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A high-density genetic linkage map of *Aegilops tauschii*, the D-genome progenitor of bread wheat

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Abstract *Aegilops tauschii* is the diploid D-genome progenitor of bread wheat (*Triticum aestivum* L. em Thell, 2n = 6*x* = 42, AABBDD). A genetic linkage map of the *Ae. tauschii* genome was constructed, composed of 546 loci. One hundred and thirty two loci (24%) gave distorted segregation ratios. Sixty nine probes (13%) detected multiple copies in the genome. One hundred and twenty three of the 157 markers shared between the *Ae. tauschii* genetic and *T. aestivum* physical maps were colinear. The discrepancy in the order of five markers on the *Ae. tauschii* 3DS genetic map versus the *T. aestivum* 3D physical map indicated a possible inversion. Further work is needed to verify the discrepancies in the order of markers on the 4D, 5D and 7D *Ae. tauschii* genetic maps versus the physical and genetic maps of *T. aestivum*. Using common markers, 164 agronomically important genes were assigned to specific regions on *Ae. tauschii* linkage, and *T. aestivum* physical, maps. This information may be useful for map-based cloning and marker-assisted plant breeding.

Key words *Aegilops tauschii* · *Triticum aestivum* · Genetic mapping · Molecular markers · Agronomically important genes

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Introduction

Aegilops tauschii (Coss.) Schmal. (2n = 2*x* = 14, DD) (syn. *Ae. squarrosa* L.; *T. tauschii*) is the diploid D-genome donor of bread wheat (*Triticum aestivum* L. em. Thell., 2n = 6*x* = 42, AABBDD) (Kihara 1944; McFadden and Sears 1946). Kam-Morgan et al. (1989) proposed that *Ae. tauschii* is ideal for genetic mapping because of its diploid inheritance, high level of polymorphism among accessions, and almost complete homology to the D-genome of bread wheat. Gill et al. (1991) constructed the first genetic linkage map of *Ae. tauschii* which consisted of 178 markers. In the present report, we provide a more extensive genetic linkage map of *Ae. tauschii* and compare it to the D-genome and consensus physical maps of bread wheat (Gill et al. 1993; Hohmann et al. 1994; Delaney et al. 1995a, b; Mickelson-Young et al. 1995; Gill et al. 1996a, b). The information on the genetic and physical location of markers related to agronomically important genes will be useful for map-based cloning and marker-assisted plant breeding.

Materials and methods

Plant materials

A population of 56 F_2 plants derived from an *Ae. tauschii* var. *meyeri* (TA1691) × var. *typica* (TA1704) cross was used for RFLP analysis (Gill et al. 1991). In some cases, DNA was isolated from pooled leaf-tissue samples of at least ten F_3 plants representing individual F_2 plants. All plant material is maintained by the Wheat Genetics Resource Center, Kansas State University, Manhattan, Kansas.

Genetic mapping

A list of all markers used for RFLP and AFLP mapping and their location on the *Ae. tauschii*, *T. aestivum*, *H. vulgare and T. monococcum* maps can be found on the internet at < http://wheat.pw.usda.gov/ggpages/Ae.tauschii.markers/ >. Mapping was performed with 368 anonymous clones, including 255 wheat clones (64 cDNAs and 191 gDNAs), 85 barley clones (35 cDNAs and 50 gDNAs), and four miscellaneous clones. Clones representing genes of known function were pTaadh3′ (alcohol dehydrogenase), cxp1 (carboxypeptidase), dhn2, dhn3, dhn5 (dehydrins), gsp (grain softness protein), pTa71 (18S and 26S rRNA), and ten protein clones as previously described (Gill et al. 1991). The population also segregated for an unnamed leaf rust resistance gene (Gill et al. 1991).

For the 53 AFLP markers, scored by J.S. Ziegle (Perkin–Elmer, Applied Biosystems Division), the adapter oligonucleotides for the *Eco*RI-ligated ends were:

Primer 1: CTC GTA GAC TGC GTA CC,
Primer 2: AAT TGG TAC GCA GTC.

The adapter oligonucleotides for the *Mse*I ligated ends were:

Primer 1: GAC GAT GAG TCC TGA G,
Primer 2: TAC TCA GGA CTC AT.

The core sequence for the selective primer for the *Eco*RI side was GAC TGC GTA CCA ATT C. The selective bases to the 3′ end of the *Eco*RI side were CAC for the *Xpea1*, *Xpea3* and *Xpea4* class of markers, and CCA for the *Xpea2* class of markers. The core sequence for the selective primer for the *Mse*I side was GAT GAG TCC TGA GTA A. The selective bases to the 3′ end of the *Mse*I side were CTC for *Xpea1*, ATC for *Xpea2*, ACA for *Xpea3*, and ACT for *Xpea4*.

All procedures in this study were previously described in Gill et al. (1991). All clones were obtained from members of the ITMI (International Triticeae Mapping Initiative). Lab designators for these laboratories are listed in McGuire and Qualset (1997) and McIntosh et al. (1998).

Autoradiograms for each probe were scored independently by three individuals. In case of any disagreement in scoring, the autoradiogram was re-checked and scored by consensus. The linkage map was generated from F_2 data of Gill et al. (1991) and data collected in present study using the Mapmaker 2.0 computer program (Lander et al. 1987). The markers grouped at a LOD threshold of 6.0 were used for construction for the basic map (LOD > 2.0). The positions of the remaining markers on the basic map were placed using the command "Try". If more than one marker was assigned between two markers of the basic map, their order was determined with the command "Compare". These markers are positioned on the map in the most-likely order without considering the map distances between them. Map distances between markers were computed using the Kosambi mapping function (Kosambi 1944). Markers with distorted segregation ratios were identified using the chi-square test for a fit to 1:2:1, 1:3, or 3:1 ratios.

The arm orientation and location of the centromeric region were inferred by comparing the positions of markers shared by the *Ae. tauchii* linkage and the *T. aestivum* physical maps, which were constructed using deletion lines of wheat (Gill et al. 1993; Hohmann et al. 1994; Delaney et al. 1995a, b; Mickelson-Young et al. 1995; Endo and Gill 1996; Gill et al. 1996 a, b).

Results

The linkage map of the seven *Ae. tauschii* chromosomes consists of 546 loci and includes 176 loci that constitute the basic map (LOD > 2.0) (Table 1, Fig. 1 a–g). One hundred and thirty two markers (24%) gave distorted segregation ratios ($P < 0.05$). Sixty nine probes (13%) detected multiple (2–12) copies in the genome. The majority of sets of multiple loci (78%) were detected with genomic DNA probes. The mapping pattern of these loci did not reveal any ancient pattern of tandem duplications. Forty one of the 53 AFLP markers were mapped on all seven chromosomes, and appeared to be distributed at random. Twelve AFLP markers were unlinked. The linkage maps of individual chromosomes are briefly described below.

Chromosome 1D: The map of chromosome 1D (Fig. 1) consists of 68 loci. Sixteen loci in both arms showed segregation distortion. A DNA marker for a grain softness protein (*XGsp*) and a gene encoding gliadin (*Gli-D1*) are mapped in the short arm. A glutenin gene (*Glu-D1*) and an alcohol dehydrogenase [*Xcsd19(Adh)*] gene are in the long arm.

There are 17 common markers between the 1D genetic and physical maps. The linear order of markers on both maps is identical, although the order of markers between deletion breakpoints on a physical map is not known. The location of *XGsp* (GSP detected only one major band in each parent) on 1D is anomalous compared to its location in hexaploid wheat. The fragment detected by the GSP probe was physically mapped in the telomeric region on group-5 chromosomes of *T. aestivum* (Gill et al. 1996 a) and genetically to 5DS in *Ae. tauschii* (Lagudah et al. 1991 a; Gill et al. 1996 b). In our study, when the markers were grouped using a

Table 1 Number of loci mapped, number of multilocus markers and number of markers showing segregation distortion for each of the seven chromosomes (1D to 7D) of *Ae. tauschii*

Chromosome	Loci on map	Multilocus markers	Markers with segregation distortion
1D	68	17	16
2D	76	22	5
3D	87	21	29
4D	54	15	11
5D	107	28	38
6D	83	16	11
7D	72	20	21

two-point linkage analysis (LOD = 6.0), *XGsp* went to the group-1D short-arm markers, and was mapped distal to *Xbcd1434*, *Gli-D1* and *XksuD14*.

Chromosome 2D: The map (Fig. 1) consists of 76 loci. Only five markers showed distorted segregation ratios. Of 20 markers common to the genetic and physical maps, 17 are colinear. However, *XksuG30* (five fragments, only one locus mapped genetically), which maps on 2DS of *Ae. tauschii*, is located on the long arm of the physical map in *T. aestivum.*

Chromosome 3D: The map contains 87 loci (Fig. 1). The 29 markers with distorted segregation ratios are located in the interstitial regions of both arms. Leaf esterase (*Est-D1*) and glutamic oxaloacetic transaminase (*Got-D2*) loci are located in the centromeric region, and a seed esterase locus (*Est-D5*) in a distal region of the long arm. Of 27 common markers, 22 are colinear between the genetic and physical maps. The order of five short-arm markers on the *Ae. tauschii* map (*XksuF34*, *XksuI32-3D.1*, *Xglk724-3D.1*, *XksuE2*, *XksuH7*) is reversed on the 3D physical map of *T. aestivum.*

Chromosome 4D: The map (Fig. 1) consists of 54 loci. Eleven loci on both arms showed segregation

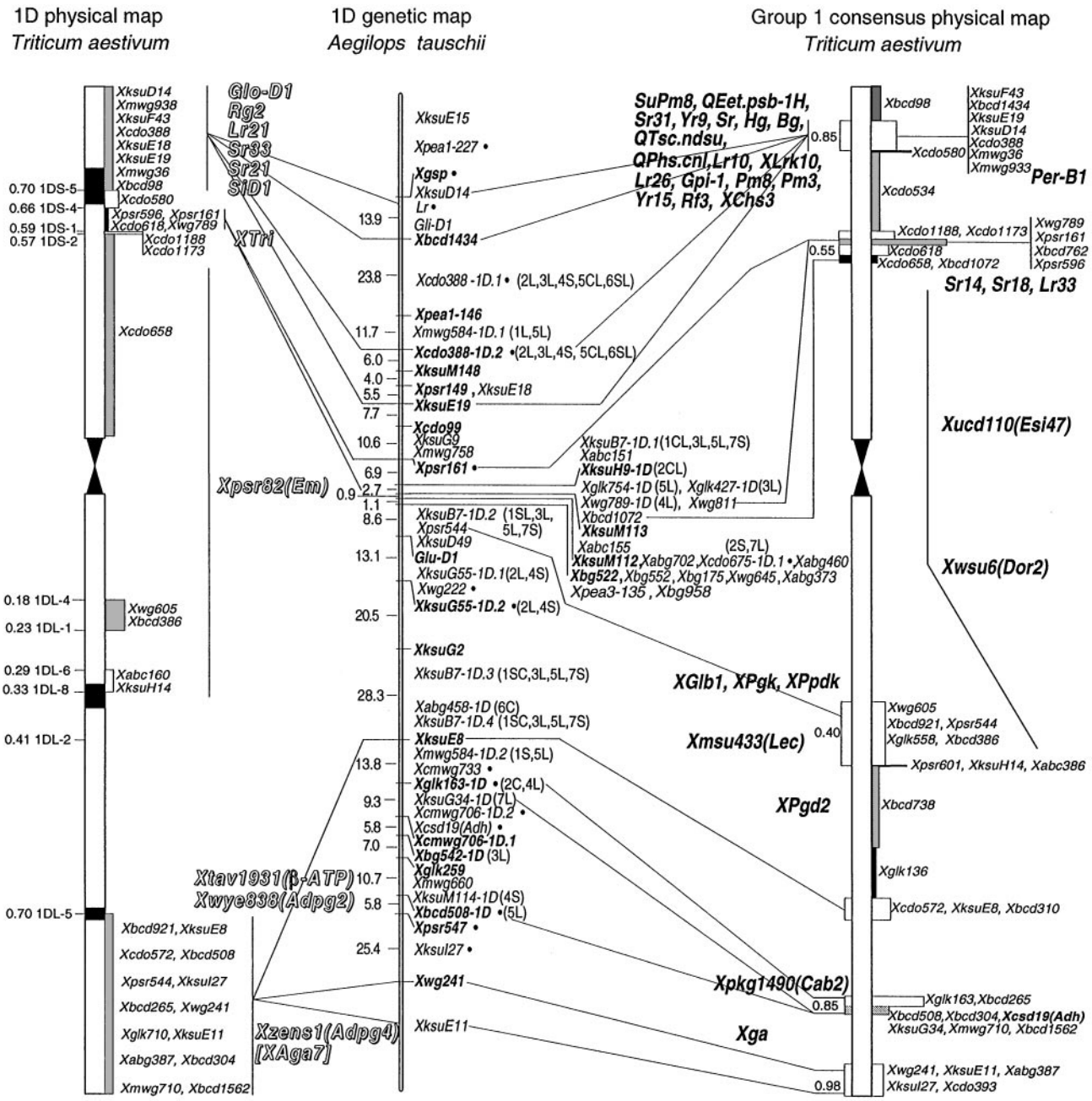

Fig. 1 See page 24 for legend

distortion. The order of 17 loci is identical between the linkage and physical maps with the exception of *Xpsr157*, which mapped in the short arm of the genetic map and in an interstitial region of the long arm in the physical map.

Chromosome 5D: The map (Fig. 1) contains 106 loci, including loci for dehydrins (*XDhn3* and *XDhn2*) and a NOR. Chromosome 5D has 39 loci with distorted segregation ratios, the highest number among all the *Ae. tauschii* chromosomes. Eight of the 39

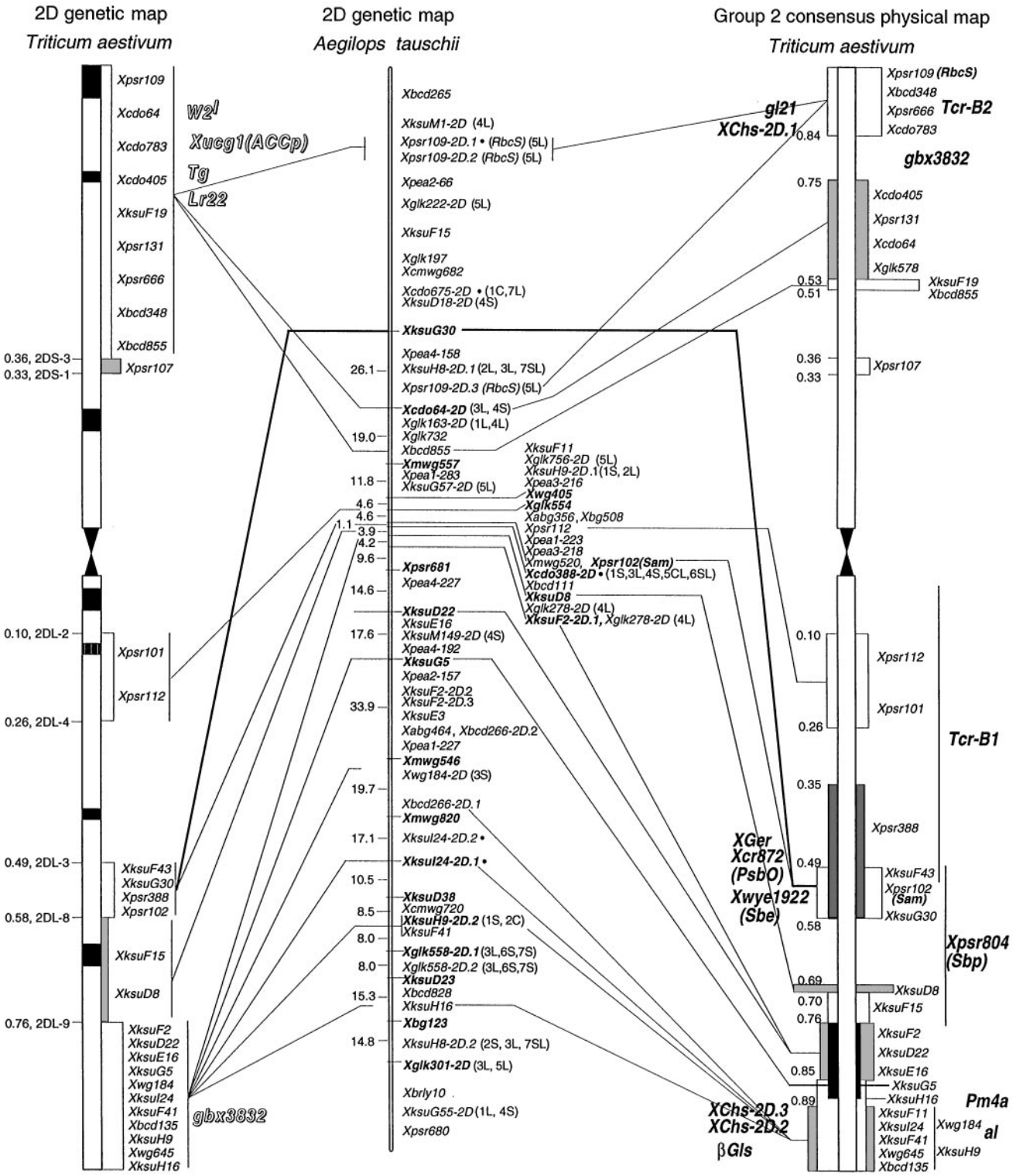

Fig. 1 Continued (see page 24 for legend)

loci common to the *Ae. tauschii* genetic map and the *T. aestivum* 5D physical map, and 18 of the 47 loci common to the *Ae. tauschii* genetic map and the *T. aestivum* consensus physical map, are in different locations.

Chromosome 6D: The map (Fig. 1) contains 83 loci, including loci for a carboxypeptidase (*XCxp1*), a low-molecular-weight gliadin (*Gli-D2*), a dehydrin (*XDhn5*), and a glutamate oxaloacetic transaminase (*Got-D1*). The 6D chromosome has 11 loci with distorted segregation ratios. There is no conclusive evidence for rearrangements in 6D of *Ae. tauschii* compared to the *T. aestivum* group-6 chromosomes.

Chromosome 7D: The map (Fig. 1) consists of 72 loci, 2l of which showed distorted segregation ratios. There is no evidence of rearrangements in the genetic map as compared to the group-7 physical map of *T. aestivum.*

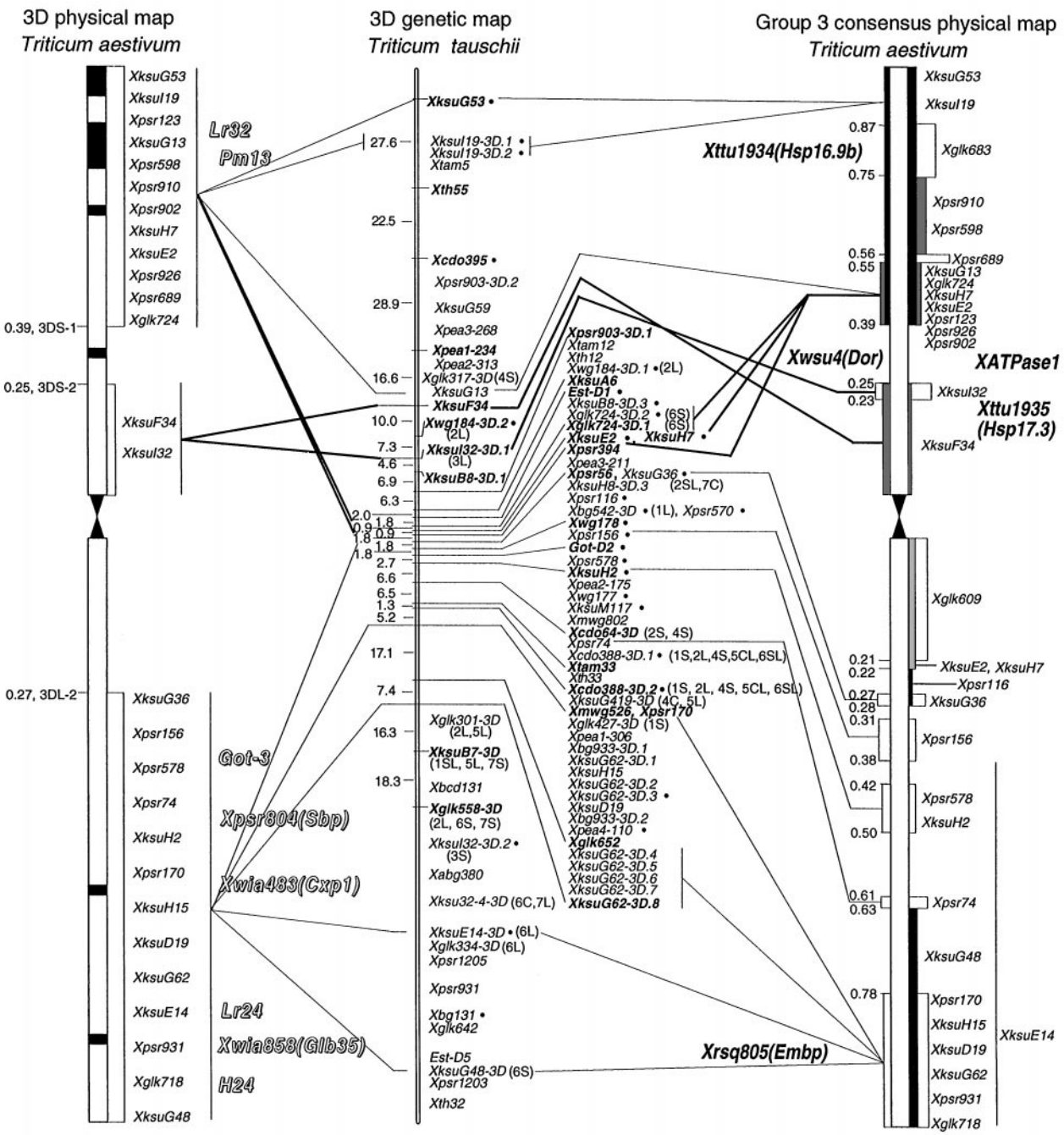

Fig. 1 Continued (see page 24 for legend)

Discussion

Marker order

Of 157 markers, 123 are colinear between the *Ae. tauschii* genetic and *T. aestivum* physical maps. Several factors should be considered when evaluating the significance of the discrepancies in the colinear order for the remaining markers.

(1) The LOD score used for mapping of the markers.
(2) The relative order of markers with different locations. If the anomalous markers are randomly distributed, the discrepancy may not reflect structural rearrangements of the chromosome.
(3) Multilocus markers that detect fragments at different locations. Probes used in constructing genetic and physical maps may detect different loci. If the same fragment(s) was (were) mapped, the discrepancy may reflect differences between the *Ae. tauschii* and *T. aestivum* chromosomes or differences between the *Ae. tauschii* accessions used as parents of the mapping population.

The markers responsible for differences between the *Ae. tauschii* genetic and the *T. aestivum* physical maps in some regions of chromosomes 4, 5, 6 and 7 were mapped at LOD < 2.0. Additional mapping of markers in these regions is necessary to provide further evidence for chromosome rearrangements. Some single-marker differences (chromosome 2) may occur because different fragments of the probe were genetically and physically mapped.

The order of five markers (*XksuF34*, eight fragments; *XksuI32*, three fragments; *Xglk724*, three fragments; *XksuE2*, nine fragments; and *XksuH*, six fragments) in the 3D short arm of the *Ae. tauschii* map is reversed as compared to the 3D and group-3 *T. aestivum* physical maps. The order of *XksuH7* (six fragments), *Xpsr903* (five fragments), and *XksuA6* (eight fragments) in the *Ae. tauschii* map of 3D is also reversed relative to the *T. aestivum* 3A and 3B genetic maps (Nelson et al. 1995 a). Even though none of the probes used to detect these eight loci had a single-fragment hybridization pattern, if does not seem possible that different fragments of each probe were mapped physically and genetically. We assume that the results indicate a possible inversion

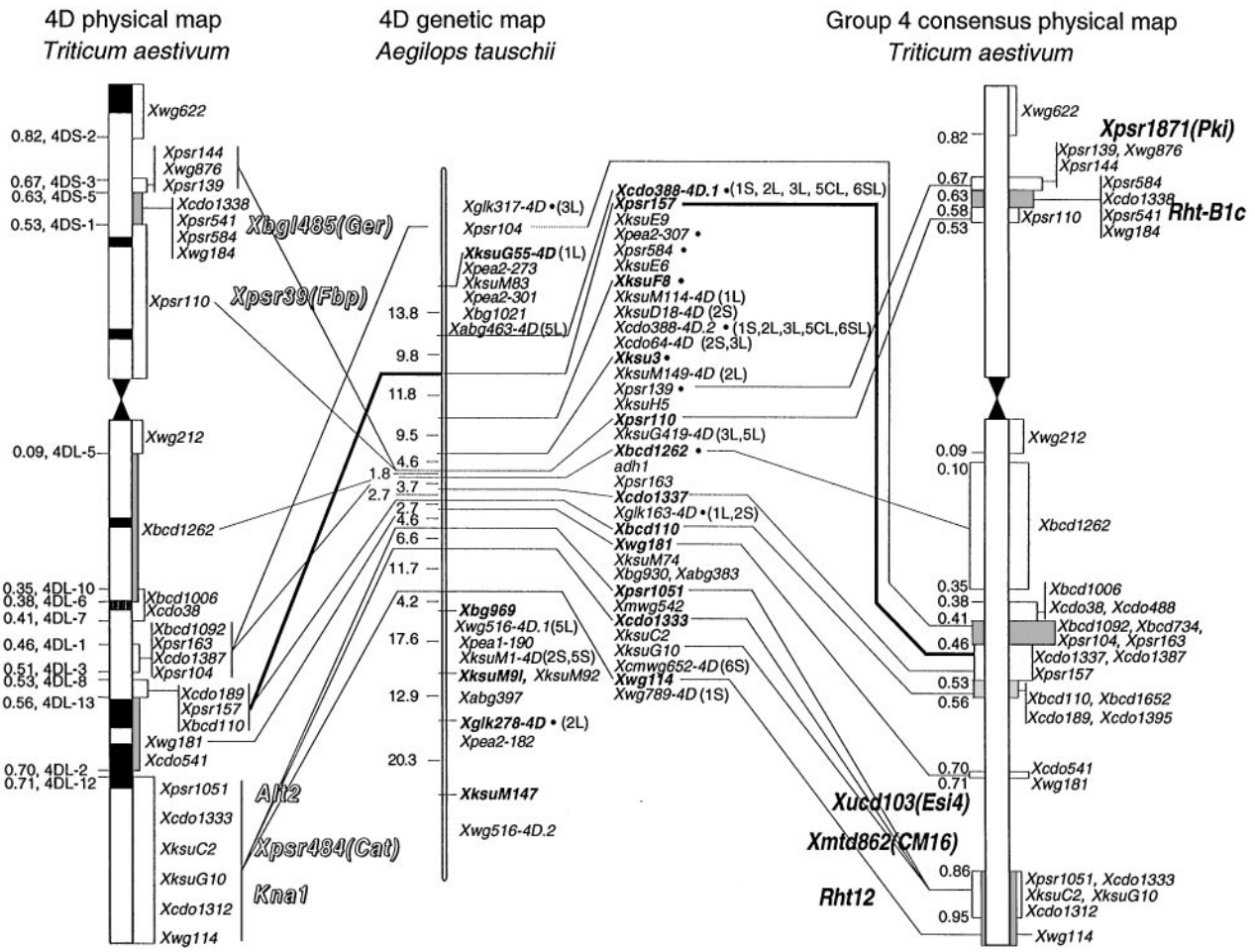

Fig. 1 Continued (see page 24 for legend)

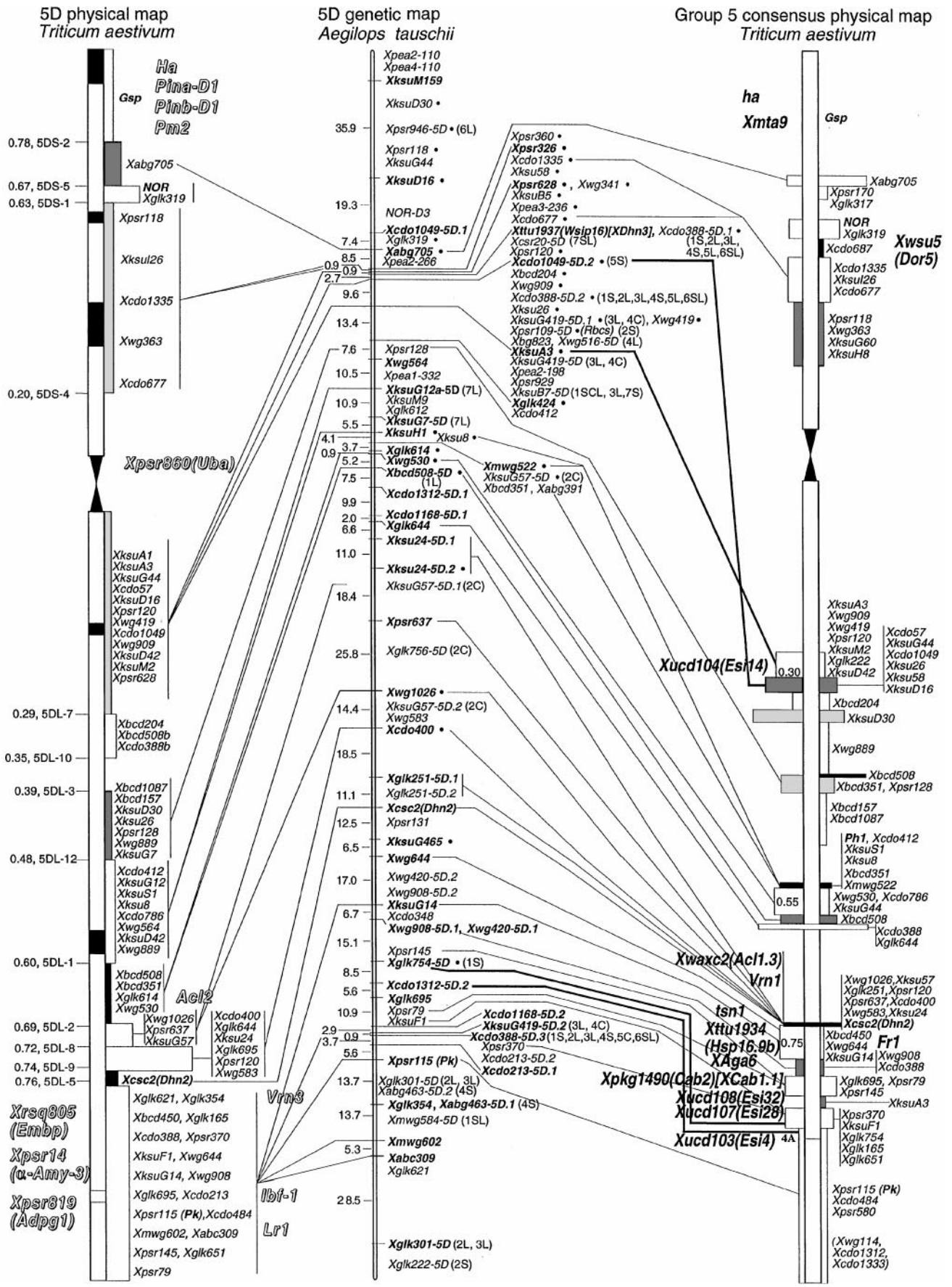

Fig. 1 Continued (see page 24 for legend)

that distinguishes varieties *meyeri* and *typica* (both contain the inversion) from the var. *strangulata* that is considered to be the D-genome donor of *T. aestivum* (Jaaska 1981; Lagudah et al. 1991 b).

There is a discrepancy in the order of several markers on the *Ae. tauschii* genetic maps of 4D and 5D as compared to the corresponding genetic and physical maps of *T. aestivum*. The markers *Xpsr104*, *Xpsr157*

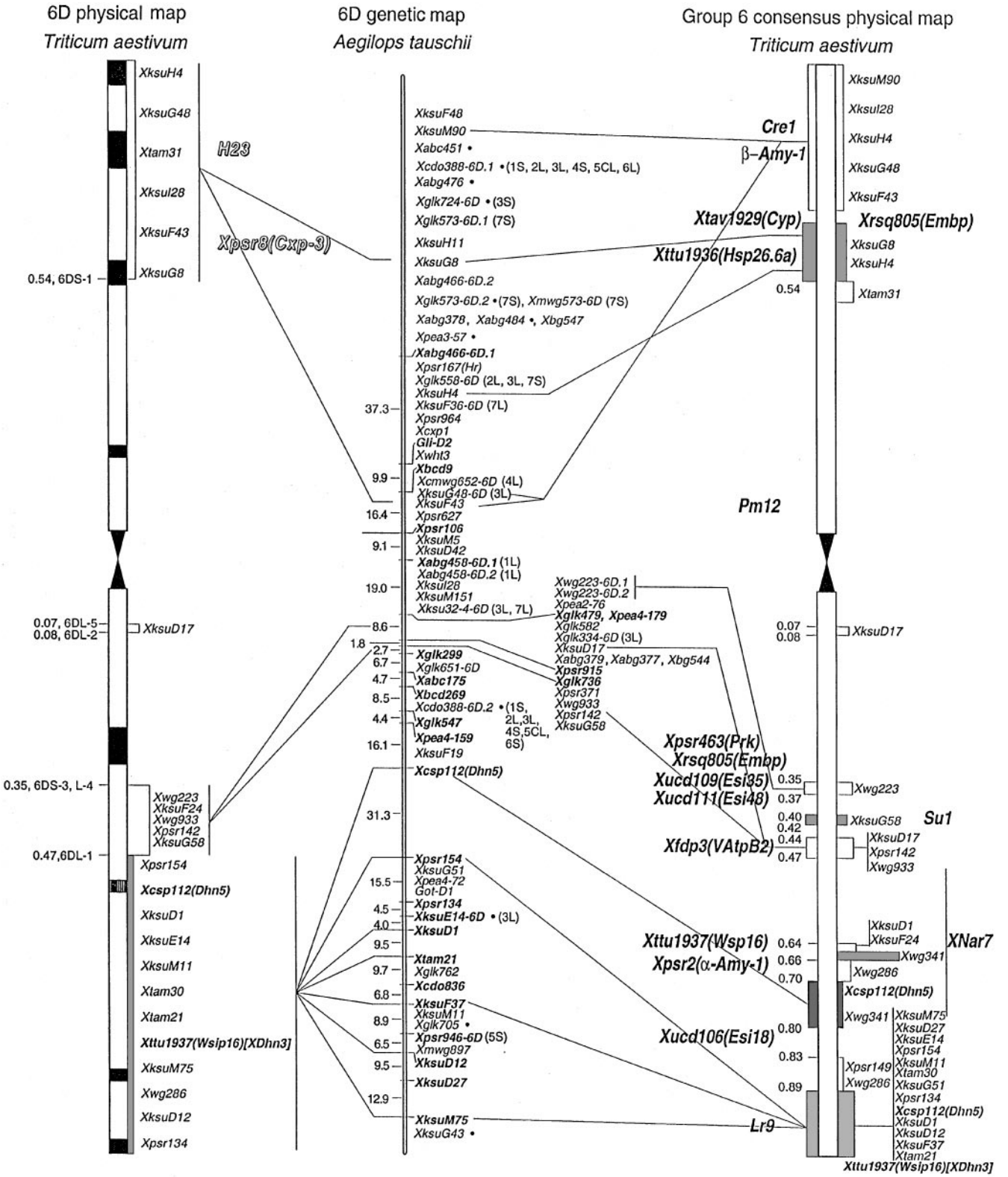

Fig. 1 Continued (see page 24 for legend)

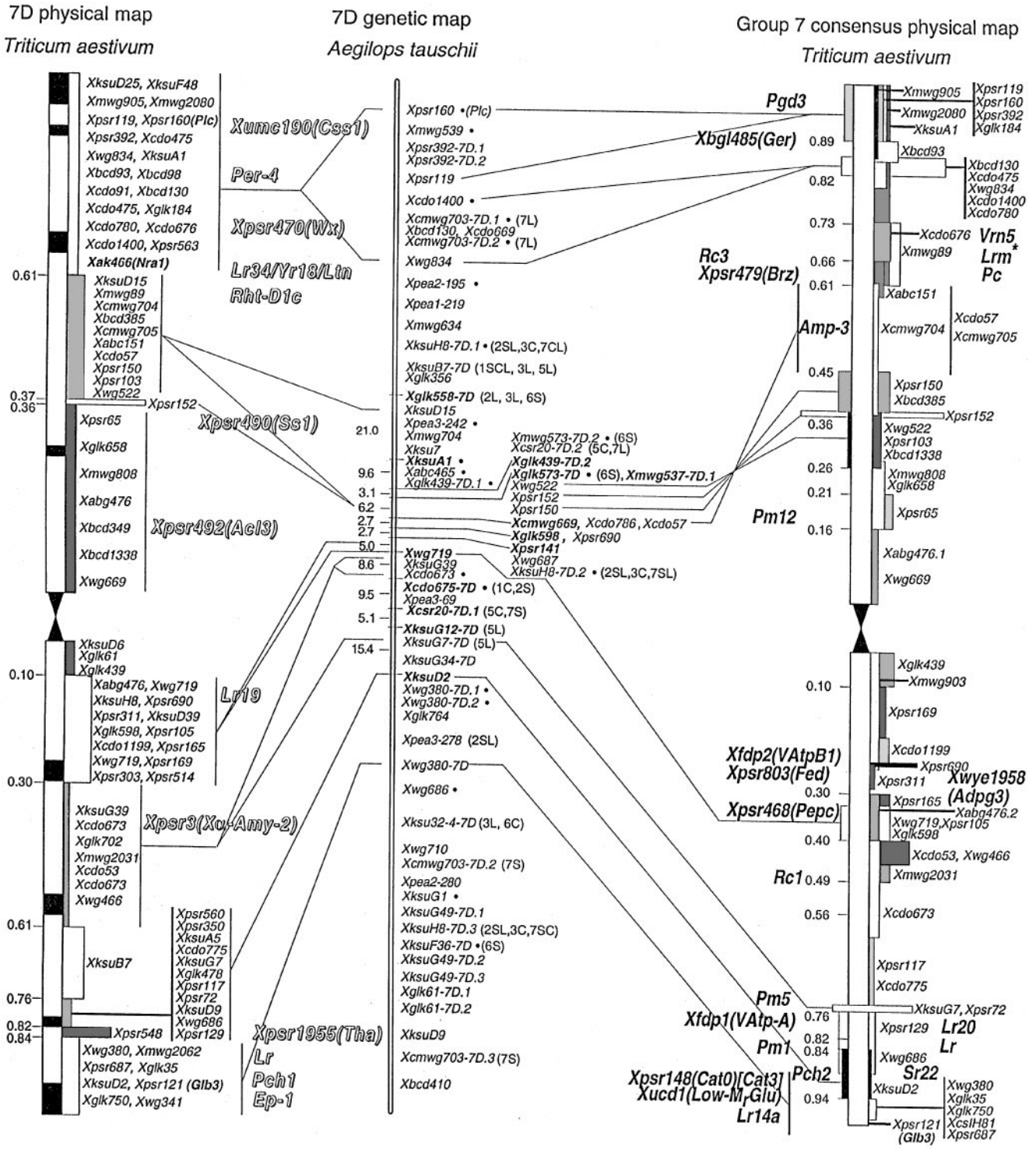

Fig. 1 Comparison of seven (1D–7D) *Ae. tauschii* genetic maps with the D-genome and consensus physical maps of *T. aestivum*. The position of the loci in the basic genetic map constructed at LOD > 2.0 are indicated in *bold*. The markers mapping at LOD < 2.0 are placed in the intervening regions and were ordered using the command "Compare" • indicates a locus with distorted segregation; *thin lines* join markers common between the *Ae. tauschii* genetic and *T. aestivum* physical maps; *thick lines* join markers of the basic map that are in a different order on the *Ae. tauschii* genetic and *T. aestivum* physical maps; .1, .2, .3 etc identify multilocus markers; the chromosome locations of multilocus markers are indicated in brackets; agronomically important genes, genes that encode proteins, and morphological markers mapped in the Triticeae by other authors are shown in *outlined letters* for the D-genome and in *bold letters* for the other genomes; the *Xpea* symbol identifies AFLP markers, *numbers 1–4* indicate the combination of selective bases (see Materials and methods), two- or three-digit numbers indicate the size of a mapped fragment

and *XksuF8*, that map in the short arm of 4D in *Ae. tauschii*, map in the long arm in the genetic and physical map of wheat 4D (Gale et al. 1995; Mickelson-Young et al. 1995; Nelson et al. 1995 b). There are other markers (*XksuD16*, *XksuD30*, *XksuG44*, *Xpsr360*, *Xpsr929*, *Xpsr628*, *Xcdo1049, XksuA3* and *Xcdo1312*) that also have an anomalous map location (see the 4D and 5D maps in Fig. 1). Further work is needed to verify these anomalies.

Segregation distortion

One hundred and thirty two loci (24% of the mapped loci) showed significant deviation from the expected segregation ratios. The greatest number of these loci were in chromosomes 5, 3 and 7 (36%, 34% and 28% of the loci mapped in each chromosome, respectively), followed by chromosomes 1, 4, 6 and 2 (23%, 21%, 13% and 7% respectively). Faris et al. (1998) analyzed this phenomenon using the same population with segregation data for 194 codominant markers, 57 of which had segregation ratios that deviated significantly from the expected ratios. It was shown that there are at least three segregation distortion loci in 5DL. Chromosomes 1D, 3D, 4D and 7D each contain at least one locus that causes deviations from the expected segregation (Faris et al. 1998).The map of the *Ae. tauschii* genome which is presented here has 2.8-times more markers, and 2.3-times more markers with distorted segregation ratios. The analysis of these data may reveal additional segregation distortion loci on these chromosomes.

Practical application of the maps

One hundred and sixty four pest-, disease-, and stress-resistance genes, proteins, and morphological markers have been assigned to regions of both the *Ae. tauschii* linkage map and the *T. aestivum* physical map using markers common between these and recently published maps (Donini et al. 1995; Chen Q et al. 1996; Mohler and Jahoor, 1996; Ben Amer et al. 1997; Faris et al. 1997; Han et al. 1997; Korzun et al. 1997; William et al. 1997; Hollenhorst and Joppa 1983; Zhang et al. 1998; the references can also be found in McGuire and Qualset 1997; McIntosh et al. 1998). Only 58 of these loci mapped to the D-genome of wheat. Others may be mapped in the D-genome using the information on their approximate location in the *Ae. tauschii* and/or *T. aestivum* maps (Fig. 1). There are 148 pest-, disease-, and stress-resistance genes (40 for the D-genome) that are assigned to chromosomes of the Triticeae. The chromosome locations of these genes in the *Ae. tauschii* and/or *T. aestivum* genomes have yet to be determined. The high-density genetic linkage map of the *Ae. tauschii* genome reported here may be used to achieve this goal.

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References

Ben Amer IM, Korzun V, Worland AJ, Börner A (1997) Genetic mapping of QTLs controlling tissue-culture response on chromosome 2B of wheat (*Triticum aestivum* L.) in relation to major genes and RFLP markers. Theor Appl Genet 94:1047–1052

Chen Q, Conner RL, Laroche A (1996) Molecular characterization of *Haynaldia villosa* chromatin in wheat lines carrying resistance to wheat curl mite colonization. Theor Appl Genet 93:679–684

Delaney DE, Nasuda S, Endo TR, Gill BS, Hulbert SH (1995 a) Cytologically based physical maps of the group-2 chromosomes of wheat. Theor Appl Genet 91:568–573

Delaney DE, Nasuda S, Endo TR Gill BS, Hulbert SH (1995 b) Cytologically based physical maps of the group-3 chromosomes of wheat. Theor Appl Genet 91:780–782

Donini P, Koebner RMD, Ceolony C (1995) Cytogenetic and molecular mapping of the wheat-*Aegilops longissima* chromatin breakpoints in powdery mildew-resistant introgression lines. Theor Appl Genet 91:738–743

Endo TR, Gill BS (1996) The deletion stocks of common wheat. J Hered 87:295–307

Faris JD, Anderson JA, Francl LJ, Jordahl JG (1997) RFLP mapping of resistance to chlorosis induction by *Pyrenophora tritici-repentis* in wheat. Theor Appl Genet 94:98–103

Faris JD, Laddomada B, Gill BS (1998) Molecular mapping of segregation distortion loci in *Aegilops tauschii*. Genetics 149:319–327

Gale MD, Atkinson MD, Chinoy CN, Harcourt RL, Jia J, Li QY, Devos KM (1995) Genetic map of hexaploid wheat. In: Li ZS, Xin Zy (eds) Proc 8th Int Wheat Genetics Symp, Beijing, China, 1993, pp. 29–40

Gill KS, Lubbers EL, Gill BS, Raupp WJ, Cox TS (1991) A genetic linkage map of *Triticum tauschii* (DD) and its relationship to the D genome of bread wheat (AABBDD). Genome 34:362–374

Gill KS, Gill BS, Endo TR (1993) A chromosome region-specific mapping strategy reveals gene-rich telomeric ends in wheat. Chromosoma 102:374–381

Gill KS, Gill BS, Endo TR, Boyko EV (1996 a) Identification and high-density mapping of gene-rich regions in chromosome group 5 of wheat. Genetics 143:1001–1012

Gill KS, Gill BS, Endo TR, Taylor T (1996 b) Identification and high-density mapping of gene-rich regions in chromosome group 1 of wheat. Genetics 144:1883–1891

Han F, Kleinhofs A, Kilian A, Ullrich SE (1997) Cloning and mapping of a putative barely NADPH-dependent HC-toxin reductase. Mol Plant-Microbe Interact 10:234–239

Hohmann U, Endo TR, Gill KS, Gill BS (1994) Comparison of genetic and physical maps of group-7 chromosomes from *Triticum aestivum* L. Mol Gen Genet 245:644–653

Hollenhorst MM, Joppa LP (1983) Chromosomal location of genes for resistance to greenbug in 'Largo' and 'Amigo' wheats. Crop Sci 23:91–93

Jaaska V (1981) Aspartate aminotransferase and alcohol dehydrogenase isoenzymes: intraspecific differentiation in *Aegilops tauschii* and the origin of the D-genome polyploids in the wheat group. Plant Syst Evol 137:259–273

Kam-Morgan LNW, Gill BS, Muthukrishnan S (1989) DNA restriction fragment length polymorphisms: a strategy for genetic mapping of the D-genome of wheat. Genome 32 : 724–732

Kihara H (1944) Discovery of the DD-analyzer, one of the ancestors of *vulgare* wheats. Agric Hort 19 : 889–890

Korzun V, Röder M, Worland AJ, Börner A (1997) Intrachromosomal mapping of genes for dwarfing (*Rht12*) and vernalization response (*Vrn1*) in wheat by using RFLP and microsatellite markers. Theor Appl Genet 116 : 227–232

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12 : 172–175

Lagudah ES, Appels R, Brown AHD, McNeil D (1991 a) The molecular-genetic analysis of *Triticum tauschii*, the D-genome donor to hexaploid wheat. Genome 34 : 375–386

Lagudah ES, Appels R, McNeil D (1991 b) The *Nor-D3* locus of *Triticum tauschii*: natural variation and genetic linkage to markers in chromosome 5. Genome 34 : 387–395

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1 : 174–181

McFadden ES, Sears ER (1946) The origin of *Triticum spelta* and its free-threshing hexaploid relatives. J Hered 37 : 81–89

McGuire PE, Qualset CO (1997) Progress in genome mapping of wheat and related species. Joint Proc 5th and 6th Public Wkshps of the International Triticeae Mapping Initiative, Sept 1995, Norwich UK, Aug 1996, Sydney, Australia, Published by Genetic Resources Conservation Program, Division of Agriculture and Natural Resources, University of California, Report No 18

McIntosh RA, Hart GE, Devos KM, Gale MD, Rogers WJ (1988) Catalogue of gene symbols for wheat. Proc 9th Int Wheat Genet Symp, 2–7 August 1998, Saskatoon, Saskachewan, Canada, vol 5

Mickelson-Young L, Endo TR, Gill BS (1995) A cytogenetic ladder-map of the wheat homoeologous group-4 chromosomes. Theor Appl Genet 90 : 1007–1011

Mohler V, Jahoor A (1996) Allele-specific amplification of polymorphic sites for the detection of powdery mildew resistance loci in cereals. Theor Appl Genet 93 : 1078–1082

Nelson JC, Van Deynze AE, Autrique E, Sorrells ME, Lu YH, Negre S, Bernard M, Leroy P (1995 a) Molecular mapping of wheat. Homoeologous group 3. Genome 38 : 525–533

Nelson JC, Sorrells ME, Van Deynze AE, Lu YH Atkinson M, Bernard M, Leroy P, Faris JD, Anderson JA (1995 b) Molecular mapping of wheat: major genes and rearrangements in homoeologous groups 4, 5 and 7. Genetics 141 : 721–731

William HM, Hoisington D, Singh RP, Gonzalez-de-León D (1997) Detection of quantitative trait loci associated with leaf rust resistance in bread wheat. Genome 40 : 253–260

Zhang H, Jia J, Gale MD, Devos KM (1998) Relationships between the chromosomes of *Aegilops umbellulata* and wheat. Theor Appl Genet 96 : 69–75