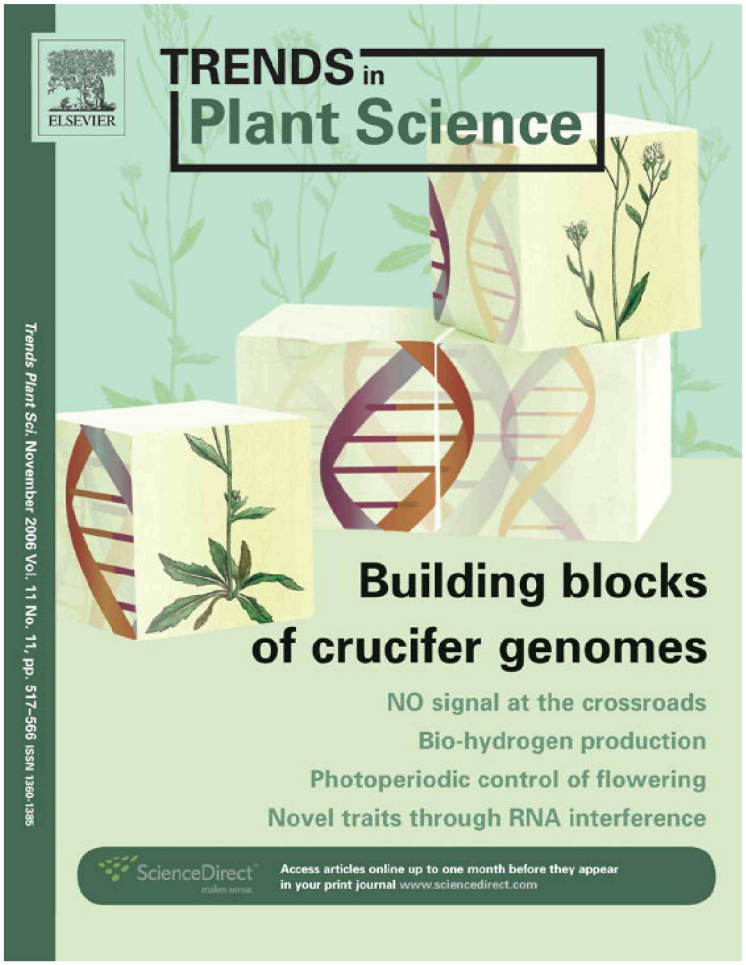

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The ABC's of comparative genomics in the Brassicaceae: building blocks of crucifer genomes

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In this review we summarize recent advances in our understanding of phylogenetics, polyploidization and comparative genomics in the family Brassicaceae. These findings pave the way for a unified comparative genomic framework. We integrate several of these findings into a simple system of 24 conserved chromosomal blocks (labeled A–X). The naming, order, orientation and color-coding of these blocks are based on their positions in a proposed ancestral karyotype (*n* = 8), rather than by their position in the reduced genome of *Arabidopsis thaliana* (*n* = 5). We show how these crucifer building blocks can be rearranged to model the genome structures of *A. thaliana*, *Arabidopsis lyrata*, *Capsella rubella* and *Brassica rapa*. A framework for comparison between species is timely because several crucifer genome-sequencing projects are underway.

A unified comparative genomic framework for the Brassicaceae

The angiosperm family Brassicaceae (the mustard family) contains several important research and agricultural species, the foremost being the model species *Arabidopsis thaliana* (*Arabidopsis*) and the *Brassica* crops. In addition, several related species are the focus of active research communities, including *Arabidopsis lyrata*, *Capsella rubella*, and other genera such as *Boechera*, *Lepidium*, *Thellungiella* (also known as *Eutrema*) and *Thlaspi*. Comparative genomics in the Brassicaceae has largely focused on direct comparisons between *A. thaliana* and the species of interest. However, several of the factors that made *Arabidopsis* ideal for genome sequencing, particularly its reduced genome size and chromosome number (157 Mb, $n = 5$) [1], reduce its utility as a standard in comparative genomics. *Arabidopsis* shows extensive genome and chromosome reshuffling compared with other Brassicaceae species. Several recent studies have tackled these obstacles, providing useful insights into the history and organization of crucifer genomes.

Our goal is to discuss these recent findings, focusing on advances in our understanding of phylogenetics, polyploidization and comparative genomics, which pave the way for a unified comparative genomic framework across the Brassicaceae. We integrate several of these findings into a simple system of structural sub-divisions representing chromosome blocks that are conserved in the species of Brassicaceae characterized to date. These crucifer building blocks can be rearranged to model the genome structures of *A. thaliana*, *A. lyrata*, *C. rubella* and *Brassica rapa*. This block system can be used to visualize comparative genome structure of other crucifer species as additional genetic mapping, cytogenetic and genomic data accumulate. A framework for comparison between species is particularly timely because genome-sequencing projects are currently underway for *A. lyrata*, *C. rubella*, *Thellungiella halophila* and *B. rapa*.

Comparative genomics in plants: the Crop Circle and beyond

The seminal comparative genetic mapping done in the grass family (Poaceae), which includes many important domesticated cereal and forage crops, resulted in the synthesis of the 'Crop Circle' [2–6]. This approach placed the small-genome of rice at the center of the circle and then aligned the maps of larger genome grass crops (including corn, sorghum, wheat, oat, fox millet and sugar cane). A large degree of colinearity was found among genomes (however, see Ref. [7]). The rice genome (~400 Mb, $n = 12$) can be subdivided into ~30 blocks that can be shuffled to represent the other grass genomes, such as

Glossary

Acrocentric chromosomes: chromosome arms of significantly unequal length with the centromere near to one chromosome end.
Comparative Chromosome Painting (CCP): in plant cytogenetics CCP is fluorescence *in situ* hybridization (FISH) of chromosome-specific large-insert DNA clones, microdissected or flow-sorted DNA probes of a reference species to chromosomes of another species.
Metacentric chromosomes: both arms are of roughly equal length with the centromere in the middle. Submetacentric chromosomes have one arm slightly shorter than another. In crucifer cytogenetics, short and long chromosome arms are usually described as top and bottom arms, respectively.
Pericentric inversion: a chromosome rearrangement in which two breakpoints occur in a chromosome (one on each arm), the centerpiece including the centromere is inverted and rejoined with the rest of the chromosome. Chromosome symmetry can be altered as a result of the changed position of the centromere (metacentric chromosome converted into an acrocentric chromosome).
Reciprocal translocations: a chromosome rearrangement involving the exchange of chromosome segments between two chromosomes.

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Box 1. Chromosome number reduction via pericentric inversion–reciprocal translocation events

The relative placement of centromeres and telomeres is crucial to understanding the evolution of crucifer genomes and the definition of conserved genomic blocks. Most observations of karyotype evolution and chromosome number reduction can be explained by rearrangements via pericentric inversion followed by reciprocal translocation [33]. The basic steps involved in this cycle are as follows (Figure I):

(1) A pericentric inversion occurs that moves the centromere of a (sub)metacentric chromosome towards the end of the chromosome, creating an acrocentric chromosome.
(2) A reciprocal translocation occurs between the centric end of this acrocentric chromosome and a subtelomeric region of another chromosome.
(3) There are two products of the translocation event: a large 'fusion' chromosome and a small mini-chromosome made up mostly of the centromere of the acrocentric chromosome and of the subtelomeric segment of the other. It is hypothesized that the mini-chromosomes are free of essential genes and meiotically unstable and, hence, are eliminated. If the subtelomeric region of the second chromosome involved in the reciprocal translocation comprises a nucleolar organizing region (NOR), the NOR is lost together with the mini-chromosome.

Although this mechanism explains how centromeres can be lost and chromosome number reduced, evolutionary pathways leading to the chromosome number increase are less clear. Chromosome number can be increased by a polyploid event and the subsequent loss of several chromosome types, or as a result of a meiotic non-disjunction. Whether chromosome fission and neocentromere formation can play a role in karyotype evolution towards increased chromosome numbers needs to be investigated.

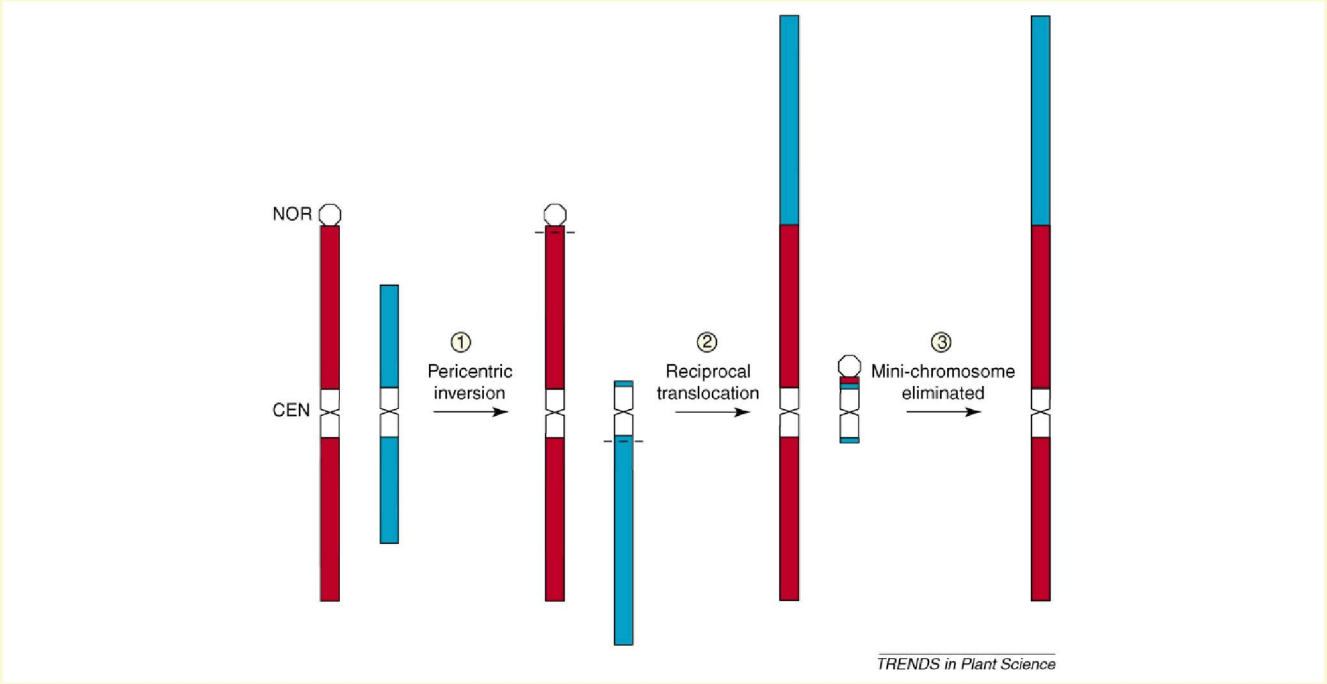

Figure I.

bread wheat (~17 000 Mb, $n = 21$). In recent years there has been a push to integrate genetic maps and genomics across other families, particularly those with several domesticated crops, such as the Fabaceae [8,9], Rosaceae [10], Solanaceae [11], Asteraceae (The Compositae Genome Project: http://compgenomics.ucdavis.edu) and Brassicaceae [12–14].

Brassicaceae: phylogeny and genome duplications

An accurate phylogeny is essential for comparative studies within the Brassicaceae. Knowledge of natural phylogenetic relationships allows estimates of: (i) derived versus ancestral states for numerous characters (morphological, cytological, biochemical), (ii) evolutionary distances and divergence times between groups and (iii) the positioning of evolutionary events to particular nodes or clades on the phylogenetic tree. Recent studies have classified the 338 genera and ~3700 species of Brassicaceae into 25 tribes [15] based on nuclear- [16] and chloroplast-encoded [15] markers. Sixteen of the 25 tribes can be further grouped into one of three lineages (referred to as Lineages I–III) [15]. Although the system is incomplete with some genera having a provisional position and some that are not analyzed yet, this taxonomic classification [15] provides the most up-to-date reference point for comparative studies in this family.

The discernment and appreciation of whole-genome duplication (polyploidy) within lineages is also crucial for comparative studies within the Brassicaceae [17]. Based on the 'traditional' definition of polyploids, it has been estimated that ~37% of Brassicaceae species are of polyploid origin (defined as $n \geq 14$) [18]. However, in recent years it has become apparent that ancient polyploidy, or paleopolyploidy, events have also played a major role in crucifer evolution. Analysis of the *A. thaliana* genome has revealed extensive intra- and inter-chromosomal segmental duplications that were interpreted as relics of a whole-genome duplication event [19–22]. Additional analyses indicate that *Arabidopsis* ancestors underwent three rounds (1–3R, or γ, β and α, respectively) of whole-genome duplications [23–25]. The most recent (3R or α) polyploidy event appears to be unique to the Brassicaceae, having

occurred ~40 million years ago (mya), after divergence from its sister family Cleomaceae [26,27].

In addition to the 3R polyploidy event occurring across the family, there is also evidence for an additional ancient triplication event that is unique to the tribe Brassiceae. Several comparative maps between *A. thaliana* and *Brassica* suggested that numerous regions homeologous to the *Arabidopsis* genome are triplicated within *Brassica* genomes because of an ancestral hexaploidy event [28]. Recently, additional evidence for the genome triplication in *Brassica* was found by sequencing [29,30], genetic [31], and cytogenetic [32,33] methods. These studies support the hypothesis of a common hexaploid ancestor in the ancestry of *Brassica* and the tribe *Brassiceae*. However, there is some controversy regarding the ancient hexaploid hypothesis because some genomic regions are present in less or more than three copies in *Brassica* genomes. Other phenomena (such as ancient tetraploidy and/or segmental duplication) could also explain the current genomic structure of *Brassica* [34,35].

Comparative mapping and genomics in the Brassicaceae

The genome sequencing of *A. thaliana* was a major landmark in plant biology and transformed a rather unassuming weed into the reference point for most comparative studies [20]. The reduced genome size and low chromosome number ($n = 5$) made *Arabidopsis* ideal for genome sequencing, but complicates its use in comparative studies. It is tempting to place *Arabidopsis* at the center of a Brassicaceae genomics circle in the same way rice was placed at the center of the Crop Circle [2–6]. However, most of the other species in its tribe, the Camelineae, have the base chromosome number $n = 8$, in common with at least 37% of Brassicaceae species [18]. Thus, when comparisons are made between an $n = 8$ taxon and the *A. thaliana* genome, chromosome rearrangements that are unique to *A. thaliana* must be (re)accounted for. Recent studies suggest that comparison with an 'ancestral karyotype' of $n = 8$ would considerably expedite genomic comparisons [33,36]. Introduction of the ancestral $n = 8$ karyotype would also facilitate comparisons between more distantly related groups within the family.

Comparative genetic maps have recently been constructed for two $n = 8$ Camelineae species, *C. rubella* [37] and *A. lyrata* [38,39], by examining the positions of *Arabidopsis* genetic markers in their genomes. This mapping has shown that both $n = 8$ genomes are largely colinear with the reduced $n = 5$ genome of *A. thaliana*, and that all three taxa share large conserved genomic blocks [37–39]. Furthermore, *A. lyrata* and *C. rubella* possess almost identical genome structure, presumably resembling an ancestral $n = 8$ karyotype of *A. thaliana* [36].

Comparative chromosome painting (CCP) (see Glossary) has been used within a phylogenetic framework to examine the chromosome number reduction that occurred in *A. thaliana* [33]. One of the most important conceptual shifts of this paper was the use of the $n = 8$ ancestral karyotype (AK), based on *A. lyrata* and *C. rubella* maps, as the reference point. The CCP analysis used chromosome-specific BAC contig probes of *A. thaliana* arranged and colored according to the colinear segments found in genetic maps of *A. lyrata* and *C. rubella* [37–39]. The CCP study also provided information about the positions of centromeres in the ancestral karyotype [33], which has been corroborated by genetic mapping in *A. lyrata* [40,41].

In addition to examining the chromosome reduction of *A. thaliana*, Martin Lysak *et al.* [33] also examined other karyotypes with reduced chromosome number ($n = 6$ and 7) of two taxa from the tribe Camelineae (*Neslia*, *Turritis*) and one taxon from Descurainieae (*Hornungia*). The results revealed that all species analyzed share conserved chromosome segments that can be related to the ancestral karyotype [33]. Furthermore, the results suggested a common mechanism for chromosome number reduction via a pericentric inversion followed by reciprocal translocation (Box 1).

Besides *Arabidopsis* and its closest relatives, comparative analyses are concentrated on economically important brassicas and some other species from the tribe Brassiceae. Comparing the *Arabidopsis* genome with those of *Brassica* species has a long and somewhat controversial history. The difficulty in establishing syntenic relationships between *Brassica* and *A. thaliana* is caused by the aforementioned derived nature of the *A. thaliana* genome, relatively large phylogenetic distance between the two genera [42], the paleopolyploid nature of Brassiceae genomes [28,31,43], and the low marker densities of some *Brassica* genetic maps.

Despite these difficulties, a superb recent study [31] has made a comprehensive comparison that places almost 90% of the *Brassica napus* mapped length into conserved syntenic blocks relative to *A. thaliana*. Isobel Parkin *et al.* [31] placed 1327 genetic loci on the 19 linkage groups of

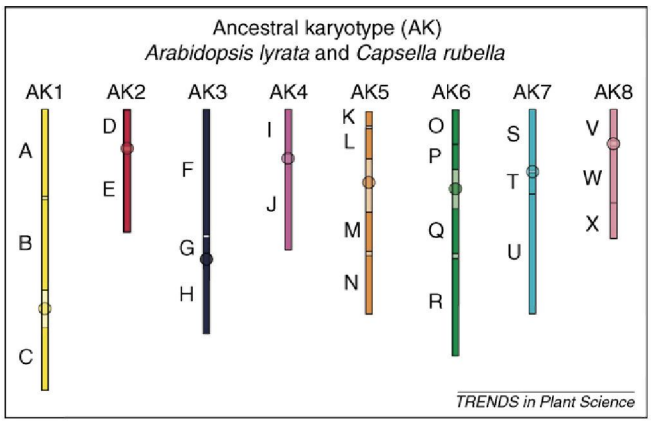

Figure 1. Genome blocks in the 'ancestral karyotype' ($n = 8$) based on cytology and genetic maps of *Arabidopsis lyrata* and *Capsella rubella*. Genome blocks are labeled A–X. The order, orientation, and color-coding of each block is based on their positions in the ancestral karyotype of Lysak *et al.* [33]. Each block is one of eight colors, with each color corresponding to one of the chromosomes, beginning with block A on the top of AK1 and ending with block X at the bottom of AK8. Each block is considered to be in the upright orientation in the ancestral karyotype. The colored circles indicate centromeric positions. Because only the *Arabidopsis thaliana* genome is currently sequenced, the boundaries of the blocks are defined by their At locus names (shown in Figure 2). Block boundaries are based mostly on the homology of probes used in a genetic mapping study in *Brassica napus* to *A. thaliana* [31]. However, we refined and defined some blocks based on the *A. lyrata* genetic mapping and cytogenetic results [33,38,39]. Specifically, we have added block K and divided two *Brassica* blocks into two (N and O, and G and H).

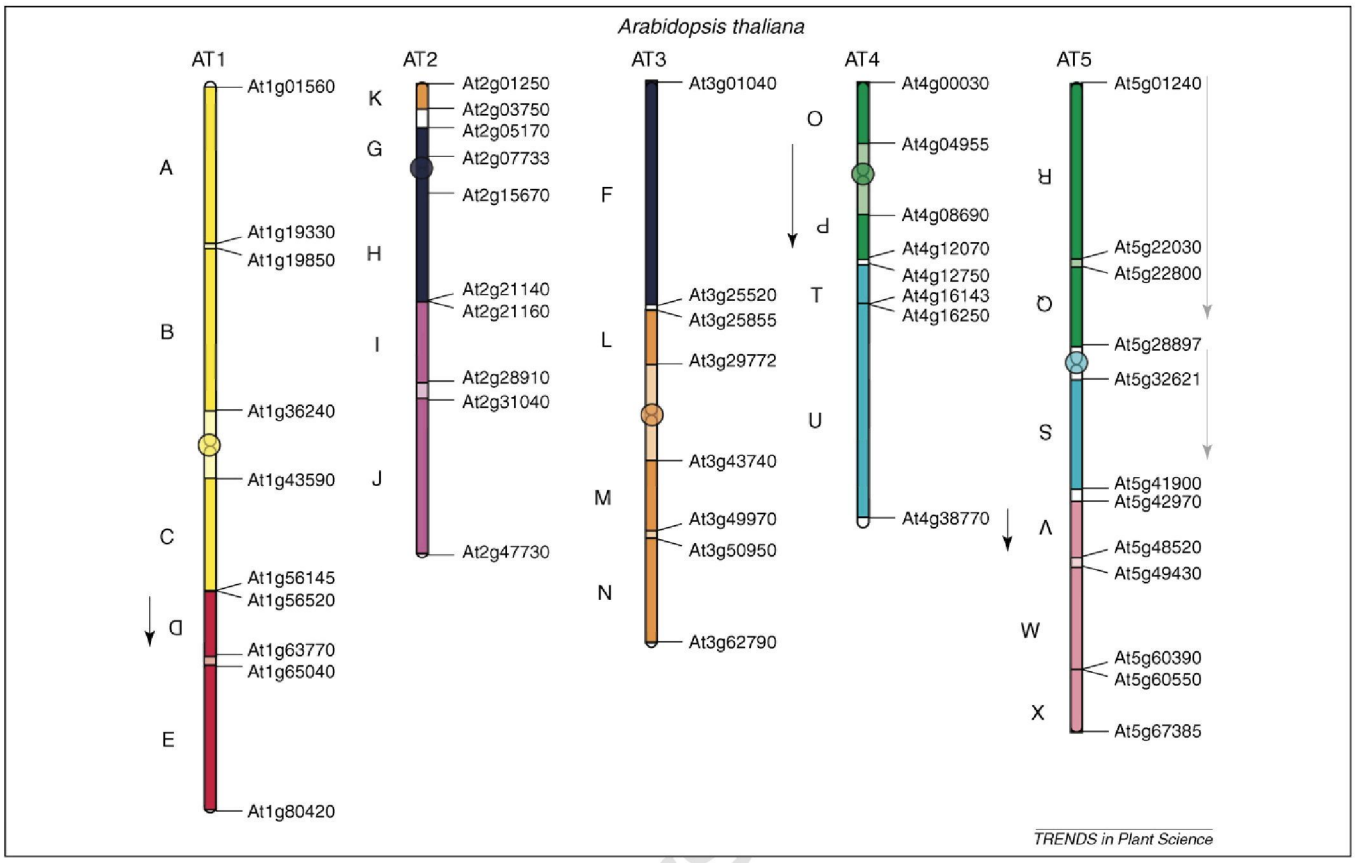

Figure 2. Genome blocks and block boundaries mapped onto the reduced karyotype ($n = 5$) of *Arabidopsis thaliana*. The genome blocks defined by their position in the ancestral karyotype ($n = 8$) (Figure 1) are reorganized to show the evolution of the reduced karyotype of *A. thaliana* ($n = 5$). The boundaries of the blocks are defined by their At locus names. Most of the chromosome fusions occurred via pericentric inversion–reciprocal translocation events involving (peri)centromeric and (sub)telomeric regions (see Box 1). Blocks that have been inverted relative to the ancestral karyotype are represented by black downward-pointing arrows on the left of the block and by the block letter being upside-down (blocks D, P and V). Blocks that are in the opposite orientation, but not inverted, relative to the ancestral karyotype are represented by a gray downward-pointing arrow on the right of the block and by the block letter being upside-down (blocks R, Q and S). Fusion of blocks from different ancestral chromosomes is shown by adjacent blocks of different colors. Of the eight ancestral karyotype centromeres, only three appear to have maintained the same flanking pericentromeric regions at both borders in *A. thaliana* (AK1 = CEN1 between blocks B and C, AK3 = CEN2 between blocks G and H, and AK5 = CEN3 between blocks L and M). The other five centromeres have been lost or rearranged by pericentric inversion–reciprocal translocation events. Three centromeres present in the ancestral karyotype species have been lost: the centromeres of AK2 (between blocks D and E), AK4 (between blocks I and J) and AK8 (between blocks V and W) are no longer present in *A. thaliana*. There is only one major non-centromere-associated translocation, namely the reciprocal translocation of blocks K and F between AK3 and AK5 during the evolution of AT2 and AT3.

allopolyploid *B. napus*. These 19 linkage groups, which are labeled N1–19, correspond to the ten chromosomes of *B. rapa* (N1–10) and the nine chromosomes of *B. oleracea* (N11–19). This analysis identified 21 syntenic blocks shared by *B. napus* and *A. thaliana* genomes that could be duplicated and rearranged to represent 90% of the *B. napus* genome. These conserved blocks (with an average size of ~4.8 Mb in *A. thaliana*) represent colinear regions that have been maintained since the divergence of the *Arabidopsis* and *Brassica* lineages ~20 mya [31,44]. The identification of such conserved blocks, along with recent comparative mapping in *A. lyrata* and *C. rubella* [37–39], and the definition of the ancestral karyotype [33] has paved the way for genomic comparisons across the Brassicaceae.

ABC's: the conserved blocks of crucifer genomes

An important step toward a unified comparative genomics system across the Brassicaceae can be accomplished by integrating the colinear regions identified between *B. napus* and *A. thaliana* [31] with the concept of the $n = 8$ ancestral karyotype shared by *A. lyrata* and *Capsella* [33]. We propose a set of 24 genomic blocks (A–X) within the ancestral karyotype that represent an extension to the set of 21 blocks proposed for *Brassica* by Parkin *et al.* [31]. These 24 blocks represent the conserved segments that can be identified among the ancestral karyotype (Figure 1), *A. thaliana* (Figure 2) and the *B. rapa* component (A genome = N1–N10) of *B. napus* (Figure 3). This expanded genomic block system reflects our current understanding of the conserved nature of crucifer genomes. A summary of the blocks and characteristics in the three species is also summarized in Table 1.

The order, orientation, and color-coding of these blocks are based on their positions in the ancestral karyotype [33]. Because only the *A. thaliana* genome is currently sequenced, the boundaries of the blocks are defined by their At locus names (Figure 2, Table 1). Furthermore, we refine and define several additional blocks based on mapping and cytogenetic comparisons between the ancestral karyotype and *A. thaliana* [33,38,39].

Bridging *Arabidopsis thaliana* and *Brassica* via the ancestral karyotype

Recognition of the ancestral karyotype and these genomic building blocks will facilitate comparisons between *A. thaliana* and *Brassica* and provide a basis

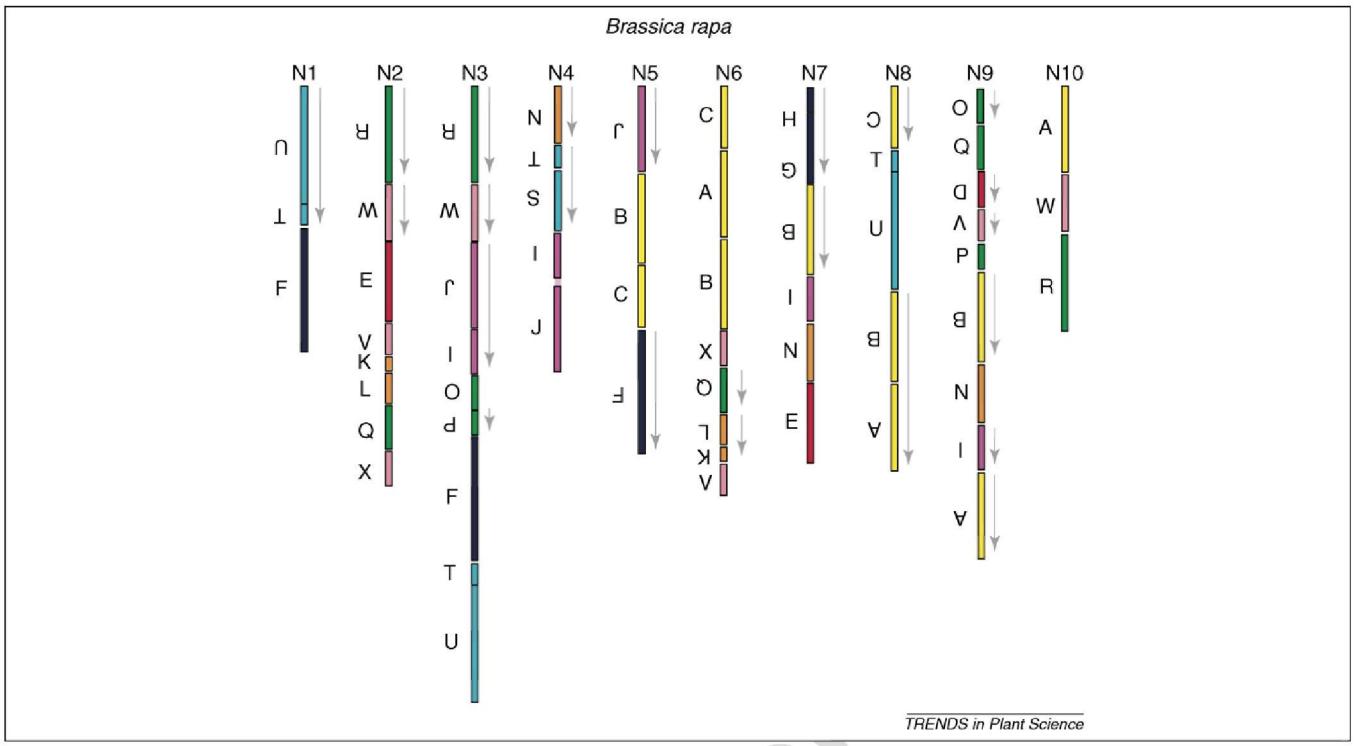

Figure 3. Genome blocks shown for the A genome species *Brassica rapa* ($n = 10$). The genome blocks defined by their position in the ancestral karyotype ($n = 8$) (Figure 1) are shown for *B. rapa*. The position of the genome blocks for the *B. rapa* genome is based on the comparative mapping that has been done between *B. napus* (the A genome component of *B. napus* = N1–N10) and *Arabidopsis thaliana* by Parkin *et al.* [31]. Blocks that are in the opposite orientation, but not inverted, relative to the ancestral karyotype are represented by a gray downward-pointing arrow on the right of the block and by the block letter being upside-down. By comparison to the ancestral karyotype, we are able to make several refinements to our understanding of *Brassica* genome evolution. Several block boundaries that exist in *A. thaliana* are not seen in *Brassica*, such as the C–D fusion or the H–I fusion. We have included some new blocks, such as the placement of block K next to block L on linkage groups N2 and N6. Also, many blocks are found in triplicate as predicted by the hypothesis of an ancient hexaploidy ancestry of the group [28,31,43].

for family-wide comparative genomics in the Brassicaceae. Although it is well known that *A. thaliana* and *Brassica* genomes differ by many rearrangements [28,45–47], the pattern underlying these changes is less clear. In particular, the *Brassica* genome is less rearranged relative to the ancestral karyotype compared with that of *A. thaliana*. Several block boundaries that exist in *A. thaliana* are not seen in *Brassica*. This is because these are derived states found in *A. thaliana*, and not the ancestral karyotype. There are several refinements that can be identified by comparing *Brassica* to the ancestral karyotype. For example, a conserved region corresponding to block K on N2 and N6 (Figure 3) was not incorporated into the analysis of *B. napus* [31], probably because of its derived position on the top of At2. Block K is fused with block L in the ancestral karyotype (Figure 1), which suggests that block K is adjacent to block L in *Brassica* as well. Indeed, when the genetic markers adjoining block K on linkage groups N2 and N6 in the *B. napus* map [31] are scrutinized, homology to block L can be identified (Figure 3). Further support for the placement of block L next to block K comes from a separate study reporting a detailed molecular analysis of *B. rapa* [48].

Comparison to the ancestral karyotype also highlights several potentially conserved centromeric locations in *Brassica* based on colinearity. However, these regions are often the sites for rearrangements (Box 1). Parkin *et al.* [31] mapped groups of markers that corresponded to pericentromeric genes in *A. thaliana*. Taking a conservative approach we can identify four chromosomes (N3, N4, N5 and N7) with non-rearranged blocks that flank a centromere in the ancestral karyotype and the block order is the same in the *Brassica* A genome. The potentially conserved centromeres on N3 and N4 are only apparent by comparison to the ancestral karyotype. The centromeres on N5 and N7 are potentially conserved between *Brassica*, the ancestral karyotype and *A. thaliana*. On N5, one would predict a centromere between blocks B and C. On N7, a conserved centromere is predicted between blocks G and H. Support for this hypothesis comes from the cytological observation that *B. oleracea* linkage group O7 (the homeolog of N7) is acrocentric and homologous to the top of At2 [49].

Finally, presenting the *B. rapa* genome with the ancestral blocks can be used to visualize blocks that are, or are not, present in three copies as predicted by the ancient polyploidy hypothesis for the tribe (Figure 3, Table 1). Several blocks are present in triplicate, and have been well characterized in previous studies. For example, block R is triplicated (on N2, N3 and N10) and has been analyzed in several studies [30,46,50]. Triplicated blocks U (on N1, N3 and N8) and V (on N2, N6 and N9) and their homeologs in *B. oleracea* have been examined recently [29,51]. Block U, which has also been examined using CCP [43], is triplicated across most of the tribe Brassiceae. However, as noted earlier, there are blocks that seem to occur only once, for instance blocks G and H are present only on N7 (Figure 3, Table 1).

Table 1. Block summary

Block	~Interval	Al LG[a]	Al order[b]	Al orient.[c]	At LG[d]	At order[e]	At orient.[f]	*Brassica* block[g]	Frequency in Br[h]
A	At1g01560–At1g19330	1	1	+	1	1	+	C1A	4
B	At1g19850–At1g36240	1	2	+	1	2	+	C1B	5
C	At1g43590–At1g56145	1	3	+	1	3	+	C1C	3
D	At1g63770–At1g56520	2	4	+	1	4	–	C1D	1
E	At1g65040–At1g80420	2	5	+	1	5	+	C1E	2
F	At3g01040–At3g25520	3	6	+	3	11	+	C3A	3
G	At2g05170–At2g07733	3	7	+	2	7	+	C2A	1
H	At2g15670–At2g21140	3	8	+	2	8	+	C2A	1
I	At2g21160–At2g28910	4	9	+	2	9	+	C2B	4
J	At2g31040–At2g47730	4	10	+	2	10	+	C2C	3
K	At2g01250–At2g03750	5	11	+	2	6	+	C2A	2
L	At3g25855–At3g29772	5	12	+	3	12	+	C3B	2
M	At3g43740–At3g49970	5	13	+	3	13	+	C3C	0
N	At3g50950–At3g62790	5	14	+	3	14	+	C3D	3
O	At4g00030–At4g04955	6	15	+	4	15	+	C4A	2
P	At4g12070–At4g08690	6	16	+	4	16	–	C4A	2
Q	At5g28897–At5g22800	6	17	+	5	20	–	C5B	3
R	At5g22030–At5g01240	6	18	+	5	19	–	C5A	3
S	At5g41900–At5g32621	7	19	+	5	21	–	C5C	3
T	At4g12750–At4g16143	7	20	+	4	17	+	C4B′	4
U	At4g16250–At4g38770	7	21	+	4	18	+	C4B	2
V	At5g48520–At5g42970	8	22	+	5	22	–	C5D	3
W	At5g49430–At5g60390	8	23	+	5	23	+	C5E	3
X	At5g60550–At5g67385	8	24	+	5	24	+	C5F	2

[a] *Arbidopsis lyrata* linkage group (LG).
[b] Order of blocks along *A. lyrata* LG.
[c] Relative orientation of blocks along *A. lyrata* LG.
[d] *Arabidopsis thaliana* linkage group.
[e] Order of blocks along *A. thaliana* LG.
[f] Relative orientation of blocks along *A. thaliana* LG. Blocks that have been inverted relative to the ancestral karyotype (blocks D, P and V) and blocks that are in the opposite orientation but not inverted (blocks R, Q and S) are indicated by a minus symbol.
[g] Corresponding block identified in *Brassica napus* by Parkin *et al.* [31].
[h] Number of times the block occurs within the *B. rapa* (Br) genome.

Concluding remarks and future directions

Future research should lead to the refinement of the boundaries and definitions of many of the blocks to more precisely delineate syntenic relationships. If future studies require additional genomic subdivisions we recommend the division of the present blocks (A–X) into enumerated sub-blocks (e.g. A_1 and A_2). Also, there are likely to be minor species-specific differences in microcolinearity within the blocks that will become apparent from fine-mapping studies or by analyzing DNA sequence. For example, it is already known from the genetic mapping results in *B. napus* [31] that there are four inversions within blocks of the A genome. Nevertheless, we hope that this set of genomic building blocks derived from the comparative work between *Brassica* and *A. thaliana* [31] that we have linked to the $n = 8$ ancestral karyotype represent a useful framework for comparative genomics across the Brassicaceae. Cytogenetic and genetic investigations revealed these conserved genomic blocks in species from tribes Camelineae (*Arabidopsis, Capsella, Neslia, Turritis*), Descurainieae (*Hornungia*) [33] and Brassiceae [30,31]. A crucial goal in the future will be the integration of genetic maps and cytogenetic findings from additional species, particularly from tribes more distantly related to either Camelineae or Brassiceae. Several conserved chromosome segments partly colinear to ancestral chromosomes AK6 and AK7 have been revealed in *Arabis alpina* ($n = 8$), belonging to Arabideae [52]. Furthermore, the genome structure of *Boechera stricta* ($n = 7$) belonging to Boechereae, as revealed by genetic linkage mapping, can also be fully accounted for using our blocks (M.E. Schranz and T. Mitchell-Olds, unpublished). Finally, analyzing taxa from the tribe Aethionemeae, which is sister to the rest of the extant Brassicaceae tribes [18], should cast more light on the ancestral structure of crucifer genomes, and should facilitate comparisons to its sister family the Cleomaceae [26].

It will be important to address whether patterns of chromosomal repatterning (or diploidization) that occurred after the 3R ancient polyploidy event are shared across the family [53]. If much of the genome changes occurred shortly after the polyploidization, then we would expect to find conservation of the genomic blocks across many tribes. However, if the diploidization process occurred independently within individual lineages, than the genomic block system will be less informative. Furthermore, a major objective will be to understand the significance of the inversion–translocation mechanism involved

in chromosome fusions and whether chromosome number reduction, perhaps associated with genome diploidization, is a prevailing evolutionary process within Brassicaceae. In conclusion, we hope that the underlying simplicity of the presented model will aide in future comparative genomics studies in the Brassicaceae, and facilitate the transfer of knowledge from model species to crop species.

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Plant Science Conferences in 2007

Plant and Animal Genome XV Conference
13–17 January 2007
San Diego, California, USA
http://www.intl-pag.org/pag/

Gordon Conference on Plant–Herbivore Interaction
18–23 February 2007
Ventura, California, USA
http://www.grc.org/programs/2007/planthrb.htm

49th Annual Maize Genetics Conference
22–25 March 2007, St. Charles, Illinois, USA
http://www.maizegdb.org/maize_meeting/

The 2nd International Conference on Plant Molecular Breeding
23–27 March 2007
Sanya, Hainan, China
http://www.icpmb.org

Keystone Meeting: Plant Cell Biology
23–28 March 2007
Coeur d'Alene, Idaho, USA
http://www.keystonesymposia.org/Meetings/ViewMeetings.cfm?MeetingID=844

SEB Main Meeting 2007
31 March – 4 April 2007
Glasgow, UK
http://www.sebiology.org/Meetings/pageview.asp?S=2&mid=91