B chromosomes in plants: escapees from the A chromosome genome?

Neil Jones[1] and Andreas Houben[2]

[1]The Institute of Biological Sciences, The University of Wales Aberystwyth, Cledwyn Building, Aberystwyth, UK SY23 3DD
[2]The Institute of Plant Genetics and Crop Plant Research (IPK), 06466 Gatersleben, Germany

B chromosomes are dispensable elements that do not recombine with the A chromosomes of the regular complement and that follow their own evolutionary track. In some cases, they are known to be nuclear parasites with autonomous modes of inheritance, exploiting 'drive' to ensure their survival in populations. Their 'selfishness' brings them into conflict with their host nuclear genome and generates a host–parasite relationship, with anti-B-chromosome genes working to ameliorate the worst of their excesses in depriving their hosts of genetic resources. Molecular studies are homing in on their sequence organization to give us an insight into the origin and evolution of these enigmatic chromosomes, which are, with rare exceptions, without active genes.

Supernumerary B chromosomes are recognized by three criteria: (i) they are dispensable and can be present or absent from individuals within a population; (ii) they do not pair or recombine with any members of the standard diploid (or polyploid) set of A chromosomes at meiosis; and (iii) their inheritance is non-mendelian and irregular. These criteria were embodied into the definition of a B chromosome as a 'dispensable supernumerary chromosome that does not recombine with the A chromosomes and which follows its own evolutionary pathway', which arose out of the First B-Chromosome Conference, held in Madrid in 1993 [1]. The simplicity of the definition belies the complexity of a diverse range of B-chromosome systems, which are found in many of the major groups of plants and animals. Earlier reviews (Table 1) contain the full story from the 1920s to the present but, to give this article some context, we profile the properties of B chromosomes, with their many generalities and exceptions (Box 1), and then deal with the more recent work that focuses on the question of the origin of B chromosomes and on aspects of their transmission and population dynamics.

Significance of B chromosomes

The significance of B chromosomes is to be found in their widespread occurrence in hundreds of flowering plants, and also in gymnosperms and in some lower forms such as ferns, bryophytes and fungi (they are also common in animals, including mammals) [2]. Owing to their particular properties, B chromosomes have been used to elucidate

the function of post-translational histone modifications, such as histone H3 phosphorylation [3] and methylation [4]. They are of particular interest in maize (*Zea mays*), in which they have been extensively used in genetic analysis involving A–B translocations for mapping [5,6] and for the identification of centromere structure and size [7,8]. In other species, there is interest in their capacity to behave as diploidizing agents for chromosome pairing in certain allopolyploid hybrids [9,10] and their influence on recombination through the modulation of chiasma frequency and distribution in the A chromosomes (e.g. in rye) [2].

The question of their adaptive significance in natural populations has been argued over for decades, with the final position showing little if any substantial evidence to support such a role, with the possible exception of chives (*Allium schoenoprasum*) [11–13] and the fungal pathogen *Nectria haematococca* [14]. The emerging view in plants, principally from rye and maize, is that the B chromosomes are parasitic elements that maintain their polymorphism by DRIVE (see Glossary) and that there is a host–parasite relationship between the A and B chromosomes. The idea that B chromosomes are nuclear parasites is fascinating. It places them in the arena with other forms of selfish DNA

Table 1. Chronological list of selected reviews of B chromosomes

Date	Content of review
1982	Research monograph based on the world literature in plants and animals up to 1980, including references to all earlier reviews and an atlas of species with B chromosomes [2]
1982	B chromosomes in plants, particularly good on effects on chiasma frequency and chromosome pairing in hybrids [9]
1986	General review of the B chromosome of maize [59]
1988	The maize B chromosome as a model system for nondisjunction [60]
1990	Muller's Ratchet and the evolution of B chromosomes [61]
1990	Review of the Red Queen theory in the context of B chromosomes as parasites that induce changes in host recombination [62]
1991	Cytogenetics and plant breeding applications of B–A translocations in maize [5]
1991	B–A translocations and chromosome manipulations in maize [6]
1991	Cytogenetics of B chromosomes in crop plants, including species hybrids [63]
1991	Review of B chromosome 'drive' [64]
1993	B chromosomes of rye, Secale cereale [65]
1995	B chromosomes in plants [48]
2000	B chromosome evolution [32]
2002	Recent advances and insights on origin and evolution [26]

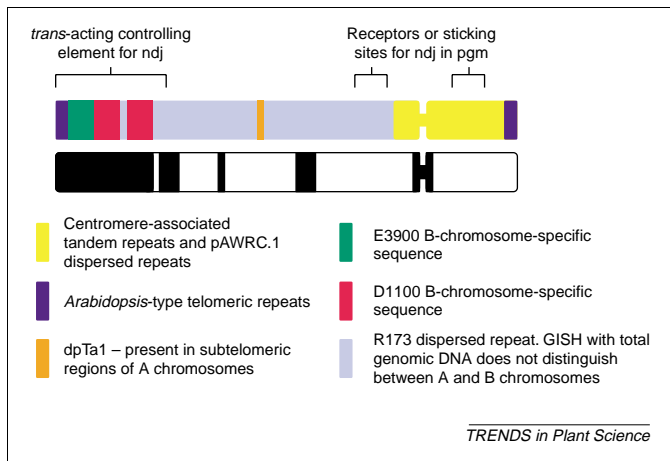*Corresponding author:* Neil Jones (rnj@aber.ac.uk).

Fig. 1. The sequence, genetic and chromatin organization of the B chromosome of rye. The lower chromatid indicates C-band heterochromatic regions [65]. References: E3900 C-chromosome-specific sequence [45]; centromere-associated tandem repeats and pAWRC.1 dispersed repeats [66]. Abbreviations: ndj, nondisjunction; pgm, pollen grain mitosis.

Glossary

Electrophoretic karyotypes: Descriptions of chromosome number and size produced by pulse-field gel electrophoresis in species with chromosomes that are too small to be seen by light microscopy (e.g. fungi).

Isochromosome: A chromosome with two genetically identical arms that are mirror images of each other.

Drive: With reference to B chromosomes, drive occurs when chromosome number in the gametes is greater than mendelian expectations (i.e. >0.5). In some cases, this can occur at meiosis, when the B chromosomes can migrate to one pole of the spindle during the first anaphase and then pass preferentially into the nucleus that is destined to form the egg cell (particularly where the spindle is asymmetrical). Alternatively, drive can occur in the first pollen grain mitosis, when the B-chromatids fail to separate and both pass into the generative nucleus. Nondisjunction at the second pollen mitosis followed by preferential fertilization of the egg by the B-containing sperm is another drive mechanism.

Microchromosomes: Tiny dot-like chromosomes that are too small for their centromeres and individual arms to be resolved under the light microscope (Fig. 2).

Telocentrics: Chromosomes that have their centromere at one end.

in A-chromosome genomes (e.g. retro-elements), the difference being that they are autonomous in their inheritance and not constrained by the normal rules of chromosome behaviour. Little wonder, then, that interest is now focusing on 'transmission genes' and that a cocktail of molecular technologies is being thrown at B chromosomes in an attempt to make sense of them, especially their structure, origin and evolution.

Transmission genotypes

Östergren [15] first proposed that B chromosomes in plants could be viewed as parasitic chromosomes, based on his observations that progeny had more B chromosomes than their parents in crossing experiments. This idea did not meet with enthusiasm and much energy was invested in trying to show that their population polymorphisms could be explained in terms of Darwinian fitness and selection based on phenotypic effects. Much later, Kimura and Kayano [16] proposed an elegant model of the selfish nature of the B chromosomes of *Lillium callosum* based on meiotic drive in the female, and Nur provided convincing evidence of their parasitic nature in the grasshopper *Melanoplus femur-rubrum* [17] and the mealy bug *Pseudococcus affinis* [18,19]. Studies of the genetic control of transmission properties are best developed in rye and maize. In rye, the drive mechanism based on directed nondisjunction in gametophytes is strong and is under the control of the B chromosome itself (Figs 1,2). A computer
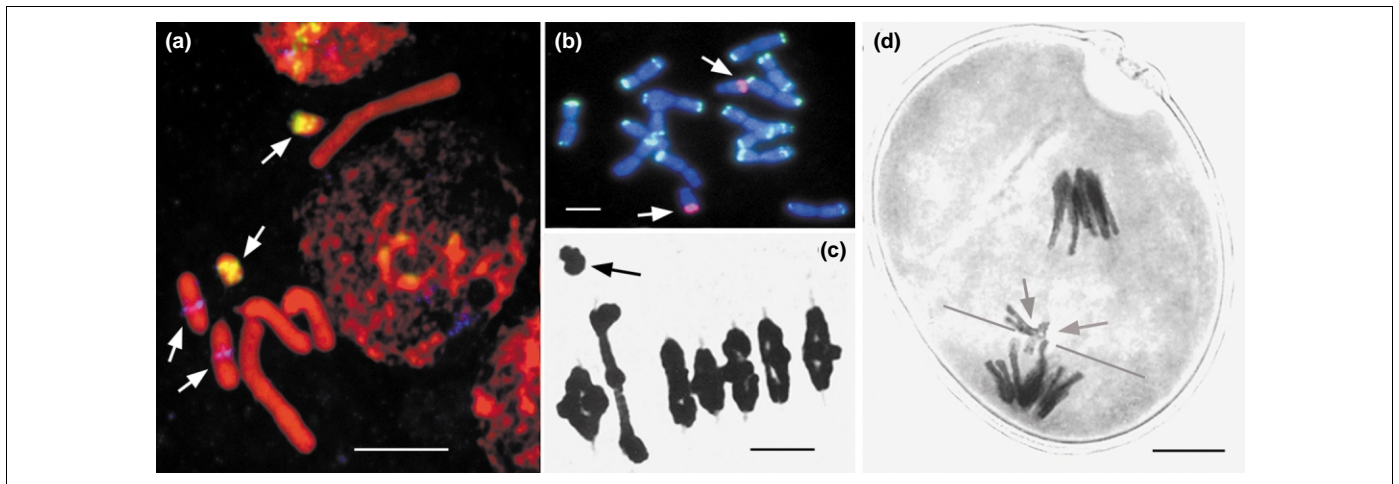

Fig. 2. B chromosomes in rye and in an Australian member of the Asteraceae, *Brachycome dichromosomatica* (synonym *Brachyscome dichromosomatica*), which has extraordinary genome plasticity. *B. dichromosomatica* is an annual outbreeder with only two pairs of A chromosomes, and it occurs in four karyotypically distinct cytodemes. In some cases, supernumerary A chromosome fragments can be present as well as different types of B chromosomes within a single plant; these are the somatically stable large B chromosomes and the somatically unstable dot-like micro-B chromosomes. (a) A mitotic cell of *B. dichromosomatica* (2n = four A chromosomes + two standard B chromosomes + two iso-micro-B chromosomes) after fluorescence *in situ* hybridization performed with a micro-B-chromosome-specific probe {Bdm29 [67], yellow (arrowed)} and a standard B-chromosome centromere-specific probe {Bd49 [68], blue (arrowed)}. (b) C metaphase in a root meristem cell of rye with two B chromosomes (arrowed) and 14 normal A chromosomes, after fluorescence *in situ* hybridization using the pSc200 probe for subtelomeric repeats, which marks the ends of the A chromosomes, and the B-chromosome-specific probe D1100 (red), which marks the end of the long arm of the B chromosomes. Notice the absence of the A chromosome subtelomeric sequences on the B chromosomes (photographs courtesy of Robert Hasterok, and reproduced, with permission, of Ref. [56]). (c) Metaphase I of meiosis in a rye plant with single B chromosome (arrowed) and seven A chromosome bivalents. (d) First pollen grain mitosis in rye, showing directed nondisjunction of a single B chromosome towards the generative nucleus. The two chromatids of the B are held together at two sensitive sticking sites, one on each side of the centromere, and the centromeres are being pulled towards the poles. The spindle is asymmetrical and B chromatids are transiently held together in such a way that they become passively included in the generative nucleus. Because the same process happens on the female side in rye, the progeny will carry four B chromosomes in a 2B × 2B cross. The broken line represents the equator of the spindle. Arrows indicate sticking sites. Scale bars = 5 μm.

Box 1. General properties of B chromosomes and exceptions to them

Form and size

B chromosomes are smaller than A chromosomes (Fig. 2) except in a few cases, in which they are of equal size. They often have distinct centromere positions and can be readily identified at mitosis. Variants include B chromosomes as ISOCHROMOSOMES or TELOCENTRICS, and, in a few species, they appear as MICROCHROMOSOMES.

Structural polymorphism

The normal situation is for only one form of a B chromosome, with variants arising at mutation frequency. However, in at least 65 plant species, two or more polymorphic forms are known.

Chromatin

B chromosomes are described as heterochromatic in about half of plants that carry them [e.g. maize (*Zea mays*)]. In general, their heterochromatic content is similar to that of their A chromosomes (Figs 1,3–5).

Gene content and sequence organization

No B-chromosome-localized gene has been isolated in plants yet but they might have ribosomal DNA, some organize nucleoli and some have genetic information controlling their own transmission (e.g. in rye and maize). The strongest evidence to date for genes on B chromosomes comes from the fungal plant pathogen *Nectria haematococca*, which infects peas. Several genes determining pathogenicity have been identified and located to the 1.6 Mb supernumerary B chromosome in this fungus [14], and ELECTROPHORETIC KARYOTYPES indicate that several fungal species carry dispensable supernumerary B chromosomes [71]. The chromosomes of these fungi are too small to be resolved by light microscopy and so we have no information about how they behave at meiosis.

Mitotic stability

B chromosomes show a constant number in all somatic tissues in about a third of species for which information is available (i.e. 60 out of 180 species). Where there is instability, this can take the form of cell-to-cell variation in number or of absence from certain tissues (e.g. as in *Aegilops mutica*, in which there are no B chromosomes in the roots).

Meiotic behaviour

The only fixed rule is that, by definition, B chromosomes never pair or recombine with A chromosomes (Fig. 2c). Where they do pair, it is among themselves, forming multivalents when more than two are

present. Two B chromosomes can have a regular meiotic process but, as univalents, they suffer elimination. There are more than 20 cases known in which B chromosomes are described as nonpairing (e.g. *Allium cernuum* and *Centauria scabiosa*) and, surprisingly, this does not lead to their loss from the populations. The meiotic properties of some B chromosomes endow them with 'drive', which is the case in female meiosis in *Lillium callosum*.

Inheritance

The inheritance of B chromosomes is non-mendelian and irregular owing to vagaries in the levels of paring, to degrees of meiotic elimination and to various drive processes. Drive is mostly caused by directed nondisjunction of sister chromatids at the first pollen mitosis, such that the generative nucleus carries the unreduced number, which then forms the sperm (e.g. many species of Gramineae). In rye, unusually, this drive happens on both the male (Fig. 2d) and the female side, and, in maize, the nondisjunction happens at the second pollen mitosis, followed by preferential fertilization by the B-chromosome-containing sperm. Meiotic drive and accumulation at earlier developmental stages in the germ line operate in a few cases. These irregularities in transmission generate a numerical polymorphism in populations, with a spectrum of B chromosome numbers including individuals with none. There is usually a modal number and an equilibrium frequency based on a balance between drive and the harmful effects caused by high numbers. Drive is by no means a universal process: it is known in ~60% of species for which transmission data are available. In the others, there is no known drive and no real understanding of how the population equilibrium frequencies are maintained.

Phenotypic effects

B chromosomes tend to be neutral in their phenotypic effects in low numbers and harmful in high numbers, affecting a wide range of nuclear [72] and exophenotypic characters. They are particularly detrimental to fertility and also have the enigmatic effect of influencing phenotype in certain cases according to their presence in odd or even-numbered combinations. Visualizing rye B chromosomes carried as an additional line in a wheat background with *in situ* hybridization probes indicates that they have a dose-dependent association at interphase, with even numbers (2B, 4B) having a greater preference for being physically associated than odd ones [72]. There might therefore be some relationship between their nuclear disposition and their phenotypic effects.

---

simulation of B-chromosome transmission in rye suggested that the main factor contributing to equilibrium B-chromosome frequencies in populations is the level of meiotic pairing among B chromosomes themselves, and is not determined solely by their negative phenotypic effects [20,21]. Subsequently, Puertas and colleagues identified high and low transmission lines from different rye populations, and developed the concept of 'high' and 'low' transmission genotypes [22]. An elegant set of experiments confirmed that the level of meiotic pairing was indeed the main factor influencing equilibrium B-chromosome frequencies in populations [23,24] and that the 'genes' controlling B-transmission rate are located on the B chromosomes themselves and that such 'genes' are the sites for chiasma formation [25,26].

The B chromosome of maize has a more complex genetic organization than that of rye, with at least four different regions (Fig. 3) that influence the nondisjunction process, which happens on the male side only. In addition, unpaired univalent B chromosomes can suppress their meiotic loss

and enhance their transmission potential [27]. Transmission genotypes were first demonstrated by Rosato *et al*. [28], and it was later suggested that the genetic elements
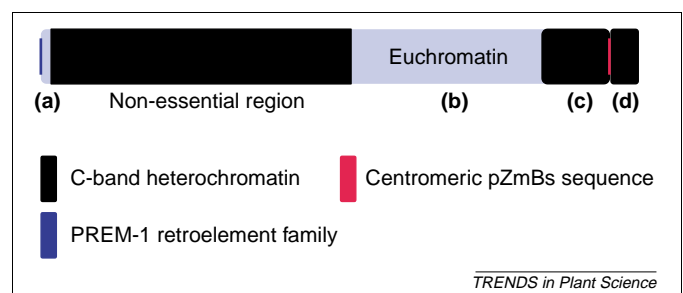

Fig. 3. The genetic, sequence and chromatin organization of the B chromosome of maize. (a) Distal euchromatic tip is *trans*-acting and essential for nondisjunction. (b) Proximal euchromatin is *trans*-acting and essential for nondisjunction. (c) Centromeric chromatin is a *cis*-acting receptor for nondisjunction. (d) Short arm and centromere region enhances nondisjunction. Loss of short arm reduces the rate of nondisjunction but does not prevent it. Regions controlling nondisjunction were identified by deletion studies [60]. References: PREM-1 retroelement family [37]; centromeric pZmBs sequence [53,54].

controlling transmission rate are located on the A chromosomes [29]. Subsequent experiments [30] determined that a single major gene in an A chromosome controls B-chromosome transmission rate in maize, and that it acts in the haploid egg cell at the time of fertilization. In high transmission lines, the H (high transmission) allele allows the B chromosome opportunistically to use the fertilization process to promote its own accumulation within populations, and the L allele works in the opposite direction to reduce B-chromosome transmission and to serve essentially as an anti-B-chromosome gene. The way that the maize B chromosome interacts with its host genome therefore constitutes a co-evolutionary host–parasite system [31]. A wider view of this topic, including some interesting animal systems, is found in two reviews [32,33].

A patchwork of A-chromosome sequences?

The origin of B chromosomes has remained a mystery since their description in the early part of the past century but the B chromosomes of different organisms probably arose in various ways. The *de novo* formation of B chromosomes must be a rare process because analyses of different B-chromosome variants within a species suggests a common origin of different B-chromosome forms [34,35]. It is widely accepted that B chromosomes could be derived from the A chromosomes (e.g. *Crepis capillaries* [36], *Z. mays* [37]) and/or from sex chromosomes in animals (e.g. *Eyprepocnemis plorans* [38]). However, there is also evidence suggesting that B chromosomes can be generated spontaneously in response to the new genome conditions following interspecific hybridization (e.g. *Coix aquaticus* and *Coix gigantea* [39], and in the parasitic wasp *Nasonia vitripennis* [40]). This view derives from new knowledge that allopolyploidization induces structural rearrangements at the chromosome level, as well as the elimination, reorganization or amplification of sequences [41,42], and there is every reason to believe that this restructuring of the genome could generate sequences that have the potential to form B chromosomes. In addition, spontaneous amplification of coding and noncoding tandem repeat sequences derived from A chromosomes seem to be strongly associated with the origin and evolution of plant B chromosomes [43–45]. Repeats arranged in tandem arrays are particularly prone to molecular events that alter the number of repeats [46], such as unequal crossing over between the sister chromatids, replication slippage and replication on a rolling circle [47].

The involvement of ribosomal RNA coding repeats does not appear to be accidental because ribosomal DNA (rDNA) loci have been detected on B chromosomes of many species [48]. In the herb *Plantago lagopus*, the origin of a B chromosome seems to be associated with massive amplification of 5S rDNA sequences after chromosome fragmentation of an aneuploid A chromosome [43]. Alternatively, but less likely, B-chromosome-localized rDNA sites could be a consequence of the reported mobile nature of rDNA [49,50], with B chromosomes as the preferred 'landing sites' owing to their neutral character.

The origin of the dot-like micro-B chromosomes of *Brachycome dichromosomatica* has also been linked to

rapidly evolving tandem repeat sequences [44] (Figs 2,4). In *Brachycome*, there is an evolutionary relationship between different types of polymorphic and heterochromatic A-chromosome regions ('supernumerary segments') and B chromosomes. The supernumerary segments are often heterochromatic and dispensable, and provide a natural platform from which B chromosomes could be formed. However, because the genomic organization of the micro-B chromosome is a patchwork or conglomerate of repetitive sequences from different polymorphic A-chromosome sites, the present micro-B chromosomes could not have originated by simple excision of an A-chromosome fragment. We propose instead that B-chromosome founder sequences were 'released' from a polymorphic A-chromosome region and were then stabilized by the addition of telomeric repeats and other sequences. The rapid accumulation of other sequences on a *de novo* micro-B chromosome would present a barrier to the similarity between the 'parent' homologous chromosome regions and thus interfere with the competence for meiotic pairing between the 'parental' and derived segments. The newly formed B chromosome can then start its independent evolution. This, of course, begs the question of how a centromere appears in a newly formed chromosome. Transposition or activation of a cryptic
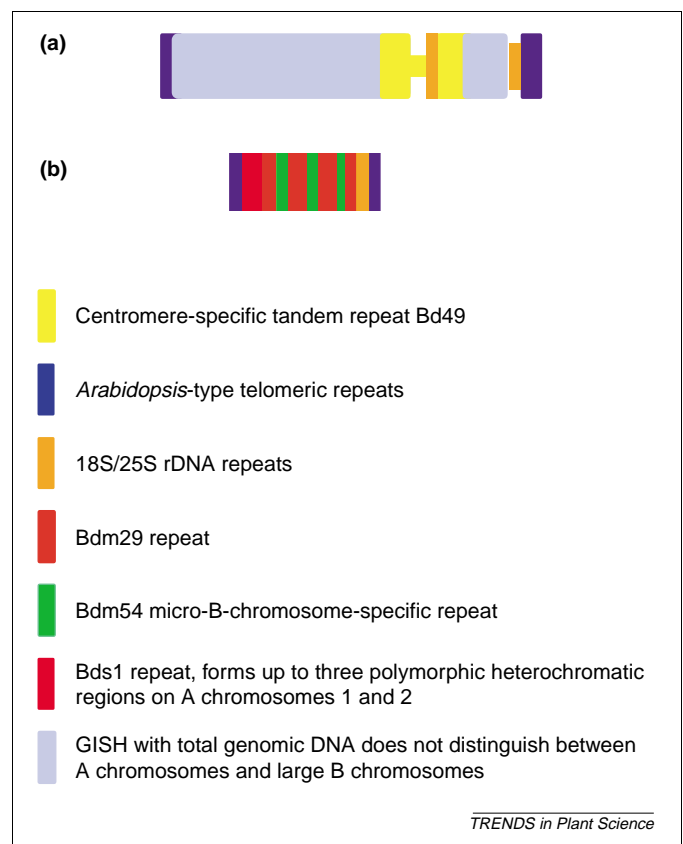

Fig. 4. The sequence and chromatin organization of the B chromosomes of *Brachycome dichromosomatica*. (a) Large B-chromosomes contain euchromatic and heterochromatic DNA, and are late replicating and hypoacetylated on histone H4 [69]. (b) Micro-B chromosomes contain heterochromatic DNA, replicate throughout S-phase, and are hypomethylated on histone H3 Lys4 and hypermethylated on H3 Lys9 [4]. The Bdm29 repeat forms a rare polymorphic heterochromatic region on A chromosome 1 [44]. 18S/25S ribosomal DNA repeats on the large B chromosomes are transcriptionally inactive [70]. Reference: centromere-specific tandem repeat Bd49 [68]. Abbreviation: GISH, genome *in situ* hybridization.
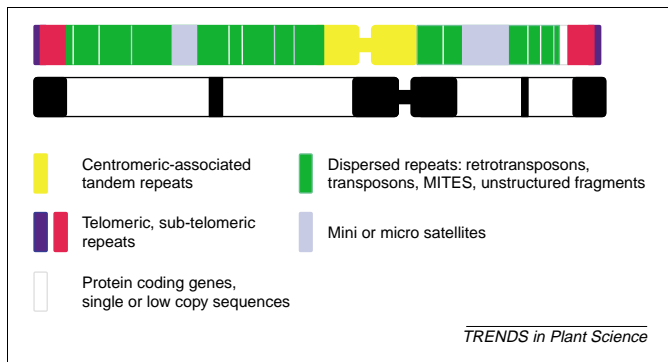
Fig. 5. The sequence organization of a representative plant A chromosome for comparison with the B chromosomes in Figs 1, 3 and 4. Abbreviation: MITES, miniature inverted-repeat transposable elements.

centromere sequence is possible, but it is more likely that an epigenetic event induced centromere activity [51].

The genetic and sequence organization of the maize B chromosome has been intensively studied (Fig. 3), as indicated earlier. Interestingly, the maize B chromosome has many sequences that originate from different A chromosomes [52,53], and also from polymorphic and heterochromatic A chromosome regions (often called 'knobs') [54] (Fig. 3). Because no such knobs are found adjacent to centromeres of A chromosomes in any karyotype of maize or its relatives [55], the B chromosome of maize could also be an amalgamation of sequences from several A chromosomes. The sequence organization of the B chromosomes of rye (Fig. 1), maize (Fig. 3) and *Brachycome dichromosomatica* (Fig. 4) can be usefully compared with the sequence organization of a representative plant A chromosome (Fig. 5).

B chromosomes are mainly transcriptionally inactive, so a greater tolerance is expected to modifications of the B chromosomes than of the A chromosomes, and B-chromosome structural polymorphisms have been reported in several different species [2]. However, there are also species (e.g. *B. dichromosomatica* [35]) with little structural variation in their B chromosomes [48]. One explanation for the observed uniformity is that the A chromosome genotypes have a low tolerance, which limits B chromosome variation to only minor changes. This suggests the existence of an A- and/or B-chromosome-derived control mechanism for the maintenance of 'suitable' B chromosomes. Also, stable B–A translocations seldom occur and it seems that there can be no crossing of the chromosome-type barrier in rye [56]. By contrast, stable B–A translocations in maize are widely used for experimental mapping purposes [57] and also to manipulate the dosage of chromosomal segments on gene expression [58], but we do not know of the existence of any such translocations in natural maize populations.

The B-chromosome centromere of maize has also been used as a model to study the DNA organization of a functional centromere. Changes in the physical structure of the B-chromosome repeat array are correlated with altered meiotic transmission [7]. There is a correlation between the size of a centromere and meiotic transmission. It is proposed that at least 55 kb is crucial for full meiotic transmission, and that the surrounding DNA, which leads

to a larger fragment of 370 kb, provides additional stabilizing DNA. Healing of broken centromeres can be achieved through the addition or fusion of telomeric repeats to the broken chromosome [8]. The elegant studies of the centromere structure of maize B chromosomes provide a convincing example of the usefulness of B chromosomes for research into genome organization.

Afterthoughts

The thrust of current research on the biology of plant B chromosomes has a sharp point. It penetrates only a handful of species and we do not know whether they are widely representative. Nonetheless, some truths are evident. We are confident that B chromosomes arise because of errors during meiosis that generate A-chromosome fragments, and that interspecific hybridization and allopolyploidization cause a plethora of genome rearrangements that provide the platform from which autonomous selfish elements can emerge. We know, too, that there are methods of sequence amplification and rearrangement that can affect A as well as B chromosomes, and that these activities can inflate genome size and provide sequence resources to make some B chromosomes 'grow'. When a B chromosome is born complete with a centromere (e.g. from a trisomic), we are confident of its developmental progression. Beyond this level, there are uncertainties yet to be resolved. How does the capacity for mitotic and meiotic drive arise, as it must do in the early post-natal phase, and what sequence information encodes such processes? What is the meaning of a 'genetic element' or a 'region of a chromosome' that controls nondisjunction? Transmission genotypes have 'genes' controlling rates of transmission, but there is still much to be learned about these 'genes' and how they act to determine the various processes that they control and how they interact and co-evolve with their A-chromosome counterparts. There is a good story unfolding here (albeit told briefly), and not just about B chromosomes themselves but also about how we might use them as tools to investigate wider issues of genome organization and evolution in plants.

References
1 Beukeboom, L.W. (1994) Bewildering Bs: an impression of the 1st B-chromosome conference. *Heredity* 73, 328–336
2 Jones, R.N. and Rees, H. (1982) *B Chromosomes*, 1st edn, Academic Press
3 Manzanero, S. *et al.* (2000) The chromosomal distribution of phosphorylated histone H3 differs between plants and animals at meiosis. *Chromosoma* 109, 308–317
4 Houben, A. *et al.* (2003) Methylation of histone H3 in euchromatin of plant chromosomes depends on basic nuclear DNA content. *Plant J.* 33, 967–973
5 Beckett, J.B. (1991) Cytogenetic, genetic and plant breeding applications of B–A translocations in maize. In *Chromosome Engineering in Plants: Genetics, Breeding, Evolution* (Part A) (Gupta, P.K. and Tsuchiya, T., eds), pp. 493–529, Elsevier
6 Birchler, J.A. (1991) Chromosome manipulation in maize. In *Chromosome Engineering in Plants: Genetics, Breeding, Evolution* (Part A) (Gupta, P.K. and Tsuchiya, T., eds), pp. 531–559, Elsevier
7 Kaszas, E. and Birchler, J.A. (1998) Meiotic transmission rates correlate with physical features of rearranged centromeres in maize. *Genetics* 150, 1683–1692
8 Kaszas, E. *et al.* (2002) Cytological and molecular analysis of centromere misdivision in maize. *Genome* 45, 759–768

9 Tanaka, M. and Kawahara, T. (1982) Cytogenetical effects of B chromosomes in plants – a review. *Report of the Plant Germplasm Institute, Kyoto University* 5, 1–18, Plant Germplasm Institute, Kyoto University, Japan

10 Jenkins, G. (1986) Synaptonemal complex formation in hybrids of *Lolium temulentum* × *Lolium perenne* (L.) III. Tetraploid. *Chromosoma* 93, 413–419

11 Holmes, D.S. and Bougourd, S.M. (1991) B chromosome selection in *Allium schoenoprasum* II. Experimental populations. *Heredity* 67, 117–122

12 Plowman, A.B. and Bougourd, S.M. (1994) Selectively advantageous effects of B-chromosomes on germination behavior in *Allium schoenoprasum* L. *Heredity* 72, 587–593

13 Bougourd, S.M. and Plowman, A.B. (1996) The inheritance of B chromosomes in *Allium schoenoprasum* L. *Chromosome Res.* 4, 151–158

14 Han, Y. *et al.* (2001) Genes determining pathogenicity to pea are clustered on a supernumerary chromosome in the fungal plant pathogen *Nectria haematococca*. *Plant J.* 25, 305–314

15 Östergren, G. (1947) Heterochromatic B chromosomes in *Anthoxanthum*. *Hereditas* 33, 261–296

16 Kimura, M. and Kayano, H. (1961) The maintenance of supernumerary chromosomes in wild populations of *Lillium callosum* by preferential segregation. *Genetics* 46, 1699–1712

17 Nur, U. (1977) Maintenance of a 'parasitic' B chromosome in the grasshopper *Melanoplus femur-rubrum*. *Genetics* 87, 499–512

18 Nur, U. and Brett, B.L.H. (1988) Genotypes affecting the condensation and transmission of heterochromatic B chromosomes in the mealy bug *Pseudococcus affinis*. *Chromosoma* 96, 205–212

19 Nur, U. and Brett, B.L.H. (1987) Control of meiotic drive of B chromosomes in the mealy bug *Pseudococcus affinis (obscurus)*. *Genetics* 115, 499–510

20 Matthews, R.B. and Jones, R.N. (1982) Dynamics of the B chromosome polymorphism in rye. I. Simulated populations. *Heredity* 48, 345–369

21 Matthews, R.B. and Jones, R.N. (1983) Dynamics of the B chromosome polymorphism in rye. II. Estimates of parameters. *Heredity* 50, 119–137

22 Jimenez, M.M. *et al.* (1995) Genetic control of the rate of transmission of rye B-chromosomes. 2. 0B × 2B crosses. *Heredity* 74, 518–523

23 Jimenez, M.M. *et al.* (1997) Genetic control of the rate of transmission of rye B chromosomes. 3. Male meiosis and gametogenesis. *Heredity* 78, 636–644

24 Jimenez, G. *et al.* (2000) Relationship between pachytene synapsis, metaphase I associations, and transmission of 2B and 4B chromosomes in rye. *Genome* 43, 232–239

25 Puertas, M.J. *et al.* (1998) Genetic control of the rate of transmission of rye B chromosomes. IV. Localization of the genes controlling B transmission rate. *Heredity* 80, 209–213

26 Puertas, M.J. (2002) Nature and evolution of B chromosomes in plants: a non-coding but information-rich part of plant genomes. *Cytogenet. Genome Res.* 96, 198–205

27 Carlson, W.R. and Roseman, R.R. (1992) A new property of the maize B-chromosome. *Genetics* 131, 211–223

28 Rosato, M. *et al.* (1996) Genetic control of B chromosome transmission rate in *Zea mays* ssp *mays (Poaceae)*. *Am. J. Bot.* 83, 1107–1112

29 Chiavarino, A.M. *et al.* (1998) Localization of the genes controlling B chromosome transmission rate in maize (*Zea mays* ssp. *mays*, Poaceae). *Am. J. Bot.* 85, 1581–1585

30 Chiavarino, A.M. *et al.* (2001) Is maize B chromosome preferential fertilization controlled by a single gene? *Heredity* 86, 743–748

31 Gonzalez-Sanchez, M. *et al.* (2003) One gene determines maize B chromosome accumulation by preferential fertilization; another gene(s) determines their meiotic loss. *Heredity* 90, 122–129

32 Camacho, J.P.M. *et al.* (2000) B-chromosome evolution. *Philos. Trans. R. Soc. London Ser. B* 355, 163–178

33 Frank, S.A. (2000) Polymorphism of attack and defense. *Trends Ecol. Evol.* 15, 167–171

34 Cabrero, J. *et al.* (1999) Common origin of B chromosome variants in the grasshopper *Eyprepocnemis plorans*. *Heredity* 83, 435–439

35 Houben, A. *et al.* (1999) A monophyletic origin of the B chromosomes of *Brachycome dichromosomatica* (Asteraceae). *Plant Syst. Evol.* 219, 127–135

36 Jamilena, M. *et al.* (1994) A molecular analysis of the origin of the *Crepis capillaris* B chromosome. *J. Cell Sci.* 107, 703–708

37 Stark, E.A. *et al.* (1996) Molecular analysis of the structure of the maize B-chromosome. *Chromosome Res.* 4, 15–23

38 Lopez-Leon, M.D. *et al.* (1994) Possible origin of a B chromosome deduced from its DNA composition using double FISH technique. *Chromosome Res.* 2, 87–92

39 Sapre, B. and Deshpande, S. (1987) Origin of B chromosomes in *Coix* L. through spontaneous interspecific hybridization. *J. Hered.* 78, 191–196

40 McAllister, B.F. and Werren, J.H. (1997) Hybrid origin of a B chromosome (PSR) in the parasitic wasp *Nasonia vitripennis*. *Chromosoma* 106, 243–253

41 Ozkan, H. *et al.* (2001) Allopolyploidy-induced rapid genome evolution in the wheat (*Aegilops–Triticum*) group. *Plant Cell* 13, 1735–1747

42 Liu, B. and Wendel, J.F. (2002) Non-mendelian phenomena in allopolyploid genome evolution. *Curr. Genom.* 3, 489–505

43 Dhar, M.K. *et al.* (2002) Origin of an apparent B chromosome by mutation, chromosome fragmentation and specific DNA sequence amplification. *Chromosoma* 111, 332–340

44 Houben, A. *et al.* (2001) The genomic complexity of micro B chromosomes of *Brachycome dichromosomatica*. *Chromosoma* 110, 451–459

45 Langdon, T. *et al.* (2000) *De novo* evolution of satellite DNA on the rye B chromosome. *Genetics* 154, 869–884

46 Flavell, R.B. (1985) Repeated sequences and genome change. In *Genetic Flux in Plants* (Hohn, B. and Dennis, E.S., eds) pp. 139–156, Springer

47 Wintersberger, E. (1994) DNA amplification: new insights into its mechanism. *Chromosoma* 103, 73–81

48 Jones, R.N. (1995) B chromosomes in plants. *New Phytol.* 131, 411–434

49 Schubert, I. and Wobus, U. (1985) *In situ* hybridization confirms jumping nucleolus organizing regions in *Allium*. *Chromosoma* 92, 143–148

50 Dubcovsky, J. and Dvorak, J. (1995) Ribosomal RNA multigene loci: nomads of the Triticeae genomes. *Genetics* 140, 1367–1377

51 Karpen, G.H. and Allshire, R.C. (1997) The case for epigenetic effects on centromere identity and function. *Trends Genet.* 13, 489–496

52 Page, B.T. *et al.* (2001) Characterization of a maize chromosome 4 centromeric sequence: evidence for an evolutionary relationship with the B chromosome centromere. *Genetics* 159, 291–302

53 Cheng, Y.M. and Lin, B.Y. (2003) Cloning and characterization of maize B chromosome sequences derived from microdissection. *Genetics* 164, 299–310

54 Alfenito, M.R. and Birchler, J.A. (1993) Molecular characterization of a maize B chromosome centric sequence. *Genetics* 135, 589–597

55 Buckler, E.S. *et al.* (1999) Meiotic drive of chromosomal knobs reshaped the maize genome. *Genetics* 153, 415–426

56 Hasterok, R. *et al.* (2002) The nature and destiny of translocated B-chromosome-specific satellite DNA of rye. *Chromosome Res.* 10, 83–86

57 Beckett, J.B. (1978) B–A translocations in maize. I. Use in locating genes by chromosome arms. *J. Hered.* 93, 135–138

58 Auger, D.L. and Birchler, J.A. (2002) Maize tertiary trisomic stocks derived from B–A translocations. *J. Hered.* 93, 42–47

59 Carlson, W.R. (1986) The B chromosome of maize. *CRC Crit. Rev. Plant Sci.* 3, 201–206

60 Carlson, W.R. (1988) B chromosomes as a model system for nondisjunction. In *Aneuploidy: Induction and Test Systems* (Part B) (Vig, B.K. and Sandberg, A.A., eds), pp. 199–207, Alan R. Liss, New York, NY, USA

61 Green, D.M. (1990) Muller's ratchet and the evolution of supernumerary chromosomes. *Genome* 33, 818–824

62 Bell, G. and Burt, A. (1990) B-chromosomes: germ-line parasites which induce changes in host recombination. *Parasitology* 100, S19–S26

63 Jones, R.N. (1991) Cytogenetics of B chromosomes in crops. In *Chromosome Engineering in Plants: Genetics, Breeding, Evolution* (Part A) (Gupta, P.K. and Tsuchiya, T., eds), pp. 141–157, Elsevier

64 Jones, R.N. (1991) B-chromosome drive. *Am. Nat.* 137, 430–442

65 Jones, R.N. and Puertas, M.J. (1993) The B-chromosomes of rye (*Secale cereale* L.). In *Frontiers in Plant Science Research* (Dhir, K.K. and Sareen, T.S., eds) pp. 81–112, Bhagwati Enterprises, Delhi, India

66 Wilkes, T.M. *et al.* (1995) Analysis of rye B-chromosome structure using fluorescence *in situ* hybridization (FISH). *Chromosome Res.* 3, 466–472

67 Houben, A. *et al.* (1997) A repetitive DNA sequence common to the different B chromosomes of the genus *Brachycome*. *Chromosoma* 106, 513–519

68 Leach, C.R. *et al.* (1995) Organization and origin of a B chromosome centromeric sequence from *Brachycome dichromosomatica*. *Chromosoma* 103, 708–714

69 Houben, A. *et al.* (1997) Differences of histone H4 acetylation and replication timing between A and B chromosomes of *Brachycome dichromosomatica*. *Chromosome Res.* 5, 233–237

70 Donald, T.M. *et al.* (1997) Ribosomal RNA genes specific to the B chromosomes in *Brachycome dichromosomatica* are not transcribed in leaf tissue. *Genome* 40, 674–681

71 Covert, S.F. (1998) Supernumerary chromosomes in filamentous fungi. *Curr. Genet.* 33, 311–319

72 Morais-Cecilio, L. *et al.* (1996) Painting rye B chromosomes in wheat: interphase chromatin organization, nuclear disposition and association in plants with two, three or four Bs. *Chromosome Res.* 4, 195–200