(A08)	76.3
130	SHIN-1435b	Chr.08--Chr.24	Chr.24(D08)	49.4
131	SHIN-1494a	Chr.08--Chr.24	Chr.08(A08)	148.0
132	SHIN-1494b	Chr.08--Chr.24	Chr.24(D08)	116.5
133	DC30213a	Chr.09--Chr.23	Chr.09(A09)	79.4
134	DC30213b	Chr.09--Chr.23	Chr.23(D09)	85.1
135	DC40129a	Chr.09--Chr.23	Chr.23(D09)	100.7
136	DC40129b	Chr.09--Chr.23	Chr.09(A09)	101.6
137	DC40407a	Chr.09--Chr.23	Chr.09(A09)	42.4
138	DC40407c	Chr.09--Chr.23	Chr.23(D09)	71.7
139	DPL0044a	Chr.09--Chr.23	Chr.09(A09)	96.1
140	DPL0044b	Chr.09--Chr.23	Chr.23(D09)	96.6
141	DPL0093a	Chr.09--Chr.23	Chr.09(A09)	64.2
142	DPL0093b	Chr.09--Chr.23	Chr.23(D09)	68.8
143	DPL0356a	Chr.09--Chr.23	Chr.09(A09)	25.2
144	DPL0356b	Chr.09--Chr.23	Chr.23(D09)	36.3
145	DPL0524a	Chr.09--Chr.23	Chr.09(A09)	119.1
146	DPL0524b	Chr.09--Chr.23	Chr.23(D09)	123.2
147	DPL0745a	Chr.09--Chr.23	Chr.23(D09)	78.0
148	DPL0745b	Chr.09--Chr.23	Chr.09(A09)	74.1

Continued next page

#	Marker loci	Homeologous relationship	Chromosomes	Position (cM)
149	DPL0783a	Chr.09--Chr.23	Chr.09(A09)	26.0
150	DPL0783b	Chr.09--Chr.23	Chr.23(D09)	37.1
151	SHIN-0050a	Chr.09--Chr.23	Chr.09(A09)	50.4
152	SHIN-0050b	Chr.09--Chr.23	Chr.23(D09)	54.7
153	COT119a	Chr.10--Chr.20	Chr.20(D10)	16.4
154	COT119b	Chr.10--Chr.20	Chr.10(A10)	19.1
155	DPL0037a	Chr.10--Chr.20	Chr.20(D10)	68.0
156	DPL0037b	Chr.10--Chr.20	Chr.10(A10)	90.6
157	DPL0108a	Chr.10--Chr.20	Chr.20(D10)	59.2
158	DPL0108c	Chr.10--Chr.20	Chr.10(A10)	72.5
159	DPL0149a	Chr.10--Chr.20	Chr.10(A10)	95.5
160	DPL0149b	Chr.10--Chr.20	Chr.20(D10)	87.8
161	DPL0394a	Chr.10--Chr.20	Chr.20(D10)	80.3
162	DPL0394b	Chr.10--Chr.20	Chr.10(A10)	99.2
163	DPL0707a	Chr.10--Chr.20	Chr.10(A10)	77.0
164	DPL0707b	Chr.10--Chr.20	Chr.20(D10)	56.6
165	DC40250a	Chr.11--Chr.21	Chr.21(D11)	66.4
166	DC40250b	Chr.11--Chr.21	Chr.11(A11)	49.4
167	DC40316a	Chr.11--Chr.21	Chr.21(D11)	147.4
168	DC40316b	Chr.11--Chr.21	Chr.11(A11)	162.8
169	DPL0065a	Chr.11--Chr.21	Chr.21(D11)	87.8
170	DPL0065b	Chr.11--Chr.21	Chr.11(A11)	94.1
171	DPL0103a	Chr.11--Chr.21	Chr.11(A11)	109.5
172	DPL0103b	Chr.11--Chr.21	Chr.21(D11)	96.4
173	DPL0412a	Chr.11--Chr.21	Chr.11(A11)	78.3
174	DPL0412b	Chr.11--Chr.21	Chr.21(D11)	78.2
175	DPL0522a	Chr.11--Chr.21	Chr.11(A11)	12.4
176	DPL0522b	Chr.11--Chr.21	Chr.21(D11)	19.2
177	DPL0863a	Chr.11--Chr.21	Chr.11(A11)	25.9
178	DPL0863b	Chr.11--Chr.21	Chr.21(D11)	37.2
179	C2-0115a	Chr.12--Chr.26	Chr.26(D12)	27.1
180	C2-0115b	Chr.12--Chr.26	Chr.12(A12)	37.1
181	DC30107a	Chr.12--Chr.26	Chr.12(A12)	84.2
182	DC30107b	Chr.12--Chr.26	Chr.26(D12)	73.6
183	DC30183a	Chr.12--Chr.26	Chr.12(A12)	86.9
184	DC30183c	Chr.12--Chr.26	Chr.26(D12)	75.3
185	DPL0011a	Chr.12--Chr.26	Chr.26(D12)	41.8
186	DPL0011b	Chr.12--Chr.26	Chr.12(A12)	48.0
187	DPL0057a	Chr.12--Chr.26	Chr.12(A12)	3.8
188	DPL0057b	Chr.12--Chr.26	Chr.26(D12)	0.0
189	DPL0070a	Chr.12--Chr.26	Chr.12(A12)	84.0
190	DPL0070b	Chr.12--Chr.26	Chr.26(D12)	73.8

Continued next page

#	Marker loci	Homeologous relationship	Chromosomes	Position (cM)
191	DPL0144a	Chr.12--Chr.26	Chr.26(D12)	22.5
192	DPL0144c	Chr.12--Chr.26	Chr.12(A12)	38.2
193	DPL0208a	Chr.12--Chr.26	Chr.26(D12)	85.7
194	DPL0208c	Chr.12--Chr.26	Chr.12(A12)	94.0
195	DPL0240a	Chr.12--Chr.26	Chr.12(A12)	50.3
196	DPL0240b	Chr.12--Chr.26	Chr.26(D12)	40.9
197	DPL0248a	Chr.12--Chr.26	Chr.12(A12)	38.3
198	DPL0248c	Chr.12--Chr.26	Chr.26(D12)	31.2
199	DPL0363a	Chr.12--Chr.26	Chr.12(A12)	116.9
200	DPL0363c	Chr.12--Chr.26	Chr.26(D12)	112.0
201	DPL0379a	Chr.12--Chr.26	Chr.12(A12)	75.2
202	DPL0379b	Chr.12--Chr.26	Chr.26(D12)	64.9
203	DPL0380a	Chr.12--Chr.26	Chr.12(A12)	79.7
204	DPL0380b	Chr.12--Chr.26	Chr.26(D12)	64.7
205	DPL0565a	Chr.12--Chr.26	Chr.26(D12)	63.9
206	DPL0565b	Chr.12--Chr.26	Chr.12(A12)	77.0
207	DPL0917a	Chr.12--Chr.26	Chr.26(D12)	108.1
208	DPL0917b	Chr.12--Chr.26	Chr.12(A12)	114.7
209	DPL0083a	Chr.13--Chr.18	Chr.18(D13)	55.1
210	DPL0083b	Chr.13--Chr.18	Chr.13(A13)	78.8
211	DPL0161a	Chr.13--Chr.18	Chr.13(A13)	74.5
212	DPL0161b	Chr.13--Chr.18	Chr.18(D13)	49.8
213	DPL0286a	Chr.13--Chr.18	Chr.13(A13)	34.4
214	DPL0286b	Chr.13--Chr.18	Chr.18(D13)	25.0
215	DPL0308a	Chr.13--Chr.18	Chr.13(A13)	75.7
216	DPL0308b	Chr.13--Chr.18	Chr.18(D13)	49.1
217	DPL0864a	Chr.13--Chr.18	Chr.18(D13)	48.9
218	DPL0864b	Chr.13--Chr.18	Chr.13(A13)	72.2
219	DPL0894a	Chr.13--Chr.18	Chr.18(D13)	28.8
220	DPL0894b	Chr.13--Chr.18	Chr.13(A13)	39.4
221	DPL0074a	Chr.02--Chr.14	Chr.02(A02)	66.3
222	DPL0074b	Chr.02--Chr.14	Chr.14(D03)	48.4
223	DPL0245a	Chr.02--Chr.14	Chr.14(D03)	108.2
224	DPL0245b	Chr.02--Chr.14	Chr.02(A02)	26.2
225	DPL0545a	Chr.02--Chr.14	Chr.02(A02)	124.8
226	DPL0545b	Chr.02--Chr.14	Chr.14(D03)	0.1
227	DPL0095a	Chr.03--Chr.17	Chr.17(D02)	61.9
228	DPL0095b	Chr.03--Chr.17	Chr.03(A03)	31.4
229	DPL0197a	Chr.03--Chr.17	Chr.17(D02)	59.2
230	DPL0197b	Chr.03--Chr.17	Chr.03(A03)	38.5
231	DPL0232a	Chr.03--Chr.17	Chr.03(A03)	46.7
232	DPL0232b	Chr.03--Chr.17	Chr.17(D02)	56.5

Continued next page

#	Marker loci	Homeologous relationship	Chromosomes	Position (cM)
233	SHIN-1343a	Chr.03--Chr.17	Chr.17(D02)	90.3
234	SHIN-1343b	Chr.03--Chr.17	Chr.03(A03)	11.0
235	C2-0135a	Non-homeologous	Chr.26(D12)	39.5
236	C2-0135b	Non-homeologous	Chr.14(D01)	64.2
237	C2-0135c	Non-homeologous	Chr.19(D05)	68.8
238	COT003a	Non-homeologous	Chr.13(A13)	52.7
239	COT003b	Non-homeologous	Chr.11(A11)	113.8
240	COT003c	Non-homeologous	Chr.11(A11)	106.9
241	DC40041a	Non-homeologous	Chr.09(A09)	0.0
242	DC40041b	Non-homeologous	Chr.02(A02)	83.3
243	DC40087a	Non-homeologous	Chr.12(A12)	42.4
244	DC40087b	Non-homeologous	Chr.05(A05)	156.4
245	DC40108a	Non-homeologous	Chr.08(A08)	61.0
246	DC40108b	Non-homeologous	Chr.10(A10)	63.4
247	DC40233a	Non-homeologous	Chr.07(A07)	29.1
248	DC40233b	Non-homeologous	Chr.09(A09)	9.7
249	DPL0137a	Non-homeologous	Chr.04(A04)	45.8
250	DPL0137b	Non-homeologous	Chr.19(D05)	61.1
251	DPL0173a	Non-homeologous	Chr.06(A06)	85.5
252	DPL0173b	Non-homeologous	Chr.19(D05)	60.0
253	DPL0201a	Non-homeologous	Chr.04(A04)	106.3
254	DPL0201b	Non-homeologous	Chr.13(A13)	7.3
255	DPL0243a	Non-homeologous	Chr.26(D12)	33.6
256	DPL0243b	Non-homeologous	Chr.25(D06)	53.2
257	DPL0290a	Non-homeologous	Chr.22(D04)	45.6
258	DPL0290b	Non-homeologous	Chr.25(D06)	50.4
259	DPL0390a	Non-homeologous	Chr.22(D04)	26.2
260	DPL0390b	Non-homeologous	Chr.14(D03)	79.6
261	DPL0390c	Non-homeologous	Chr.16(D07)	103.3
262	DPL0404a	Non-homeologous	Chr.26(D12)	103.4
263	DPL0404b	Non-homeologous	Chr.26(D12)	120.2
264	DPL0426a	Non-homeologous	Chr.03(A03)	89.6
265	DPL0426b	Non-homeologous	Chr.03(A03)	31.0
266	DPL0525a	Non-homeologous	Chr.10(A10)	52.5
267	DPL0525b	Non-homeologous	Chr.03(A03)	40.6
268	DPL0546a	Non-homeologous	Chr.06(A06)	78.6
269	DPL0546b	Non-homeologous	Chr.01(A01)	115.6
270	DPL0644a	Non-homeologous	Chr.01(A01)	71.2
271	DPL0644b	Non-homeologous	Chr.12(A12)	44.1
272	DPL0744a	Non-homeologous	Chr.03(A03)	57.8
273	DPL0744b	Non-homeologous	Chr.11(A11)	107.7
274	DPL0776a	Non-homeologous	Chr.26(D12)	25.4
275	DPL0776b	Non-homeologous	Chr.21(D11)	70.5

Figure 1. Genetic linkage maps of 26 allotetraploid cotton chromosomes presented in 13 At and Dt subgenome homeologous pairs (in parentheses). The names of DNA markers are shown on the right and the positions of the markers are shown in Kosambi centiMorgan (cM) on the left. A line bar connects duplicate marker loci between a pair of homeologous chromosomes. Duplicate loci within a chromosome are connected with square brackets ([ ]). Marker loci in bold, italic, and larger font are the new markers added in this study. A marker with 5% or higher residual heterozygosity is labeled with *.

Figure 1. continued.

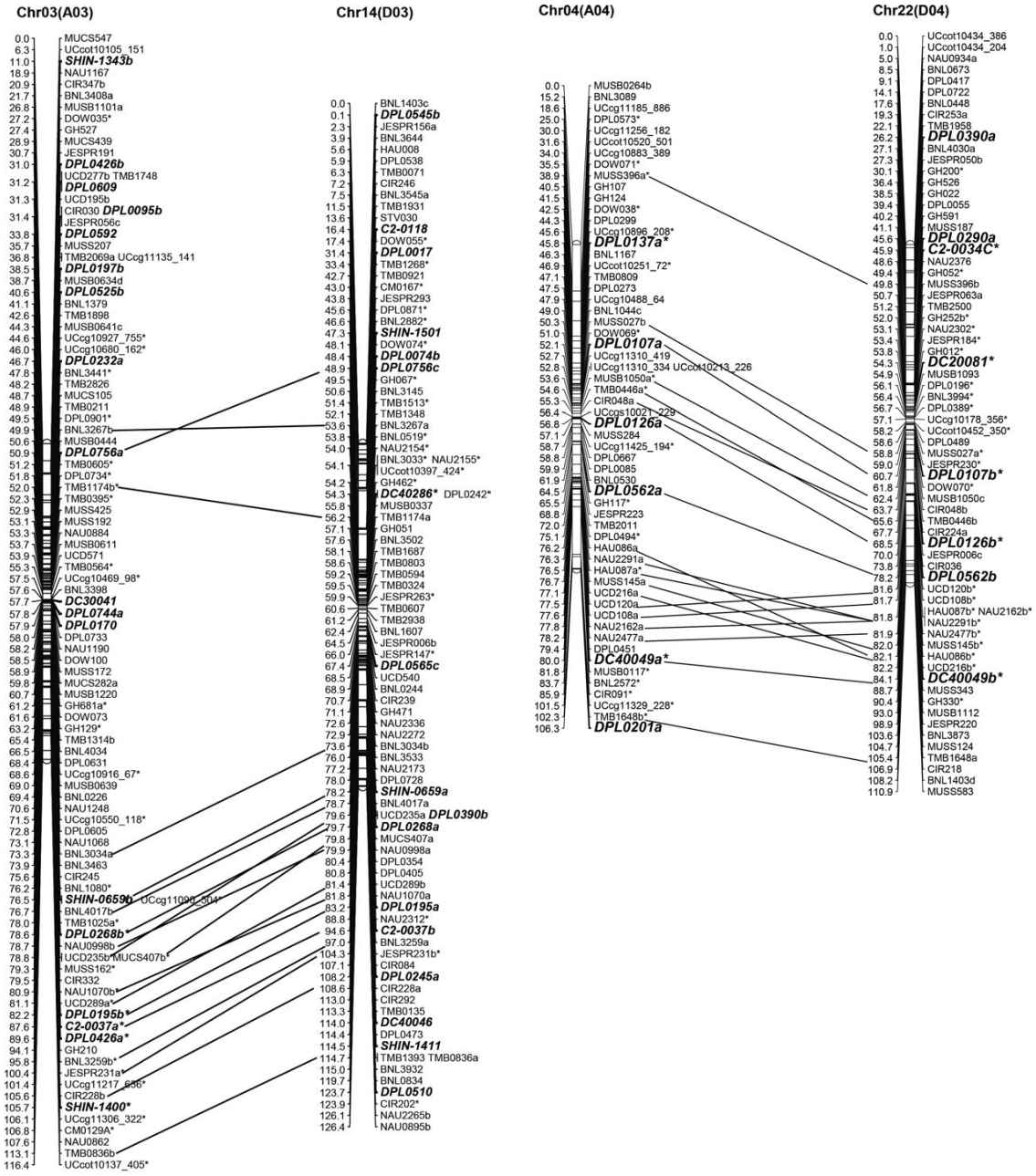


Figure 1. continued.

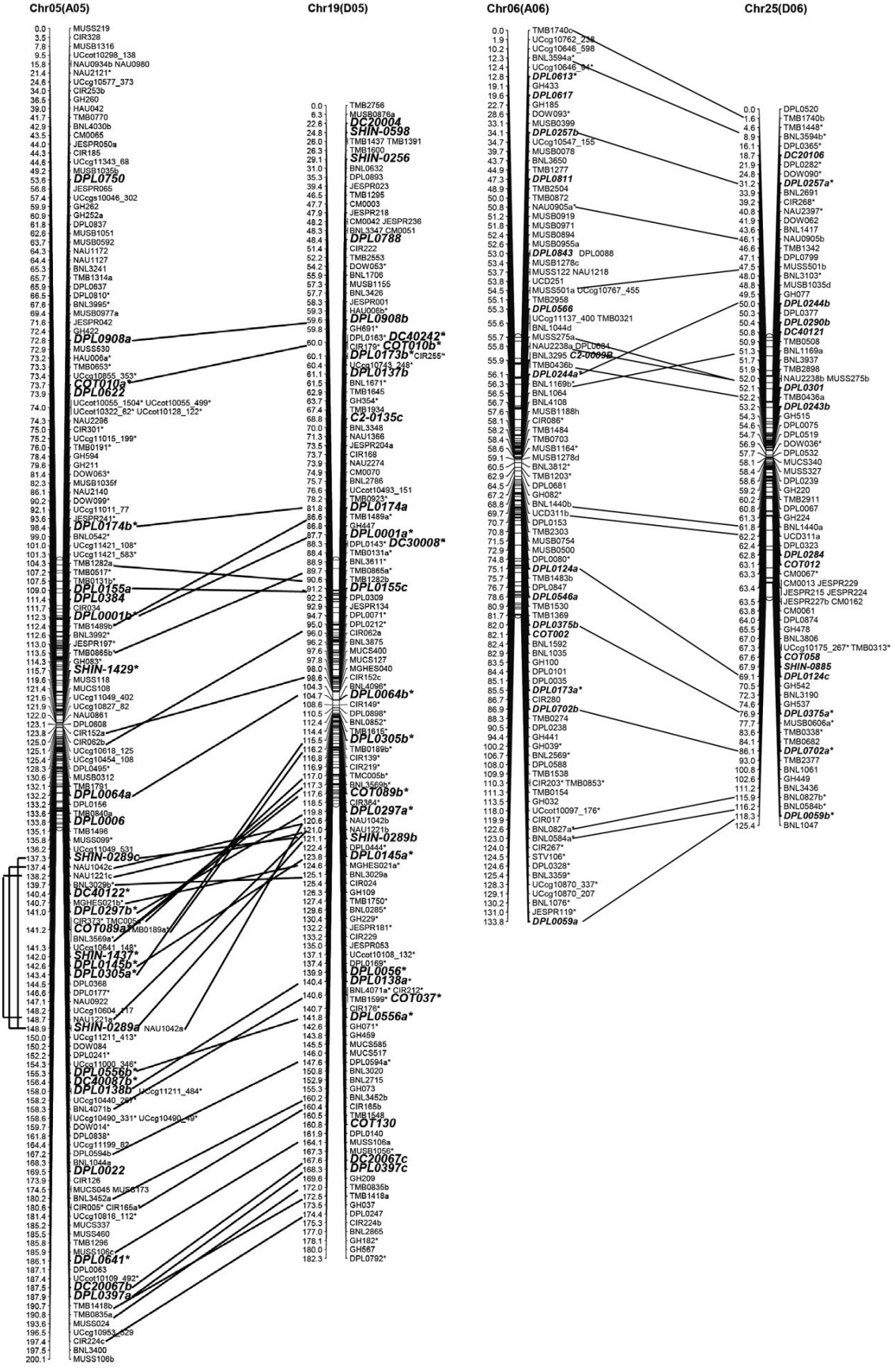


Figure 1. continued.

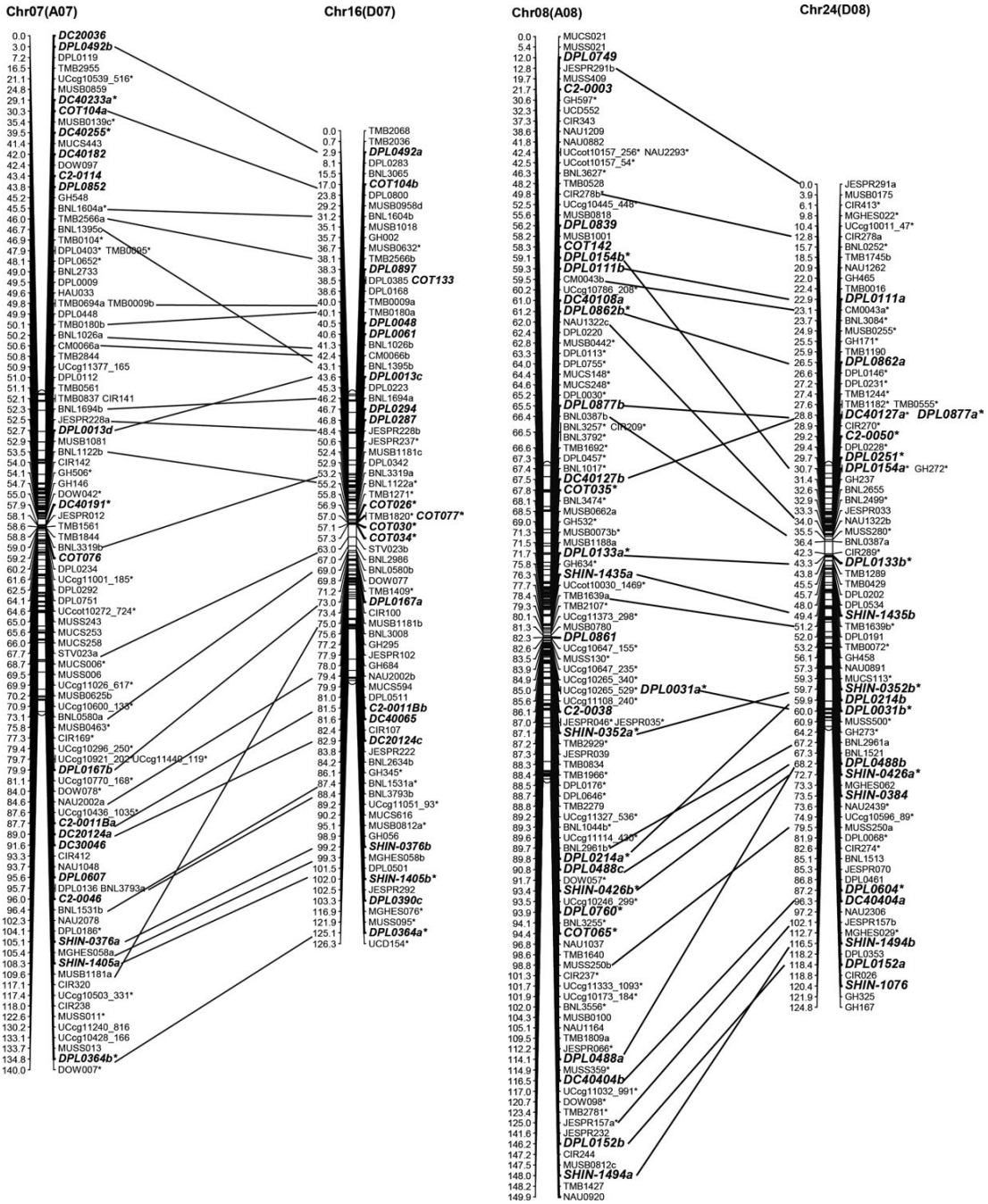


Figure 1. continued.

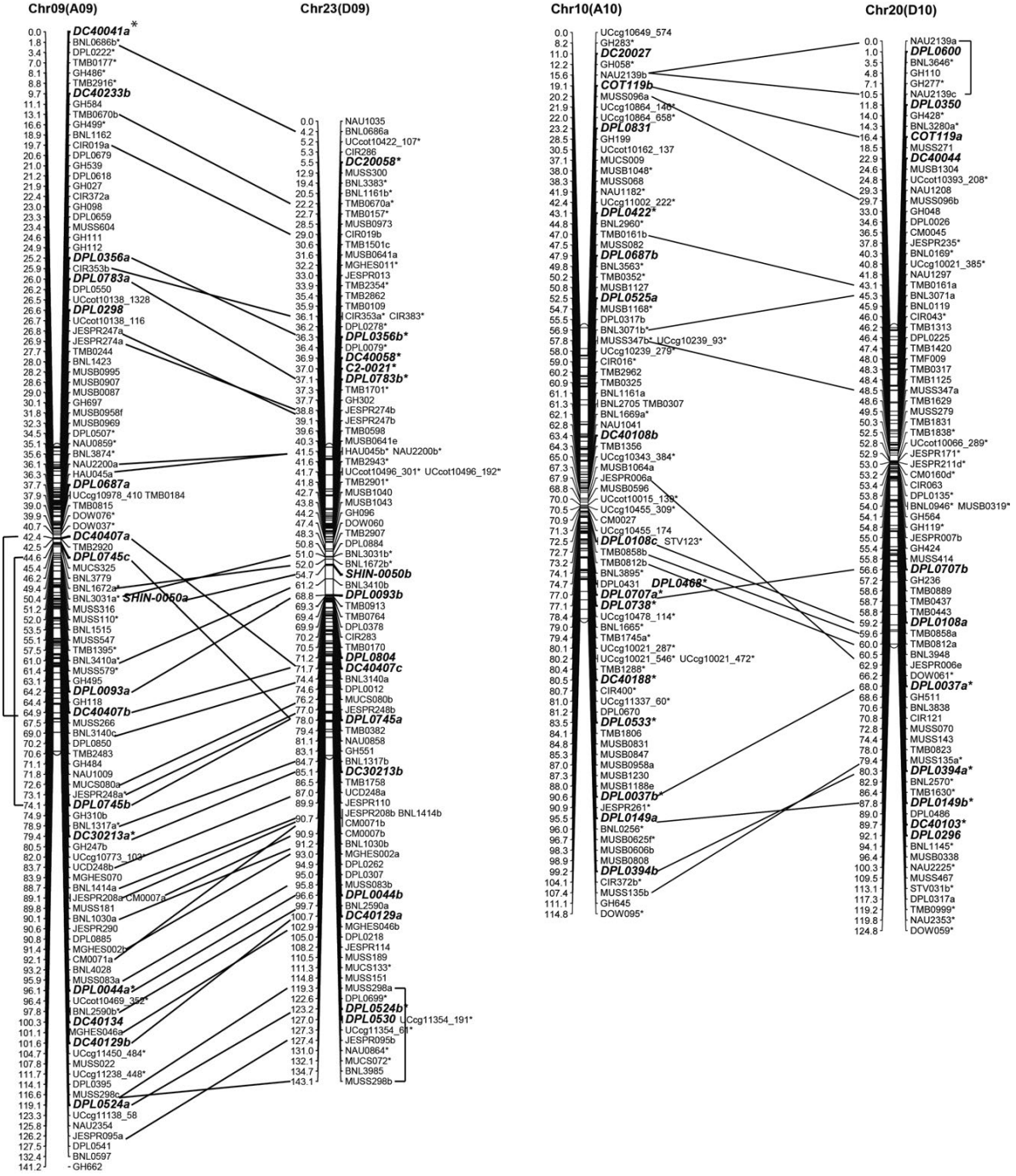


Figure 1. continued.

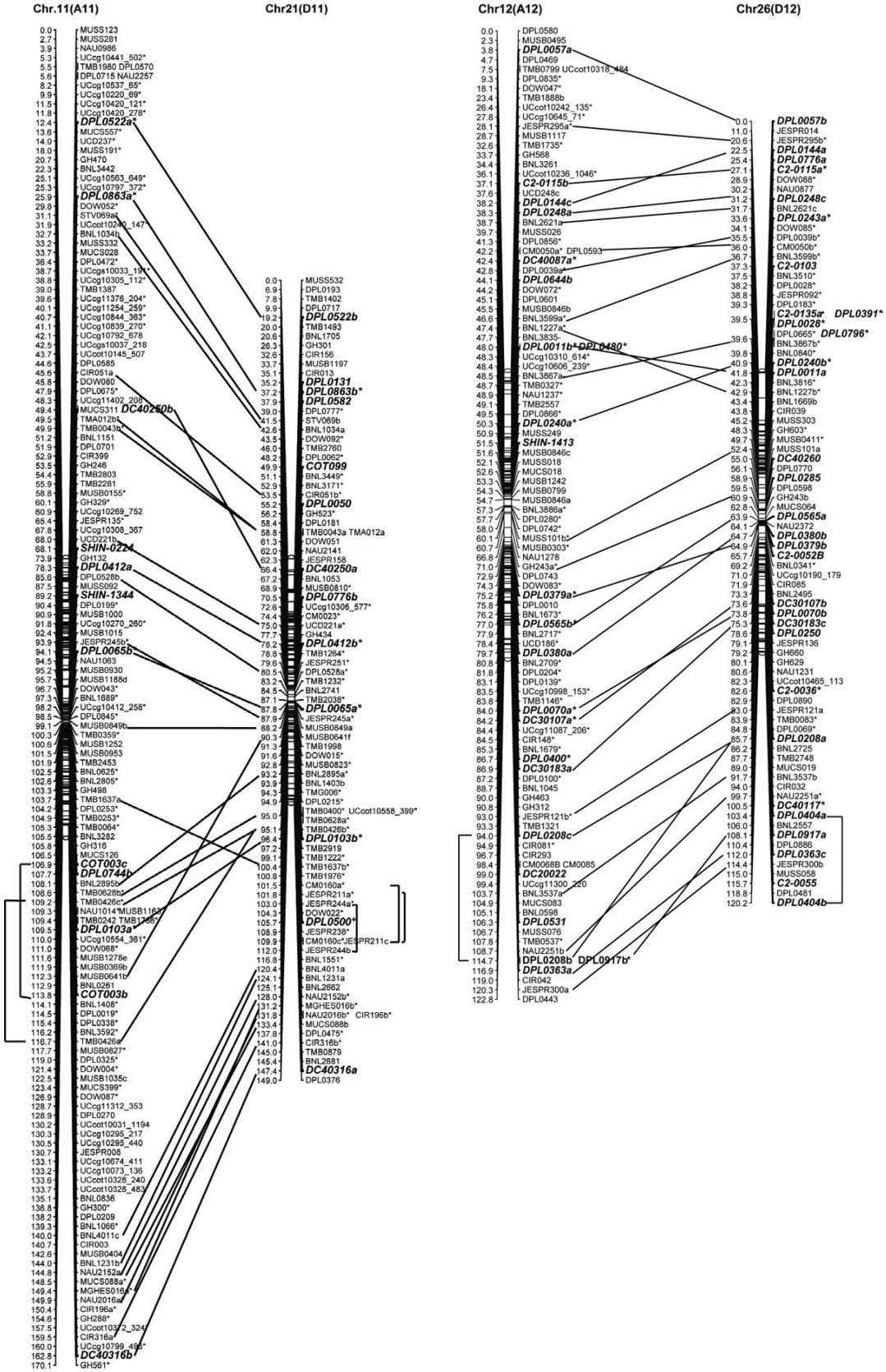
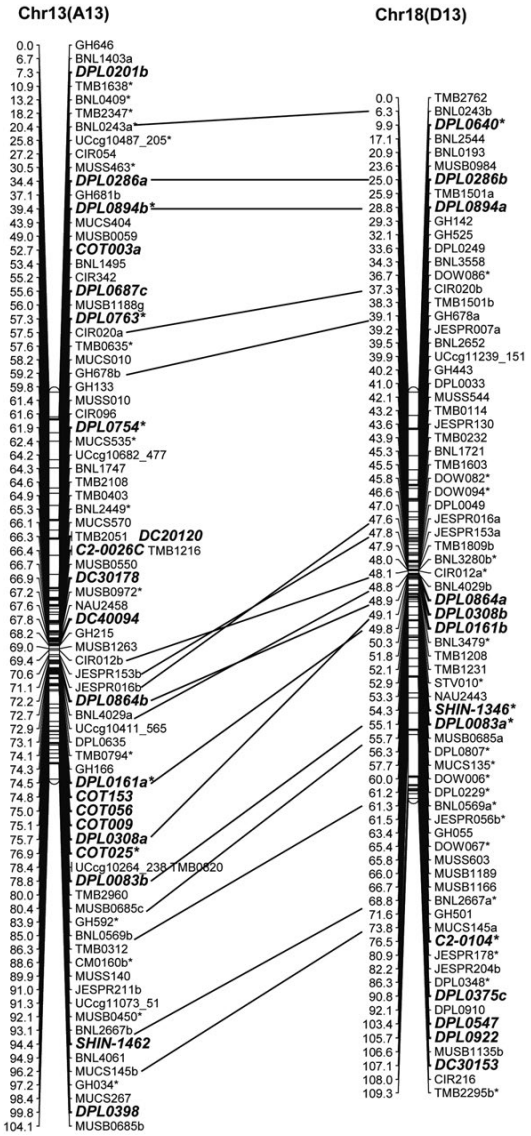


Figure 1. continued.



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