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Structural evolution of wheat chromosomes 4A, 5A, and 7B and its impact on recombination

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Abstract The construction of comparative genetic maps of chromosomes $4A^m$ and $5A^m$ of *Triticum monococcum* and chromosomes of homoeologous groups 4, 5 and 7 of *T. aestivum* has provided insight into the evolution of these chromosomes. The structures of chromosomes 4A, 5A and 7B of modern-day hexaploid bread wheat can be explained by a 4AL/5AL translocation that occurred at the diploid level and is present both in *T. monococcum* and *T. aestivum*. Three further rearrangements, a 4AL/7BS translocation, a pericentric inversion and a paracentric inversion, have taken place in the tetraploid progenitor of hexaploid wheat. These structural rearrangements and the evolution of chromosomes 4A, 5A and 7B of bread wheat are discussed. The presence of the 4AL/5AL translocation in several Triticeae genomes raises two questions – which state is the more primitive, and is the translocation of mono- or poly-phylogenetic origin?

The rearrangements that have occurred in chromosome 4A resulted in segments of both arms having different positions relative to the telomere, compared to $4A^m$ and to 4B and 4D. Comparisons of map length in these regions indicate that genetic length is a function of distance from the telomere, with the distal regions showing the highest recombination.

Key words Crossing-over · Genetic map · Inversion · Linkage · Recombination · *T. aestivum* · *T. monococcum* · Translocation

Introduction

The structure and identity of chromosome 4A in bread wheat, *Triticum aestivum* L. (2n=6x=42), has long been a source of confusion. Early attempts to assign the 21 bread wheat chromosomes to genomes were based on chromosome pairing behaviour. Chromosome pairing in AABB× AABBDD interspecific crosses with each of the 21 'Chinese Spring' (CS) monosomic lines led to the identification of the D-genome chromosomes (Sears 1954). The A-genome chromosomes were identified by their ability to pair with telocentric chromosomes in crosses of *T. aestivum* ditelosomic lines with a synthetic *T. monococcum* L.×*Ae. tauschii* Coss. (*Ae. squarrosa*) amphiploid (genomes A^mA^mDD). Chromosomes that did not pair in these crosses were assigned to the B genome (Okamoto 1962). This and subsequent work of Chapman and Riley (1966) led to the genome allocation of all bread wheat chromosomes. However, further studies showed that neither bread wheat chromosome 4A (originally IV) nor 4B (originally VIII) pair in hybrids between bread wheat telosomic lines and diploid einkorn wheats, *T. urartu* Thum. (genomes AA) and *T. monococcum* (genomes A^mA^m) (Chapman et al. 1976; Dvořák 1976; Miller et al. 1981). Later studies showed wheat chromosome IV to be a member of the B genome, as is indicated by genetic compensation by chromosome 4S from *Ae. speltoides* Tausch and other species of *Aegilops* section Sitopsis (the presumed source of the B genome of polyploid wheats), the similarity of the pattern of C-bands and a number of other lines of evidence (Dvořák 1983; Dvořák et al. 1990).

This, however, left unanswered the question as to the origin of bread wheat chromosome VIII. In situ hybridization of an interspersed repeated nucleotide sequence that preferentially hybridizes with the *T. monococcum* and *T. urartu* genomes and several other lines of evidence indicated that this chromosome is likely to be an A-genome chromosome, and it was suggested that the lack of pairing with *T. urartu* or *T. monococcum* chromosomes resulted from extensive rearrangements of this chromosome (Dvořák et al. 1990). The weight of evidence for the original misclassification of the group 4 chromosomes led, in 1988 at the VIIth International Wheat Genetics Symposium, to the reassignment of chromosome 4A (IV) as 4B and 4B (VIII) as 4A (Anonymous 1988), as used below.

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Evidence for the involvement of chromosome 4A in translocations was provided by meiotic pairing studies in wheat×rye hybrids lacking the *Ph1* locus (Naranjo et al. 1987) and was confirmed by isozyme and restriction fragment length polymorphism (RFLP) studies (Kobrehel and Feillet 1975; Kobrehel 1978; Benito and Pérez de la Vega 1979; Ainsworth et al. 1983; Anderson et al. 1992; Liu et al. 1992). Pairing of chromosome arms 5AL with 4BL and 4DL, 4AL with 7AS and 7DS, and 7BS with 5BL and 5DL (Naranjo et al. 1987) and the presence of markers from the 4L synteny group on 5AL, from the 5L synteny group on 4AL and from the 7S synteny group on 4AL (Anderson et al. 1992; Liu et al. 1992) all suggested two translocation events – first a translocation between 4AL and 5AL, followed by a second translocation between 7BS and the chromosome 5A segment previously translocated to 4A. Furthermore, as the longer arm of chromosome 4A is at least partly homoeologous with 4BS and 4DS, while 4AS is at least partly homoeologous with 4BL and 4DL (Hart and Langston 1977; Benito et al. 1984; Naranjo et al. 1987; Liu et al. 1992), it is likely that a pericentric inversion has taken place, during which a segment of 4AL was transferred to 4AS, thereby reversing the 4AS/4AL arm ratio. The presence of *Xpsr115* loci on chromosome arms 4AL, 5BL and 5DL in hexaploid bread wheat and 4A of *T. urartu* (King et al. 1995), the A-genome donor of tetraploid and hexaploid wheat (Konarev et al. 1979; Nishikawa 1984; Dvořák et al. 1988, 1993), indicated that the 4AL/5AL translocation took place before the polyploidization of wheat. It was not known if the inversion also took place at the diploid stage and whether the inversion preceded or followed the 4AL/7BS translocation.

In summary, the identity of wheat chromosome 4A has been resolved; it is a chromosome with some affinity to the A genome and some homoeology with 4B and 4D. This chromosome is, however, complex in that it carries translocated segments from 5A and 7B. Moreover, the arm ratios have been reversed so that the arm with markers in common with those on 4BS and 4DS is now called 4AL and the arm with homoeology to 4BL and 4DL is called 4AS. The construction of genetic maps of chromosomes $4A^m$ and $5A^m$ of *T. monococcum* and the chromosomes of homoeologous groups 4, 5 and 7 of *T. aestivum*, as described in this paper, allows us to determine the translocation breakpoints and also to more precisely reconstruct the course of events that led to the current structure of chromosome 4A of bread wheat.

Materials and methods

Genetic stocks

Genetic maps of chromosomes $4A^m$ and $5A^m$ of diploid wheat were constructed using a population of 74 F_2 plants or bulked F_3 families derived from a cross between cultivated *T. monococcum* ssp. *monococcum* (DV92) and wild *T. m.* ssp. *aegilopoides* from Lebanon (G3116). The homoeologous group 4, 5 and 7 chromosomes of *T. aestivum* were mapped in a population of 120 F_2 plants or bulked F_3 families derived from a cross between CS and a synthetic hexaploid wheat (the amphiploid *T. turgidum* ssp. *dicoccon* (Schrank) Thell.×*Ae. tauschii*) (McFadden and Sears 1946; Sears 1976).

DNA probes

Wheat, barley, oats and *Ae. tauschii* genomic and cDNA clones of unknown function developed at the John Innes Centre, UK (PSR-clones), Cornell University, USA (BCD-, CDO-, WG-clones), Institute for Resistance Genetics, Germany (MWG-clones), Kansas State University, USA (KSU-clones) and North American Barley Genome Project (ABC-, ABG-clones) were used for the construction of the diploid and hexaploid wheat maps.

RFLP technology

Methods for DNA extraction, restriction digestion, Southern blotting, probe labelling and hybridization were as previously described by Devos et al. (1992) and Dubcovsky et al. (1994).

Results

The diploid wheat map

Maps of *T. monococcum* chromosomes $4A^m$ and $5A^m$(Fig. 1) were compared with maps of homoeologous barley chromosomes 4H and 5H (Heun et al. 1991; Kleinhofs et al. 1993; Kleinhofs et al. in Matthews and Anderson 1994). Five markers are shared by chromosomes $4A^m$ and 4H (*Xwg622*, *Xcdo669*, *Xmwg635*, *Xabg484*, *Xwg464*) and seven by chromosome arms $5A^m$L and 5HL (*Xwg541*, *Xwg889*, *Xcdo57*, *Xbcd351*, *Xwg644*, *Xwg908* and *Xabg391*). The order of these markers is colinear. The markers in the distal part of chromosome $4A^m$L and $5A^m$L do not follow this $4A^m$-4H and $5A^m$-5H synteny. The distal part of $4A^m$L is colinear with the distal part of chromosome 5HL (*Xabc310*, *Xabg390*, *Xcdo484*, *Xabg463*, *Xmwg851*), and the distal part of $5A^m$L is colinear with the distal part of 4HL (*Xwg114*, *Xwg199*, *Xbcd402*, *β-Amy-1*). The $4A^m$L/$5A^m$L translocation breakpoint was determined to lie between *Xmwg2180* and *Xabc310*, and the $5A^m$L/$4A^m$L breakpoint was shown to lie in the interval *Xabg391–XksuC2*. A comparison of *T. monococcum* chromosomes $4A^m$ and $5A^m$ with *T. aestivum* chromosomes of homoeologous groups 4 and 5 (Fig. 2) showed that $4A^m$S and a proximal segment of $4A^m$L are colinear with the short arms and proximal segments of the long arms of chromosomes 4B and 4D (*Xpsr921*, *Xwg622*, *Xpsr922*, *Xpsr153*, *Xpsr920*, *Xpsr1051*), while the distal segment of $4A^m$L is colinear with the distal segment of 5BL and 5DL (*Xabc310*, *Xpsr115*, *Xcdo484*, *Xpsr1316* and *Xpsr567*). The distal segment of chromosome $5A^m$L is colinear with the distal segment of 4BL and 4DL (*XksuC2*, *Xpsr164*, *Xwg114*, *β-Amy-1*). The non-colinearity of the *Xpsr375* loci in *T. monococcum* and *T. aestivum* is most probably due to the non-homoeology (paralogy) of these loci, as PSR375 detects multiple sequences in wheat.

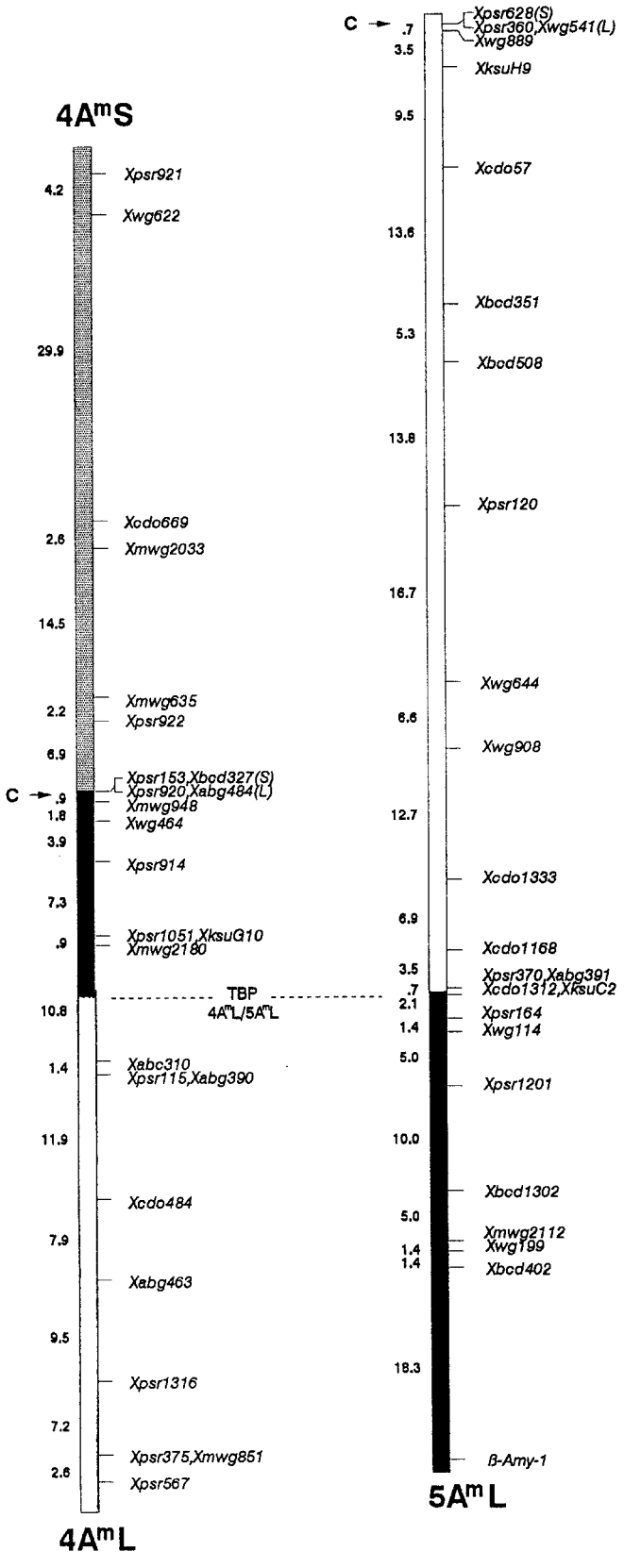

Fig. 1 The genetic maps of chromosome $4A^m$ and the long arm of $5A^m$ of *T. monococcum*. Note: Positions of centromeres are indicated by *arrows*. *TBP* translocation breakpoint

The hexaploid wheat map

A linkage map of chromosome 4A of *T. aestivum* is shown in Fig. 2. Features of this map are discussed in Gale et al. (1995). A comparison of the linkage maps of chromosomes 4A, 4B and 4D showed that the short arm of chromosome 4A is colinear with the proximal segments of 4BL and 4DL, while the proximal segment of 4AL is colinear with the proximal segments of 4BS and 4DS (Fig. 2). Adjacent to this latter segment is a segment of more than 30 cM, which includes loci *Xabc310*, *Xpsr115*, *Xpsr1206*, *Xcdo484* and *Xpsr1316*, that is colinear with the distal regions of 5BL and 5DL. However, although colinear, the order of loci is inverted relative to the centromere on the other group 5 chromosomes (Fig. 2). PSR1051, a probe that detects loci on chromosome arms $4A^mL$, 4BL and 4DL maps distal to this inverted segment in 4AL, and this location confirms the map position obtained by deletion mapping (Mickelson-Young et al. 1995). Finally, in the most distal part of the long arm of chromosome 4A is a segment spanned by loci *Xpsr160(Plc)* and *Xpsr604* that is homoeologous to the distal segments of 7AS and 7DS (Fig. 2). This 4AL segment is in the same orientation relative to the centromeres of 7A and 7D.

Discussion

Evolution of bread wheat chromosomes 4A, 5A, and 7B

Previous reports have identified two reciprocal translocations between bread wheat chromosome arms 4AL and 5AL and between 4AL and 7BS, and a pericentric inversion in bread wheat chromosome 4A. The translocation involving 4AL and 5AL was thought to have taken place at the diploid level, while the other rearrangements likely took place at the tetraploid level. A comparison of the linkage maps of chromosomes $4A^m$ and $5A^m$ of *T. monococcum* with the consensus marker order of the chromosomes of homoeologous groups 4 and 5 in *T. aestivum* and barley indeed showed the presence of a distal region of chromosome arm 5L in $4A^mL$ and a distal segment of chromosome arm 4L in $5A^mL$, with identical (within the limits of the analysis) breakpoints in *T. monococcum* chromosomes $4A^m$ and $5A^m$ and *T. aestivum* chromosomes 4A and 5A.

The 4AL/5AL translocation was the first in a series of rearrangements that led to the present composition of chromosomes 4A, 5A and 7B of bread wheat (Fig. 3). Chromosome 4A underwent a pericentric inversion with one breakpoint between *Xpsr914* and *Xpsr1051* in the original 4AL arm and the other breakpoint distal to *Xwg622* in the original 4AS segment. This pericentric inversion probably occurred at the polyploid level since it is absent in the *T. monococcum* genome and resulted in the effective transfer of the translocated 5AL segment (i.e. the segment spanned by the loci *Xpsr567*, *Xpsr1316*, *Xabg463*, *Xcdo484*, *Xpsr1206*, *Xpsr115*, *Xabg390* and *Xabc310*) and a small segment of the original 4AL, carrying locus *Xpsr1051* and

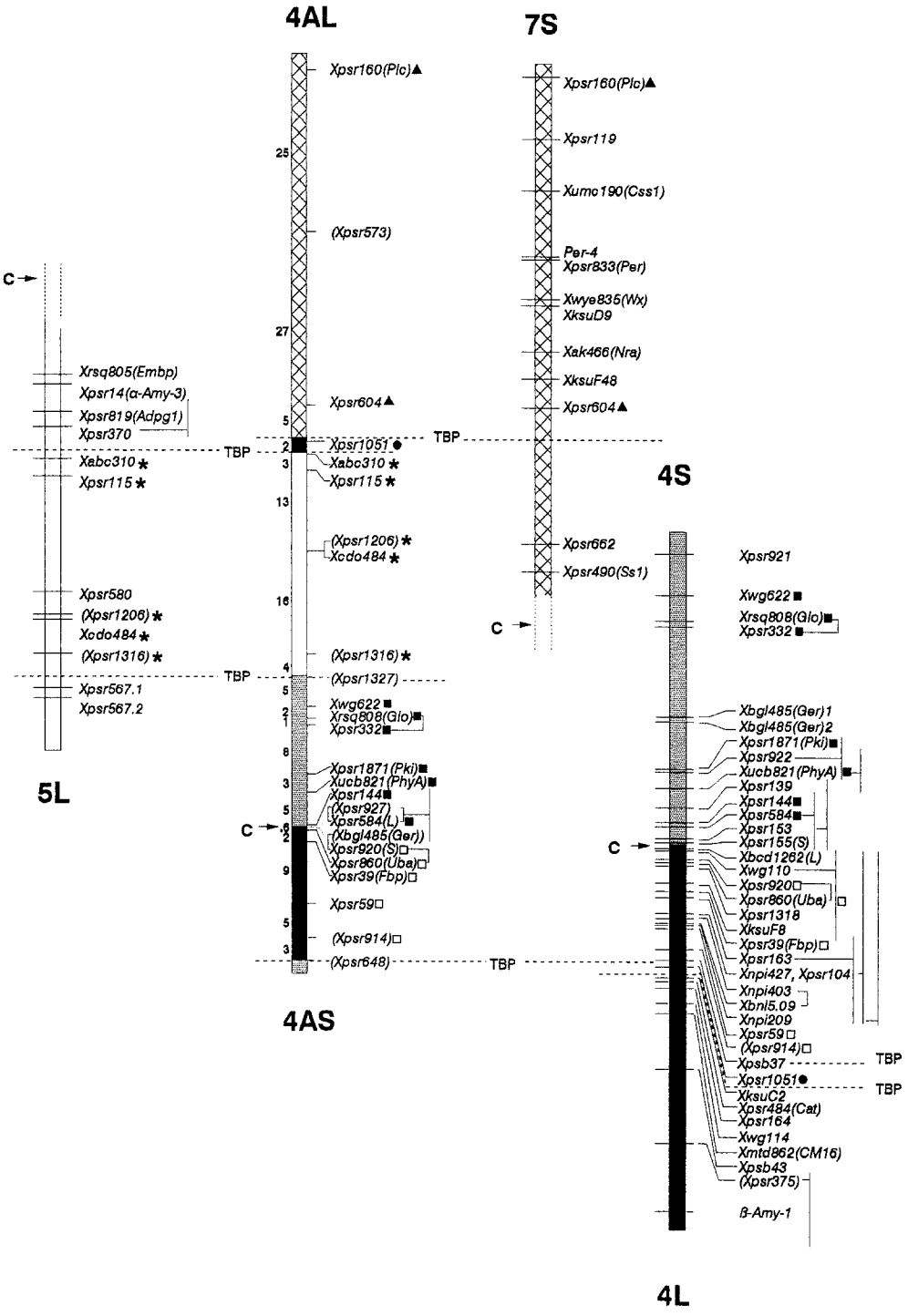

Fig. 2 The genetic map of chromosome 4A of *T. aestivum* and segments of the consensus maps of chromosome groups 4, 5 and 7. Note: The best fit relative locations of all marker loci are shown; those that could not be ordered unequivocally are identified with a *vertical bar* extending over the region of possible ambiguity. Paralogous loci are shown in *parenthesis* ( ). Positions of centromeres are indicated by *arrows*. *TBP* translocation breakpoint

probably also *XksuG10* (Mickelson-Young et al. 1995), which is completely linked to *Xpsr1051* in the *T. monococcum* map, to most or all of the original chromosome arm 4AS. This resulted in the inversion of the physical arm ratio of this chromosome, so that the cytological short arm of chromosome 4A became homoeologous to 4BL, 4DL and $4A^mL$, and part of the long arm homoeologous to 4BS, 4DS, and $4A^mS$. We have, to date, found no probes that detect homoeologous loci on the modern chromosome arms 4AS, 4BS and 4DS, so we have no evidence that the inversion breakpoint was proximal to the telomere of the original 4AS. *Xpsr648-4A* is not informative in this matter since PSR648 detects paralogous genome-specific fragments on 4AS, 1BL and 7DL (Fig. 2). The presence of a small segment of the original 4AS in the modern 4AS is, nevertheless, suggested by the observation of pairing, albeit at low frequency, of the distal segment of chromosome arm 4AS with 4BS and 4DS (Naranjo et al. 1987).

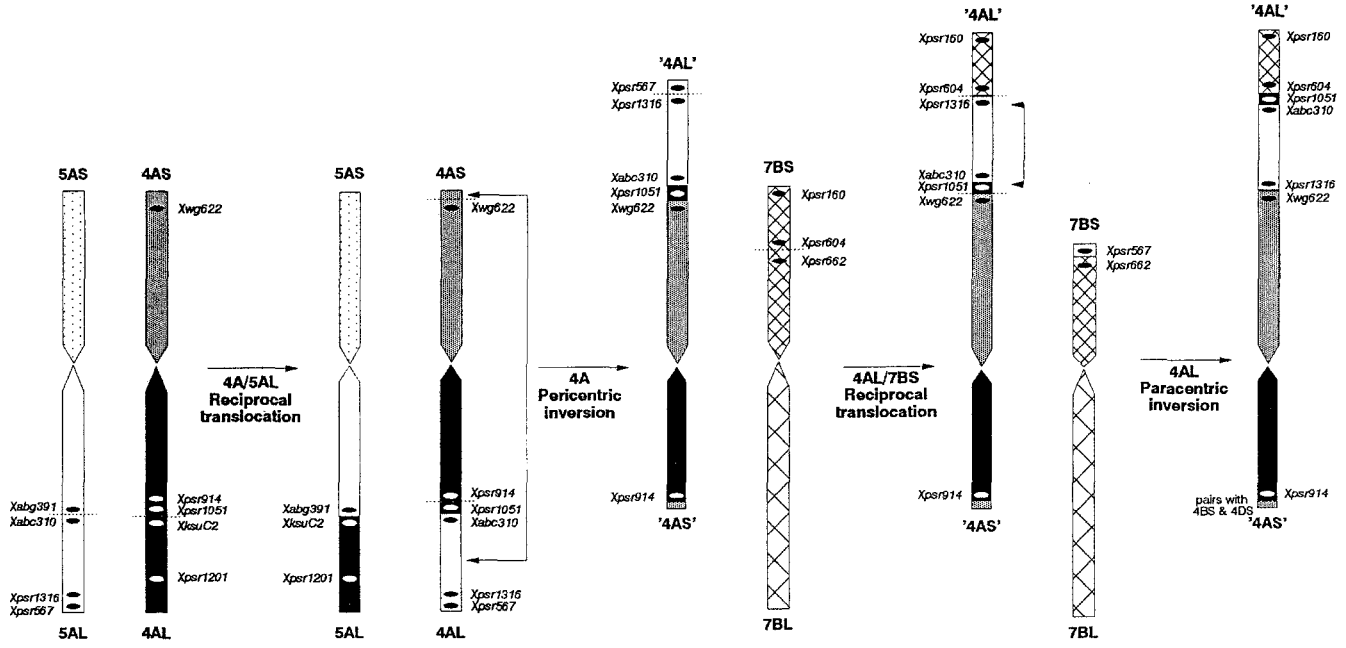

Fig. 3 The evolution of modern-day chromosome 4A. Note: loci defining the translocation breakpoints are indicated

This pericentric inversion was either preceded or followed by a reciprocal translocation between the now longer arm of 4A and 7BS, with breakpoints between *Xpsr567* and *Xpsr1316* on the segment of chromosome 5AL translocated to chromosome 4A, and between *Xpsr604* and *Xpsr662* on the short arm of chromosome 7B.

The three previously described rearrangements should have given rise to a chromosome 4A long arm consisting of, from the telomere, a segment of 7BS, a segment of 5AL, a segment of the original 4AL and a proximal segment of the original 4AS. The genetic map of chromosome 4A of hexaploid bread wheat confirms that the long arm of this chromosome is composed of, from distal to proximal, a large (>52 cM) segment of 7BS, a very small segment of the original 4AL, a substantial (36cM) segment of the original 5AL and a densely mapped segment with homoeology to the short arms of 4B and 4D (Fig. 2). The observed map differs in two points from the expected map. The small 4AL segment of the original 4AL arm is distal to 5AL, not proximal as expected, and the segment that was translocated from 5AL is inserted in inverted orientation, with *Xabc310* being the most distal marker and *Xpsr1316* being the most proximal marker. *Xabc310* is the most proximal marker in the translocated segment on the long arm of chromosome $4A^m$ of *T. monococcum*. Thus, a paracentric inversion including a segment translocated from 5AL and the juxtaposed segment from the original 4AL appears to have taken place. Locus *Xpsr1327-4A* maps between the original 5AL segment and the original 4AS segment on 4AL. However, because this locus does not have homoeologous loci on other chromosomes of group 4 and because of the inability of this probe to detect polymorphism between the parents of the *T. monococcum* mapping population, the origin of the *Xpsr1327-4A* locus must remain uncertain.

Evolutionary sequence of the rearrangements

The 4AL/5AL translocation has similar breakpoints in *T. monococcum* and *T. aestivum* (present data) and in *Secale cereale* (Devos et al. 1993a). Furthermore, evidence for the presence of a 4L/5L translocation with breakpoints between *Xpsr104* and *Xpsr115* on 4L and *Xpsr370* and *Xpsr164* on 5L has also been obtained in *T. urartu*, *Ae. umbellulata*, *Dasypyrum villosum* and *Thinopyrum bessarabicum* (King et al. 1994, and unpublished results). Synteny mapping of *Xpsr164* and *β-Amy-1* in the long arm of chromosome 4E and *Xabc310* and *Xpsr1316* in the long arm of chromosome 5E in substitution lines of *Lophopyrum elongatum* in wheat clearly showed, however, that a translocation between 4E and 5E is not present in *L. elongatum*, which is closely related to *Th. bessarabicum*. A 4L/5L translocation is also absent in barley. The presence of 4L/5L translocations in a range of Triticeae species raises two questions that must remain unanswered for the time being. Firstly, which state is the most primitive? Probably, an answer will be provided by the detailed analysis of the locations of markers in regions spanning the translocation breakpoints in other grass genomes such as rice and maize. The second question is how many times has the translocation been fixed within the Triticeae? A monophyletic hypothesis results in groups of species that contradict our present views of taxonomy within the tribe. A hypothesis which fits today's taxonomic classification would, on the other hand, require an identical reciprocal translocation to have been fixed several times. As a precedent, recurrent structural changes are known to occur in *Drosophila melanogaster* where they are mediated by P elements (Engles and Preston 1984).

The absence of multivalents in chromosome pairing studies in *T. aestivum*×*T. dicoccoides* and *T. aestivum*×*Ae. tauschii* hybrids indicates that no fixed structural rearrangements have taken place between the A and B genomes and the D genome chromosomes since the formation of hexaploid wheat (Riley et al. 1967). These results are consistent with our mapping data obtained in an F_2 population from a cross between 'Chinese Spring' and a synthetic hexaploid, where no linkages were found indicative for the presence of rearrangements that differentiate the parents. Both the pairing and RFLP data suggest that the 4AL/7BS translocation and the peri- and paracentric inversions arose in the tetraploid progenitor of hexaploid bread wheat. The temporal order of the three events, however, can not be fully resolved with the current dataset, although the 4AL/7BS translocation had to take place before the paracentric inversion. This is indicated by the interstitial and inverted position of the 5AL segment in bread wheat chromosome arm 4AL. The pericentric inversion, however, could have taken place before or after the 4AL/7BS translocation, or even after the paracentric inversion.

Recombination in chromosome regions with altered positions relative to chromosome ends

It is clear, particularly in wheat, that recombination along the physical length of a chromosome is not randomly distributed. Evidence employing physical locations of *Nor* loci and C-bands (Dvořák and Chen 1984; Lukaszewski and Curtis 1993; Snape et al. 1985), in situ locations of mapped RFLP clones (Leitch and Heslop-Harrison 1993), the distribution of loci on dense genetic maps (Devos et al. 1992) and the alignment of genetic maps with deletion analysis (Werner et al. 1992) all indicate that recombination takes place less frequently in proximal than in distal regions. It is not clear, however, whether this distribution is a function of the chromosome segments themselves, e.g. the relative proportion of repeated sequences, or their location relative to the centromere and telomere. The group 4 chromosomes provide a model whereby these questions can be approached.

Chromosome arm 4AS, which can be compared to 4DL, lacks the terminal segment translocated to 5AL, and the long arm, 4AL, which has an additional terminal segment from 5AL and 7BS, can be compared to 4DS. Chromosome 4B of CS cannot be used for comparison because of a pericentric inversion of centromeric heterochromatin in that chromosome (Dvořák et al. 1984), which may have affected the relative arm lengths.

Physical arm lengths, adjusted for the overall 13% greater length of the A genome relative to the D genome, have been calculated from the data provided by Dvořák et al. (1984). These figures indicate that 4AS is 23% shorter than 4DL, and that 4AL is more than twice as long or 207% the length of 4DL. Recombination in the two common segments *Xpsr914–centromere* and *centromere–Xwg622* can also be calculated taking into account the average 21% greater recombination observed in the D genome chromosomes relative to the A genome (Devos et al. 1993b and unpublished results). These figures show that the loss of the terminal 23% of 4AS is associated with a 58% increase in genetic length of the proximal region, from 10 to 16 cM, and the addition of the physically long 5A-7B segment at the end of 4AL results in a 55% reduction, from 36 to 20 cM, in recombination frequency in the proximal region.

These results indicate that relative recombination rates are primarily associated with the distance of a segment from the telomere rather than any attributes of the segment itself. This result is consistent with cytological data indicating that chiasmata form more frequently in proximal regions of deleted chromosome arms (A. J. Lukaszewski, personal communication) and is possibly related to the fact that chromosome pairing starts at the telomere, thereby providing these regions with more opportunity to recombine.

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