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Linear Differentiation of Cereal Chromosomes
I. Common Wheat and its Supposed Ancestors

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Summary. Using the Giemsa technique of differential staining (the BSG test), we have studies the karyotypes and constructed the idiograms of *T. aestivum* L. var. 'Diamant' and 'Chinese Spring', *T. monococcum* L. v. 'hornemannii' ssp. roles occidentali georgicum Dek., *Aegilops squarrosa* L. v. 'Meeyeri', *T. aestivum*.

The karyotypes of 'Chinese Spring' and 'Diamant' differ drastically both in total structural heterochromatin content and its localization on the nine morphologically homeologous chromosomes. The rest of the twelve pairs of chromosomes showed no morphological similarity. This indicates considerable differences in the phylogeny of the varieties, and also an absence of unique karyotype in *T. aestivum*.

Three chromosomes of *Ae. squarrosa* are similar to those of 'Chinese Spring', yet, on the whole, the chromosomal structural specificity of the diploids studied is so high that we fail to understand the nature of the homology between common wheat and its supposed diploid ancestors.

The role of introgression in the evolution of the genomes of *Triticum* and *Aegilops*, and also the meaning of the conjugation and BSG tests in resolving the phylogeny, is discussed.

Key words: C-banding - Chromosomes - Homology - Genomes - Introgression

Introduction

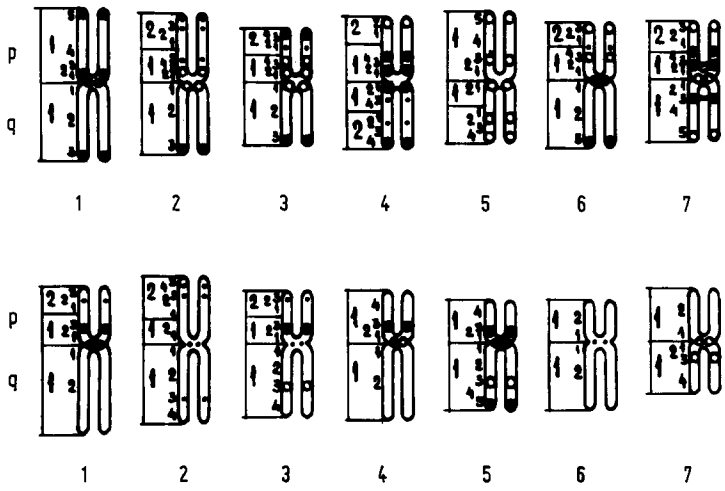
Identification of chromosomes is an obligatory stage in any cytogenetic study. To this end, an objective estimation of the possibility of identifying each chromosome, which in frequently investigated objects strongly depends on the availability of a standard cytological nomenclature, is absolutely essential.

The overall level of the chromosomal assay in wheats (and in plants in general) is markedly below that in man and animals, which seriously hinders the progress of cytogenetic studies of the phylogeny and breeding of cultivated cereals.

Quite recently it has been shown (Zurabishvili and Iordansky 1972; Zurabishvili et al. 1974), by polykaryogram analysis of the chromosomes of *Triticum monococcum* L. and *T. aestivum* L. var. 'Diamant' that, contrary to many of the earlier reports (see for review, Schulz-Shaeffer and Haun 1961; Morris and Sears 1967; Shchapova 1971; and others), no reliable identification of any pair of homologous chromosomes in the somatic cells is possible on the basis of the linear parameters. Conceivably, the considerable morphological similarity (homeomorphism) of the non-homologous chromosomes together with the occasional variations in the homologues have missled the investigators in to erroneous identification of some chromosomes, apparently similar on a given plate but actually not always homologous.

Valid identification of the wheat chromosomes became possible only with the application of the BSG technique of differential of structural heterochromatin. Using this technique, we managed to identify the chromosomes of *T. aestivum* L., to compile the cytological nomenclature, and to present the idiogram (Zurabishvili et al. 1974).

In an attempt to find the chromosome-morphological criteria for identifying the genome structure in wheats of different ploidy, and to understand the possible role of introgression in their evolution, we further extended our investigations. First of all, we were concerned with the putative diploid ancestors of common wheat and also of the variety 'Chinese Spring' most widely used in genetic studies.



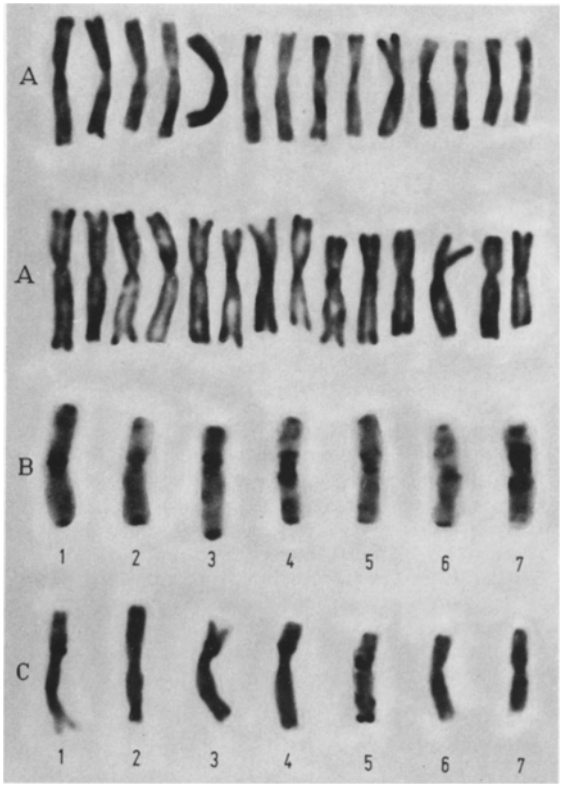


Fig. 1.a Idiogram of the differentially stained chromosomes
(A) *Ae. speltoides*, (B) *Ae. squarrosa*
b Differentially stained chromosomes
(A and B) diploid karyotypes of *T. monococcum*,
(C) haploid karyotype of *Ae. speltoides*, (D) haploid karyotype of *Ae. squarrosa*

Material and Methods

Material

Seeds of *T. monococcum* L. v. 'hornemannii' ssp. proles occidentali georgicum Del., *Aegilops speltoides* Tausch., obtained from Professor L.L. Dekaprelevich (the Georgian Agricultural Institute, Tbilisi), *Ae. squarrosa* L. v. 'Meeyeri K-4-300' and *T. aestivum* var. 'Diamant' from the collection of the N.I. Vavilov Plant Breeding Institute (Leningrad), and var. 'Chinese Spring' supplied by O.I. Maystrenko (Institure of Cytology and Genetics, the Siberian Branch of the USSR Academy of Sciences, Novosibirsk) were used.

Methods

Seeds were germinated at 25°C. The seedlings with 1 to 2 cm long rootlets were immersed in a 0.2 % colchicine solution at 25°C for 2 to 3 h. The rootlets were fixed in 45 % acetic acid at 4°C for 5 to 20 h and hydrolysed in 0.2 N HCl at 60°C for 5 min. The tips were macerated in a 1 % solution of pectinase of cellulase at 25°C for approximately 12 h. The enzyme was washed out, then the material was immersed in 45 % acetic and squash preparations made. The coverslips were removed with dry ice, then the preparations were passed through a series of alcohols at 60 to 100° for 20 to 30 min. and desiccated in heated air. Before staining, dry slides were immersed in a freshly prepared saturated solution of barium hydroxide at room temperature for 6 min, washed in 1N HCl for 1 to 2 min. and in distilled water, desiccated and immersed in a 2 × SSC solution (pH 7.0, 60°) for an hour. Then the preparations were washed in distilled water and again desiccated. Staining was performed in a Romanovsky azure-eosine solution (1:15) in phosphate buffer (pH 6.8) for 20 to 30 min. The stained preparations were washed in four changes of distilled water, desiccated, stored in xylol overnight, and mounted in Canadian balsam.

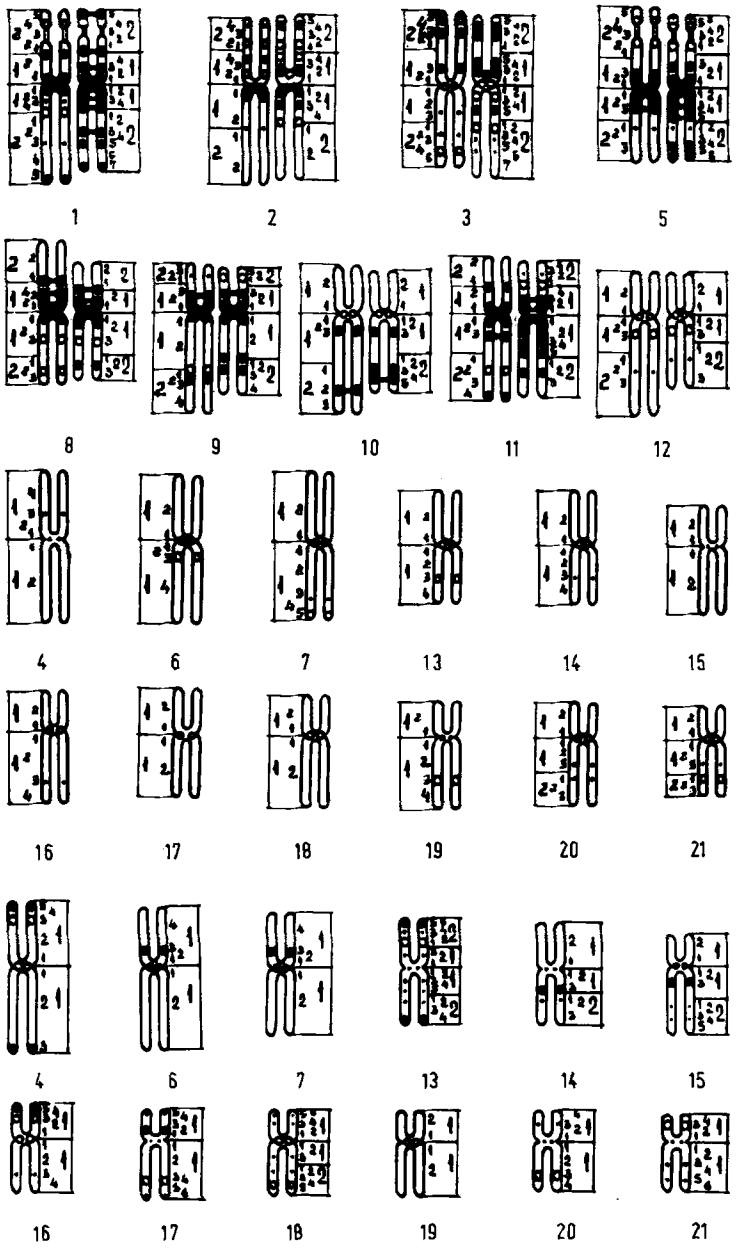
The chromosomes were photographed on Micrat-300 at a × 2900 magnification on positives.

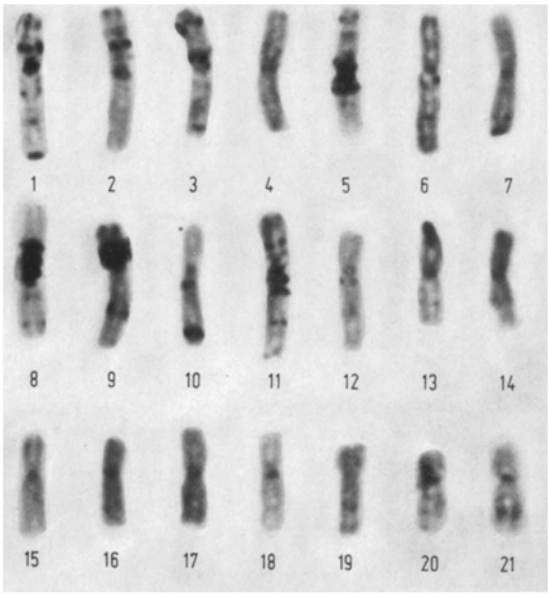
The idiograms were constructed according to the rules accepted by the Paris Converence for Chromosomes of Man (Paris Conference 1971), keeping with the previously accepted cytological nomenclature (Zurabishvili et al. 1974).

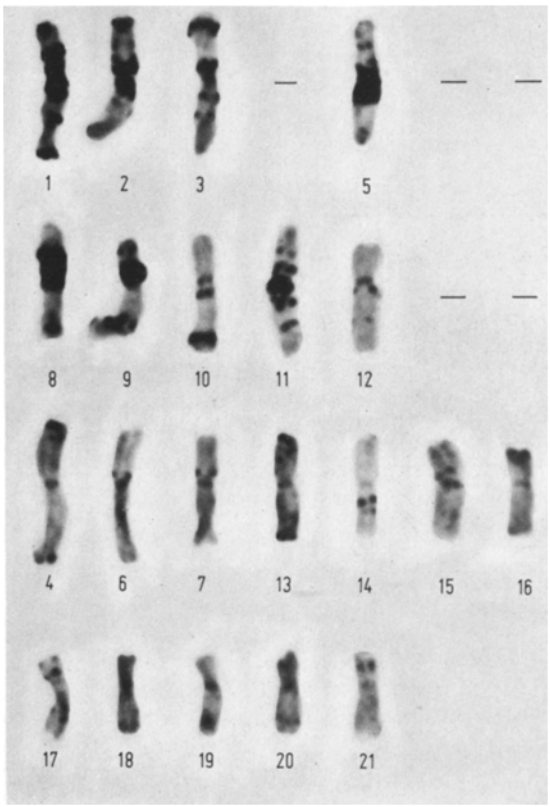
Results

T. monococcum. Using the BSG test, we failed to obtain a stable and distinct pattern of differential staining along the chromosomes (Fig. 1b(A) and (B)). Only on some plates individual chromosomes showed the tendency to a denser staining of the telomeric regions; on different plates different chromosomes had densely stained telomeres. Where two (or more) chromoso-

Fig.2.a Comparative idiogram of *T. aestivum* var. 'Diamant' and 'Chinese Spring'.
Two top rows: to the left - a chromosome of 'Diamant', to the right - its homeologue from 'Chinese Spring'. The third and the fourth rows: chromosomes of 'Diamant'. The fifth and the sixth: of 'Chinese Spring'
b Differentially stained chromosomes Karyotype of *T. aestivum* var. 'Diamant'
c Differentially stained chromosomes Karyotype of *T. aestivum* var. 'Chinese Spring'







somes of a cell are differentially stained (Fig.1b(A)) their homology is questionable.

Ae. speltoides. Constitutive heterochromatin is readily detected on all chromosomes of this species (Fig.1b(C)). Characteristically, it is localised, in most chromosomes, in the telomeric and centromeric regions. The largest blocks of heterochromatin are found in chromosomes 4 and 7.

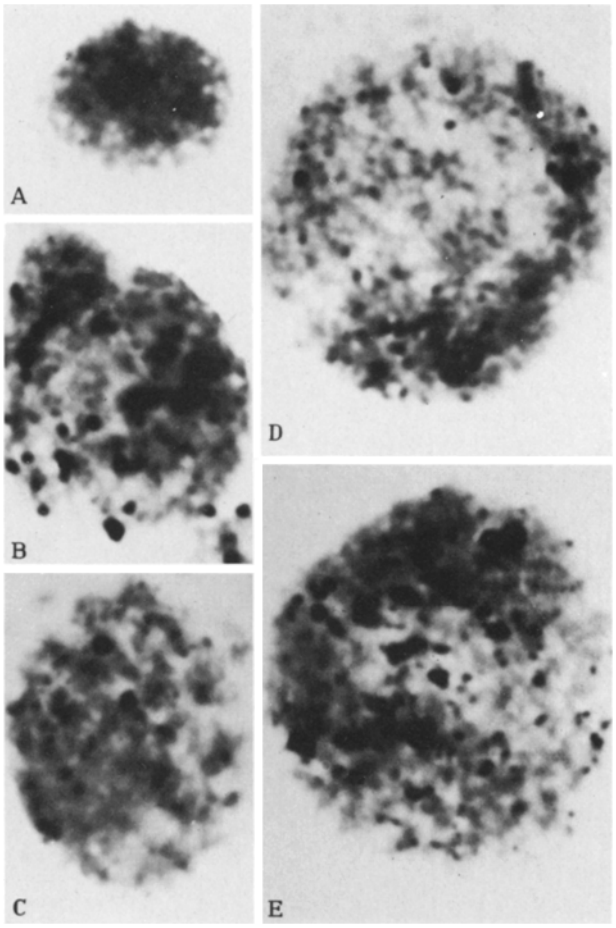


Fig.3. Differentially stained interphase nuclei (A) *T. monococcum*, (B) *Ae. speltoides*, (C) *Ae. squarrosa*, (D) *T. aestivum* var. 'Diamant', (E) *T. aestivum* var. 'Chinese Spring'

The specific distribution of densely stained regions along each chromosome together with the peculiar chromosome morphology permitted us to identify them with certainty and to construct the idiogram (Fig.1a(A)).

Ae. squarrosa. The linear differentiation of the chromosomes in this species has a clearcut specificity (Fig.1b(B)) and is markedly distinguished from that in *Ae. speltoides*. As a whole, there is less heterochromatin, and small densely stained regions are localized in the centromeres (1 and 5) and intercalary in the short arms (1,2,4 and 5). The richest in heterochromatin is chromosome 5 having a densely stained region also in the telomere of the long arm. Chromosomes 2 and 6 have little heterochromatin. The differential stain and the morphological peculiarities permit reliable identification of all chromosomes in *Ae. squarrosa* and construction of the idiogram (Fig.1a(B)).

T. aestivum var. 'Diamant'. In view of the size and number of heterochromatin regions the chromosomes of var. 'Diamant' fall into three groups (Figs. 2b and a). The first includes chromosomes abundant in heterochromatin predominantly localized in the centromeric and adjacent (1,2,5,8,9 and 11), and also in the intercalary (3 and 10) regions. The second group includes chromosomes with the median density of staining of the heterochromatin regions, localized predominantly in the centromeres and intercalary (6,7, 12,13, 19 to 20). Chromosome 7 has a telomeric heterochromatin region in the long arm. The rest of the chromosomes (4, 14 to 18) contain insignificant amounts of heterochromatin, only slightly stained and localized predominantly in the centromeres.

T. aestivum var. 'Chinese Spring'. The chromosomes differ drastically from those of 'Diamant' by the large amount of heterochromatin (Fig.2c and 2a). In addition, it has twelve chromosomes with such an original localization of heterochromatin that their homeology with any of the chromosomes of var. 'Diamant' could not be established. Among them, chromosomes 4 and 13, having a telomeric localization of heterochromatin characteristic of rye chromosomes, stand out. It is also noteworthy that chromosomes 6, 7 and 17 are similar to chromosomes 1, 4 and 3 of *Ae. squarrosa* respectively, in the heterochromatin distribution pattern and the chromosome arm length ratio.

Nine chromosomes (1 to 3, 5, 8 to 20) of 'Chinese Spring', though abundant in heterochromatin, may be treated as homeologues of respective chromosomes of the variety 'Diamant' for the general pattern of heterochromatin distribution. Yet, each of the above chromosomes has certain structural distinctions from its homeologue, as seen in the comparative idiogram (Fig.2a).

The structure of interphase nuclei. Specificity of each of the investigated species for the quantity and localization of structural heterochromatin in the karyotypes is also manifested in the structure of the interphase nuclei represented in the differentially stained preparations (Fig.3). For example, the nuclei of *T. monococcum* (Fig.3(A)) whose chromosomes have little heterochromatin, contain a few small, faintly stained chromocentres. The interphase nuclei of *Ae. speltoides* (Fig.3(B)), whose chromosomes are considerably

richer in heterochromatin, contain large, distinctly outlined and densely stained chromocentres. In this respect the nuclear structure of *Ae. squarrosa* (Fig. 3(C)) is intermediate among the species discussed.

The distinctions between the 'Diamant' and 'Chinese Spring' chromosomes in total heterochromatin are also manifested in the structure of the interphase nuclei, having markedly larger chromocentres in 'Chinese Spring' (Figs.3(D and C)).

Discussion

In the present work we hold to the cytological nomenclature for the chromosomes of common wheat accepted earlier (Zurabishvili et al. 1974), although in a work of Gill and Kimber (1974) the cytological identification was correlated with the genetic nomenclature on the basis of a study of ditelocentrics by the BSG test.

Comparing the differential stain of the chromosomes of the varieties 'Diamant' and 'Chinese Spring' (Gill and Kimber 1974), we discovered similarity between only five chromosomes. Comparing the stained 'Chinese Spring' chromosomes in our work with Fig.4 borrowed from Gill and Kimber (1974), we discovered a general similarity between only nine chromosomes. The relative lengths and the arm index of chromosomes were borrowed from Sears (1954) who obtained his data at the telophase II of meiosis. The latter circumstance leads to a marked inconsistency between the parameters of the chromosomes on the plate and in the idiogram. It is exactly what would be expected taking into account the differeing character of differential spiralisation of the chromosomes (Iordansky et al. 1975) in meiosis and mitosis (Brown 1949).

Gill and Kimber (1974) also investigated the linear differentiation of the chromosomes of the supposed diploid ancestors of common wheat.

Comparing the karyotype of *T. monococcum* L. reported by them with our observations and also with the tentative data on the linear differentiation of the chromosomes of *T. urartu*, we have not found any similar features but heterochromatin deficiency. Apparently, the authors dealt with a different form of einkorn closely related to *T. boeoticum*, since, according to our preliminary data, the differential staining of the chromosomes of the latter species is similar to that reported by Gill and Kimber (1974) for *T. monococcum*. It is noteworthy that the differential staining of the chromosomes of einkorn observed by us is similar to that observed by D. Kostov as early as 1938.

The differential staining pattern observed by us in *Ae. speltoides* and *Ae. squarrosa* is also different from that described by Gill and Kimber (1974). The only similarity was in the telomeric heterochromatin distribution in the chromosomes of *Ae. speltoides*.

Comparing the karyotypes of the diploids studied with chromosomes of hexaploids, we discovered a morphological similarity only between three individual chromosomes of *Ae. squarrosa* and 'Chinese Spring'.

The marked diffferences between the chromosomes of the varieties 'Diamant' and 'Chineses Spring', revealed by the differential staining, were quite unexpected, for they belong to the same species and the karyotpye is considered to be a fundamental and relatively stable character of a species.

The existence of the intervarietal karyotypical heteromorphism is still more surprising, as the chromosomal polymorphism in the varieties is quite low and the homologues do not actually show any morphological differences. In addition, by comparing the variety-specific chromosomes (4,6,7,13 to 21) no homeologous pairs were found, the differences between which could be explained by expected translocations (Larsen 1973). In other words, 12 chromosomes of 'Diamant' look "alien" in the karyotype of 'Chinese Spring', and vice versa. Two alternative, but not mutually exclusive, explanations of the phenomenon may be offered. The first one is the effect of introgression involving other species whose chromosomes are not yet known and therefore cannot be identified in the investigated karyotypes. Since 'Chinese Spring' is considered to be one of the most primitive wheat varieties (Sears 1954; Riley et al. 1967; Larsen 1973), it is reasonable to suppose that introgression took place in the history of 'Diamant'. This phenomenon is well-known in the evolution of many plants (Zhukovsky 1970), including *Aegilops* and *Triticum* (Zohary and Feldman 1962; Pazy and Zohary 1965; Feldman 1965, 1966; Vardi 1973, 1974), hence its role in variety formation may also be postulated.

The suggested role of introgression in the evolution of the 'Diamant' karyotype is reinforced by si-

milarity between certain chromosomes of *Ae. squarrosa* and 'Chinese Spring' and lack of similarity with 'Diamant'. This could be due to the substitution of the chromosomes originating from *Ae. squarrosa* into some unknown homeologous chromosomes of other species and forms. Such a substitution might be complete in the evolution of 'Diamant' but only partial in 'Chinese Spring'.

The second, not unreasonable explanation of the intervarietal karyotypical differences, and of those between hexaploid wheats and their supposed diploid ancestors, is that evolutionary changes took place in the pattern of constitutive heterochromatin distribution along chromosomes. The work of Vosa (1973) on *Scilla sibirica* demonstrated the possibility of heterochromatin in plants being highly variable. Therefore it may be suggested that in self-pollinators, such as sommon wheat, a change in some hterochromatin region will persist in the variety originated from such a plant and will be relatively stable.

In view of the concept of the primitive karyotype of 'Chinese Spring' and the large quantity of heterochromatin detected in it, it may be supposed that the evolutionary process tended to decrease the quantities of the genetically inactive material in the genome of more advanced wheat varieties.

The current concepts of the origin of each of the three genomes of common wheat are well known, to great extent due to the use of a conjugation test, i.e. analysis of pairing of homeologous chromosomes in different interspecific hybrids (Morris and Sears 1967; Yachevskaya 1971; Budashkina 1971).

In the first investigation in this direction, in which *T. monococcum* was identified as the donor of A-genome (Sax 1922), no quantitative estimation of conjugation was made; in later studies, as a rule, the proportion of univalents, bivalents and more complicated configurations occurring in MI hybrids was determined. As a matter of fact, the proportions were never absolutely distinct and constant for all cells and individual plants. For example, in the study of Riley and Chapman (1960), which remained until now a convincing demonstration of *Ae. squarrosa* as the donor of D-genome (Kimber and Athwal 1972), of the 100 examined F_1 cells of *T. aestivum*, var. 'Chinese Spring' × *Ae. squarrosa* only 60 cells contained 7 bivalents and 14 univalents; in the rest the number of bivalents varied from 4 to 6. The authors examined the hybrid originated from only one variety of common wheat and one collection specimen of *Ae. squarrosa*.

In some respects this work is rather typical, viz. wheat's phylogeny is resolved on the basis of rather indefinite data obtained through the conjugation test.

When in the crosses with the same 'Chine Spring' the role of *Ae. speltoides* as the donor of B-genome was analysed with several collection specimens (Kimber and Athwal 1972), they turned out to fall into three groups distinguished by the degree of conjugation with *T. aestivum* chromosomes. Conceivably, the authors were quite right to conclude that *Ae. speltoides* was not a direct donor of B-genome. However, the paper is interesting for us, above all because it demonstrated by means of the conjugation test significant polymorphism of the natural population of this species. It suggests that a rigorous estimation of the degree of homeology of chromosomes at species level cannot be afforded without a simultaneous analysis of several F_1 hybrids derived from different specimens of a diploid species. In other words, the general body of data on the chromosome conjugation in F_1 of interspecific hybrids forbids one to consider them as convincing evidence of the origin of any of the three *T. aestivum* genomes.

A novel test for estimating the homeology of chromosomes of related species is comparison of the patterns of their differential staining by the BSG method, or by peculiar distribution of constitutive heterochromatin along individual chromosomes of somatic cells. It should be taken into account that the heterochromatin regions of chromosomes are responsible for the normal process of conjugation (Barr and Ellison 1972). Complete conjugation is preceded by approximation of the heterochromatin regions (Maguire 1967; Wagenaar and Sadasivaiah, 1969) and their binding by the DNA strands (Ahokas 1971; Drets and Stoll 1974). Apparently, conjugation is a random process, depending upon the degree of homeology of the DNA carrying repeated nucleotide sequences, its quantities in the heterochromatin regions, the pattern of their distribution along chromosomes, and the effects of the residual genotype. It is worth noting that in three chromosomes of nulli-5B haploid 'Chinese Spring', which are not isochromosomes, conjugation occurs between the arms (Upadhya 1969). The differential staining

also permits detection in the karyotype of the variety three chromosomes (1,4 and 13) with a telomeric localization (symmetrical with respect to the centromere) of large heterochromatin regions. It seems probable that conjugation between the arms occurs just in these chromosomes owing to the association of the telomeric heterochromatin regions approximated at the premeiotic interphase. Approached in this way, the revealed differences in the chromosomal structure of the two varieties of *T. aestivum* L. may be compared with the previously mentioned data on polymorphism of the *Ae. speltoides* population. The differences in the degree of conjugation could be due to the polymorphism of the three groups of collection specimens of *Ae. speltoides* in the distribution pattern and the structure of the heterochromatin regions.

As a whole, the variety 'Chinese Spring' proved to be considerably richer in heterochromatin than 'Diamant'. Moreover, these two varieties of common wheat have only 9 chromosomes similar in contitutive heterochromatin pattern. Therefore their chromosomes may be expected to have differing ability conjugate in interspecific and intervarietal crossings.

Unfortunately, so far there has been no attempt to investigate the linear differentiation of the somatic chromosomes of two species (or varieties) and at the same time to make a quantitative assay of the conjugation in F_1 hybrids. Such a study would enable objective evaluation of each test in the determination of the degree of homology of homeologous chromosomes. And without it, in view of the revealed karyotypical heteromorphism of *T. aestivum* L. varieties, it seems impossible to rigorously determine the degree of homology between the chromosomes of hexaploid wheat and its putative ancestors. In this case, we may speak only about the degree of apparent similarity of the homeologues compared, not excluding the possibility of lack of homology at a genetic level. Consequently, the attempt to establish homology betwen particular chromosomes of the diploid species (*T. monococcum, Ae. speltoides, Ae. squarrosa*) and *T. aestivum* on the basis of the BSG test alone, seems unconvincing (Gill and Kimber 1974).

Using the BSG test, we would not solve unambiguously the roles of *T. monococcum, Ae. speltoides* and *Ae. squarrosa* as donors of the three genomes of *T. aestivum* L. Conceivably, to solve this problem, the BSG test should be applied to the chromosomes of a number of varieties of common wheat and a host of forms of diploid and polyploid species.

Conclusions

1. The linear differentiation of the chromosomes of *T. aestivum* var. 'Chinese Spring' and 'Diamant', and also of the diploids *T. monococcum, Ae. speltoides* and *Ae. squarrosa*, putative ancestors of common wheat, was studied by means of the BSG test.

2. The varieties studied differ drastically in their chromosome complement, only nine chromosomes manifesting morphological similarity, which indicates a lack of specific karyotype in *T. aestivum*.

3. No linear differentiation of the *T. monococcum* chromosomes has been revealed by the method used.

4. The chromosomes of *Ae. speltoides* and *Ae. squarrosa* have clearcut individual linear differentiation permitting their reliable identification.

5. The comparison of the chromosomes of diploids with those of common wheat varieties has revealed similarity only between three chromosomes of *Ae. squarrosa* and 'Chinese Spring'. No similarity has been found between the chromosomes of the variety 'Diamant' and putative ancestors of common wheat.

6. The role of introgression in the evolution of wheat and ints ancestors is discussed.

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