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Inferred Chromosome Morphology of the Ancestral Genome of *Triticum*

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Abstract: The lengths of the A, B, and D genomes of common wheat, *Triticum aestivum*, were measured from the karyotype. Relative to the B genome, standardized as length 1.000, the lengths of the A and D genomes were 0.835 and 0.722, respectively. The lengths of the chromosome arms in the A and D genomes were then multiplied by the appropriate constants so that the total lengths of each genome also equalled 1.000. These calculations revealed that homoeologous chromosomes in wheat, with a few exceptions, have similar sizes and arm ratios. The arm lengths of the three homoeologues in each homoeologous group were then averaged. These average chromosomes turned out to be remarkably similar, in size and arm ratio, to their homoeologues in the E genome of *Elytrigia elongata*. This evidence and data on cross-compatibility and morphological characteristics suggested that the genus *Triticum* is a result of adaptive radiation from the perennial genus *Elytrigia*, specifically from the complex of species possessing the E genome or one closely related to it.

The tribe *Triticeae* comprises several major genera: the annual genus *Triticum* sensu lato (including *Aegilops*), the perennial-annual genera *Secale* and *Hordeum*, and the perennial genera *Elytrigia, Elymus*, and *Leymus*. The genus *Elytrigia* comprises diploid and polyploid species of the E and S genome complexes. The genus *Elymus* contains polyploid species that originated from hybridization of an S-genome diploid(s) with a *Hordeum* species and, thus, have genome formula SH (Dewey 1982). The genus *Leymus* contains polyploid species of hybrid origin having genome formula JJXX, where J was contributed by a species of diploid genus *Psathyrostachys* whereas the origin of the X genome is

unknown (Dewey 1982). The species of *Elytrigia*, some of the species of *Elymus*, and the species of *Agropyron* sensu stricto (= *A. cristatum* complex) have often been placed in the single large genus *Agropyron* s.l. The species *Leymus* and *Psathyrostachys* have often been placed, with some species of *Elymus*, in the single genus *Elymus*. In addition to the already-mentioned *Psathyrostachys* and *Agropyron* s.str., the tribe contains several minor genera: *Dasypyrum, Eremopyrum, Heteranthelium, Crithopsis, Pascopyrum, Henrardia, Asperella,* and *Taeniatherum.*

The perennial genera *Elytrigia, Elymus*, and *Leymus* are widely distributed throughout the Old World and both Americas whereas the annuals of the genus *Triticum* are restricted to the Mediterranean, Middle East and Near East, and Central Asia. The wider geographic distribution of the perennials and the generally accepted assumption that the annual habit is derived from the perennial one have been two chief reasons for the belief that the genus *Triticum* evolved from perennial species of the tribe (Stebbins 1958, Sakamoto 1973). We report here evidence that indicates that species of *Elytrigia*, namely the E-genome group, may have been the source of this adaptive radiation.

Of the eight basic genomes occurring in the genus *Triticum*, four, the A genome of *T. monococcum* L. em. Morris & Sears and *T. urartu* Thum., the B genome of the species of section *Sitopsis* (*T. speltoides* (Tausch) Gren. ex Richter, *T. longissimum* (Schweinf. & Muschli in Muschli) Bowden, *T. sharonense* (Eig) Waines & Johnson, *T. searsii* (Kis. & Feld.) Kis. & Feld., and *T. bicorne* Forsk.), the D genome of *T. taüschii* (Coss.) Schmal., and the Z genome of *T. tripsacoides* (Jaub. & Spach) Bowden have symmetrical karyotypes lacking subacrocentric chromosomes (Senjaninova-Korczagina 1932, Chennaveeraiah 1960). Stebbins (1958) concluded that these symmetrical karyotypes are primitive whereas the asymmetric karyotypes of the remaining four genomes, the C genome of *T. dichasians* (Zhuk.) Bowden, the U genome of *T. umbellulatum* (Zhuk.) Bowden, the M genome of *T. comosum* (Sibth. & Sm.) Richter, and the N genome of *T. uniaristatum* (Sibth. & Sm.) Richter are more advanced. Three of the four symmetrical genomes, A, B, and D, constitute the chromosome complement of common wheat, *T. aestivum* L. with $2n = 6x = 42$.

All evidence available indicates that the chromosomes of the *T. aestivum* cultivar 'Chinese Spring' have not been substantially restructured relative to the chromosomes of the ancestral diploid species (see Chapman & Riley 1966, Larson 1973, Chapman & al., 1976, Dvořák 1976, 1980). It can be assumed, therefore, that the morphology of the chromosomes of the A, B, and D genomes in *T. aestivum* reflects the morphology of these chromosomes in diploid species. In our attempt to

infer the morphology of the genome ancestral to *Triticum* we, therefore, used polyploid *T. aestivum*, rather than the A, B, and D genome diploid species, because the genetic relationships among the *T. aestivum* chromosomes and chromosome arms are known (SEARS 1954, 1966, SEARS & SEARS 1979) whereas nothing is known about the genetic relationships among the chromosomes of the diploid *Triticum* species.

Materials and Methods

The karyotype of *T. aestivum* used here was established from the measurements of telosomes in C-banded root-tip cells of 'Chinese Spring' double ditelosomics. For metacentric chromosomes ditelosomics were also used. For chromosomes 1D and 7D, ditelosomics 1DL and 7DS and nulli-1A-tetra-1D and nulli-7A-tetra-7D aneuploid lines were used because double ditelosomics were not available. The double ditelosomics and other aneuploid lines of 'Chinese Spring' were provided by E. R. SEARS, Department of Agronomy, University of Missouri, Columbia. The C-banding of metaphase chromosomes in the root-tip cells was carried out accoring to a modified procedure (DVOŘÁK & APPELS 1982) of IORDANSKY & al. (1978). Since chromsome 5B can be unequivocally recognized by its banding pattern it was employed as an internal standard of length in each cell. The lengths of the telosomes and chromosome 5B were measured in approximately ten cells by use of an ocular micrometer. Each telosome measurement was divided by the average length of the two 5B chromosomes in the same cell and the resulting numbers were averaged.

The length of the karyotype of *Elytrigia elongata* (HOST) NEVSKI (DVOŘÁK & KNOTT 1974) was also standardized relative to 5B. The relative lengths of *E. elongata* telosomes 1ES, 2EL, 4EL, and 6Eα (= 6ES) added to 'Chinese Spring' (DVOŘÁK 1979), expressed as percentage of the length of arm 5BL, were first converted into the relative lengths of the entire chromosome 5B. The reason for selecting these four *E. elongata* telosomes out of the ten investigated by DVOŘÁK (loc. cit.) was that these four can be unequivocally assigned to specific chromosome arms in the *E. elongata* karyotype. The lengths of chromosome arms 1ES, 2EL, 4EL, and 6Eα in the *E. elongata* karyotype reported by DVOŘÁK & KNOTT were each divided by the 5B-relative lengths of telosomes 1ES, 2EL, 4EL, and 6Eα, respectively. The resulting numbers were averaged. This mean was then used as a coefficient to standardize the lengths of all chromosome arms of the *E. elongata* karyotype relative to the length of 5B. This was done by multiplying the length of each of the fourteen chromosome arms of *E. elongata* reported by DVOŘÁK & KNOTT by this coefficient.

Results

It is apparent from Table 1 that wheat homoeologous chromosomes in all homoeologous groups except group 4 are similar to each other, although they differ in size. In six of the seven groups, again excepting

Table 1. The lengths of *Triticum aestivum* and *Elytrigia elongata* chromosome arms relative to *T. aestivum* chromosome 5B

Genome		Chromosome							Total
		1	2	3	4*	5	6	7	
A	Short arm	0.238	0.423	0.389	0.625	0.348	0.320	0.427	2.770
	Long arm	0.466	0.563	0.550	0.368	0.557	0.378	0.473	3.355
	Total	0.704	0.986	0.939	0.993	0.905	0.698	0.900	6.125
	Arm ratio S/L	0.511	0.751	0.707	1.698	0.625	0.847	0.903	
B	Short arm	0.458	0.496	0.507	0.457	0.304	0.507	0.388	3.117
	Long arm	0.653	0.623	0.649	0.478	0.696	0.533	0.587	4.219
	Total	1.111	1.119	1.156	0.935	1.000	1.040	0.975	7.336
	Arm ration S/L	0.701	0.796	0.781	0.956	0.437	0.951	0.661	
D	Short arm	0.250	0.357	0.316	0.266	0.255	0.271	0.365	2.080
	Long arm	0.440	0.477	0.491	0.421	0.530	0.332	0.525	3.216
	Total	0.690	0.834	0.807	0.687	0.785	0.603	0.890	5.296
	Arm ratio S/L	0.568	0.748	0.644	0.632	0.481	0.816	0.695	
E	Short arm	0.273	0.439	0.313	0.348	0.283	0.351	0.460	2.467
	Long arm	0.474	0.554	0.481	0.506	0.573	0.398	0.515	3.501
	Total	0.747	0.993	0.794	0.854	0.856	0.749	0.975	5.968
	Arm ratio S/L	0.576	0.792	0.651	0.688	0.494	0.882	0.893	

* The genome allocation of chromosomes 4A and 4B was exchanged according to the proposal by DVOŘÁK (1983).

group 4, it is the B genome chromosome that is the largest of the three. In all seven groups it is always the D genome chromosome which is the smallest of the three. If the length of chromosome 5B is made the standard of 1,000, the total length of the B genome is 7.336, whereas the total lengths of the A and D genomes are 6.125 and 5.296, respectively. Thus, the total length of the A genome is 0.835 and that of the D genome is 0.722 relative to the standardized length of the B genome. To compare the morphological similarity of the homoeologous chromosomes of the three wheat genomes, these differences in genome size must be taken into account. The total lengths of the A and D genomes were therefore made equivalent to that of the B genome by multiplying the lengths of the chromosome arms of the A genome by a factor of 1.198 and those of the D genome by a factor of 1.385. These adjusted karyotypes of the wheat genomes are shown in Fig. 1.

Within six of the seven homoeologous groups of 'Chinese Spring' the three short arms are homoeologous to each other and the three long arms

are homoeologous to each other (SEARS & SEARS 1979). It was shown by DVOŘÁK (1983) that the traditional genome assignment of 4A and 4B was incorrect and should be reversed. This change will be followed throughout. It has been suggested (SEARS & SEARS 1979) that the short arm of 4B (old "4A") is homoeologous to the short arm of 4D and to the long arm of 4A (old "4B"). The evidence for this homoeology are limited

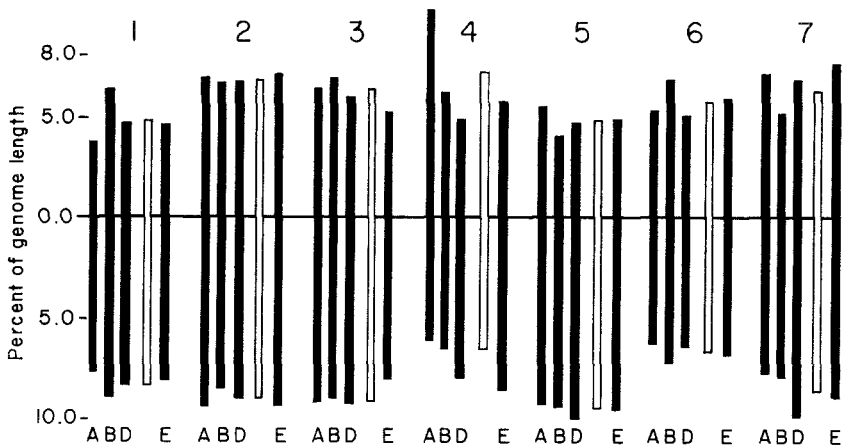

Fig. 1. Comparison of the homoeologous chromosomes of the A, B, and D genomes of *Triticum aestivum* and the E genome of *Elytrigia elongata* (solid bars). The total lengths of the A, D, and E genomes were adjusted to equal that of the B genome. The length of each chromosome arm was expressed as a percentage of the total length of the B genome which equals 1.0. The opened bars represent the average length of the adjusted homoeologous arms of the A, B, and D genomes

cytogenetic data (SEARS & SEARS 1979) and the location of homoeoalleles for certain isozymes in group 4 (HART & LANGSTON 1977). A pericentric inversion of chromosome 4A (old "4B") was suggested to explain the distribution pattern of Ag+-satellite DNA in 'Chinese Spring' (GERLACH & al. 1979). This same pericentric inversion could account for the arm length disparity and the anomalous homoeoallele distribution as well. Structural differentiation involving both chromosomes 4A and 4B (DVOŘÁK & APPELS 1982) could also contribute to the poor correspondence of homoeologous chromosomes in group 4.

Chromosome 4B is metacentric while the remaining two chromosomes of group 4 are heterobrachial. This anomaly is caused by pericentric inversion of centromeric heterochromatin in 'Chinese Spring' 4B. Chromosome 4B of other *T. aestivum* cultivars, such as 'Cheyenne'

and 'Hope' (Dvořák & Chen, unpublished) is more similar to 4D than is 4B of 'Chinese Spring'.

Chromosome arms 1BS and 6BS have secondary constrictions which are not usually discernible in the C-banded chromosomes. This probably resulted in an overestimation of the lengths of the 1BS and 6BS arms relative to their homoeologous arms in the A and D genomes which are devoid of the secondary constrictions.

Except for these few exceptions the rest of the homoeologous chromosomes of the three genomes are remarkably similar (Fig. 1). The adjusted lengths of the homoeologous chromosome arms of the three wheat genomes were averaged to reduce the effects of structural changes (such as those present in 4A and 4B) that may be present in some of the wheat chromosomes. We propose to use these average chromosomes as an estimate of the ancestral *Triticum* genome. This ancestral genome (Fig. 1) consists of two large metacentrics (chromosomes 2 and 7), three smaller, two of them more heterobrachial, metacentric chromosomes (chromosomes 1, 3, and 4), one small metacentric (chromosome 6), and one large submetacentric (chromosome 5).

In the perennial *Elytrigia-Elymus* alliance, there are two genomes, E and S, that occur among the diploid species. The E genome is present in *Elytrigia elongata* and in *E. bessarabica* (Savul. et Rayss) Dubrovik (Dvořák 1981a; McGuire, unpublished). The S genome is present in the Old World *Elytrigia tauri* (Boiss. et Bal.) Tzvelev, *E. stipifolia* (Czern. ex Nevski) Nevski, and *E. ferganensis* (Drob.) Nevski and the New World *E. spicata* (Pursh) Löve (Stebbins & Pun 1953, Dewey 1969, 1974, 1975, 1981). *Elytrigia elongata* has a symmetrical karyotype (Fig. 2) which is composed of two large metacentrics, three heterobrachial smaller metacentrics, one small satellited metacentric, and one satellited submetacentric (Cauderon 1958, Evans 1962, Dvořák & Knott 1974). *Elytrigia bessarabica*, the other diploid that has the E genome, has a very similar karyotype (Heneen & Runemark 1972). Thus, the karyotypes of the two diploid species resemble the average karyotype of *T. aestivum* shown in Fig. 1. Homoeology of the seven *E. elongata* chromosomes with wheat chromosomes has been determined (Dvořák 1980, Hart & Tuleen 1983, Tuleen, unpublished). Dvořák (Dvořák & Knott 1977, Dvořák 1979, and unpublished) also determined homoeology of most of the *E. elongata* chromosome arms with those of wheat chromosomes. It is therefore possible to ascertain whether or not the superficial morphological similarity between the wheat and *Elytrigia* chromosomes is more than just a coincidence. The total length of the *E. elongata* genome relative to chromosome 5B is 5.968 (Table 1). Thus, the total length of the E genome is between the total length of the A genome and the total length of the D genome. As was done earlier for the A and D

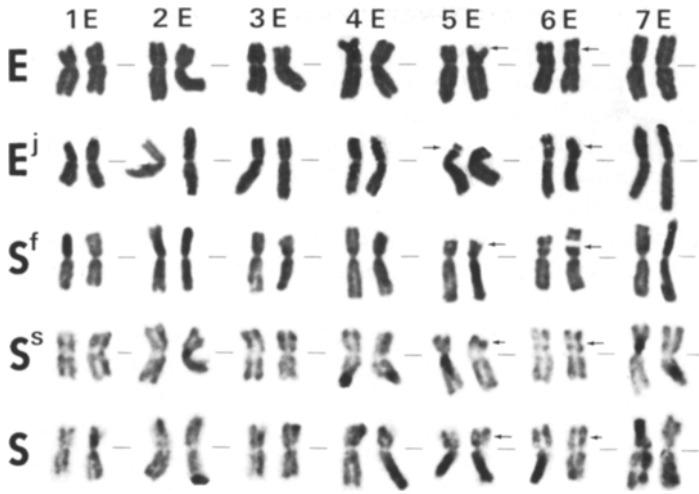

Fig. 2. Karyotypes of *Elytrigia elongata* (E), *E. bessarabica* (E), *E. ferganensis* (S^f), *E. stipifolia* (S^s) and *E. tauri* (S). The location of secondary constrictions in chromosomes 5 and 6 is specified by arrows. The location of the secondary constriction in chromosome 6 is closer to the centromere in *E. ferganensis, E. stipifolia*, and *E. tauri* than in *E. elongata* and *E. bessarabica*. Homoeologous designations refer only to the chromosomes of *E. elongata*

genomes, the total length of the E genome was adjusted to equal that of the B genome. It is apparent in the adjusted E genome (Fig. 1) that six of the seven chromosomes (1 E, 2 E, 3 E, 5 E, 6 E, and 7 E) are similar to their homoeologues in the average *T. aestivum* genome. The secondary constriction in chromosome arm 6ES (= 6Eα) which is homoeologous to arm 6BS (Dvořák 1979) is essentially in the same place as in wheat chromosome arm 6BS. The second secondary constriction is located subterminally in the chromosome 5E (Fig. 2). This constriction probably corresponds to a nucleolus organizer in chromosome 5D of *T. aestivum* and 5U of *T. umbellulatum* (Zhuk.) Bowden (Flavell & O'Dell 1976, 1979). These facts suggest that the plants that gave rise to the species of *Triticum* had to have a karyotype very similar to that of *E. elongata*.

The karyotype of three S genome diploid species, *Elytrigia ferganensis, E. stipifolia*, and *E. tauri*, are shown in Fig. 2. Both karyotypes are symmetrical, like those of the E genome, and, in general, resemble those of *E. elongata* and *E. bessarabica*. There are, however, several features by which the S genomes differ from the E genome, and, hence, also from the average *T. aestivum* genome. The position of the secondary constriction in chromosome 6 is in all species more proximal (Fig. 2) than in the E genome. A more important difference, however, is

that in the three genomes almost all chromosomes are metacentrics of a uniform size. These chromosomes are not readily separable into the four groups based on centromere position that characterize the E genome and the average *T. aestivum* genome.

All species of *Elytrigia* investigated are characterized by centromeric and terminal positions of C-bands (data not shown). In *E. ferganensis* this pattern is associated with prominent intercalary banding. Prominent terminal C-banding also characterizes the *Triticum* species of the section *Sitopsis* (B genomes) and *T. tripsacoides* (Z genome) (Gill & Kimber 1974, Gill 1981, Dvořák, unpublished). The terminal C-banding pattern is largely absent in the *Triticum* species that have asymmetric karyotypes (Dvořák, unpublished). While C-banding does not permit a decision as to whether *Triticum* genomes originated from the E or the S genome complexes of *Elytrigia*, it suggests that the symmetric genomes of *Triticum* are more primitive than the asymmetric genomes, as previously concluded by Stebbins (1958).

Discussion

Most of the species possessing the E genome hybridize easily with *Triticum*. *Elytrigia elongata* has been hybridized with several *Triticum* species (Jenkins & Mochizuki 1957, Dvořák 1971). The other diploid, *Elytrigia bessarabica*, was recently shown to hybridize easily with *T. aestivum* (Alonso & Kimber 1980). The polyploid relatives of *E. elongata* hybridize readily with species of *Triticum*—*E. scirpea* (Presl) Holub $2n = 4x = 28$ (Dvořák 1981a), *E. turcica* McGuire $2n = 8x = 56$ (Sapehin 1935), and *E. pontica* (Podp.) Holub $2n = 10x = 70$ (Wakar 1935, Peto 1936). Similarly, four of the five polyploid relatives of *E. bessarabica* have been hybridized with wheat—*E. junceiformis* Löve et Löve, $2n = 4x = 28$ (Östergren 1940), *E. disticha* (Thunb.) Prokudin ex Löve $2n = 4x = 28$ (Pienaar 1979), and *E. diae* (Runemark) nom. nud. $2n = 8x = 56$ (Mendlinger, unpublished). *Elytrigia caespitosa* (C. Koch) Nevski $2n = 4x = 28$ and *E. intermedia* (Host) Nevski $2n = 6x = 42$ fall neither into the *elongata* nor the *bessarabica* complex of species. Both species, nevertheless, appear to have two genomes that are related to the E genome (Dvořák 1981b) and both hybridize readily with wheat (Gaul 1953, Cauderon 1958, Dvořák 1981b). In spite of extensive efforts (Dvořák, unpublished) none of the S genome species has been hybridized with any species of *Triticum*. In fact, it is difficult to hybridize the S genome diploid and polyploid species even with the *Elytrigia* species possessing the E genome (Matsumura & al. 1958, Dvořák 1918b).

Comparisons of the tribe *Triticeae* with the related tribes of the grass family suggest that the archetype of *Triticeae* was probably a cross-fertilizing perennial with long spikes that had several multifloreted spikelets per node. These are the characteristics of *Psathyrostachys*, *Leymus*, and some of the species of *Elymus*. If it is assumed that *Psathyrostachys* (J genome) occupied a central position in the phylogeny of *Triticeae* (SAKAMOTO 1973), then the annual species of *Triticum* must be derivatives of an evolutionary radiation that was associated with the progressive loss of the generalized characteristics and acquisition of specialized characteristics. The species of *Elytrigia*, which differ from the J genome group by loss of the multiple spikelets per node of the spike, represent the first step in the progressive loss of the generalized characteristics. The self-fertilizing *Triticum* annuals having asymmetric karyotypes represent the most specialized forms since they show reduced numbers of seeds per spikelet and spike, loss of disarticulation of the spikelets, and evolution of elaborate systems of awns aiding spike dispersal and implantation.

All *Triticum* species have truncated glumes usually with one or more tooth-like appendages. The truncated, oblong, or obtuse glumes are characteristic for all species of *Elytrigia* of the E genome complex. All *Elytrigia* species of the S genome complex and all species of *Elymus* have lanceolate glumes. Thus, the shape of glumes also suggests a closer relationship between *Triticum* and the E genome complex of *Elytrigia* than between *Triticum* and the S genome complex.

It was shown here that the karyotype that best approximates three of the four symmetric *Triticum* genomes (the fourth one, of *T. tripsacoides*, could not be employed in this study because the homoeology of its chromosomes with the chromosomes of the other symmetric genomes is not known) is remarkably similar to that of the E-genome diploid species of *Elytrigia*. In addition to the above data, the E genome chromosomes pair at metaphase I relatively well with the *Triticum* chromosomes when the effect of the diploidizing gene is absent (DVOŘÁK 1979). It is unfortunate that no data are available on pairing of the S-genome chromosomes with those of the *Triticum* genomes under the same conditions. These facts are interpreted to mean that the genus *Triticum* evolved from a group of species having attributes of modern *Elytrigia* species which have the E genome or a closely related genome.

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