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Cytological analysis on the distribution and origin of the alien chromosome pair conferring blue aleurone color in several European common wheat (*Triticum aestivum* L.) strains

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Summary. Meiotic chromosome pairing and Giemsa C-banding analyses in crosses of several European blue-grained wheat strains with Chinese Spring double ditelosomic and other aneuploid lines showed that *Triticum aestivum* Blaukorn strains "Berlin," "Probstdorf," "Tschermak," and "Weihenstephan" are chromosome substitutions, in which the complete wheat chromosome *4A* pair is replaced, whereas the strains "Brünn" and "Moskau" are *4B* substitutions. The alien chromosome pair in all of these strains is an A genome chromosome (*4A*) from diploid *Triticum monococcum* or *T. boeoticum* not present in common tetraploid and hexaploid cultivated wheats. The Blaukorn strain Weihenstephan "W 70a86" possesses, in addition to a rye chromosome pair *5R* compensating for the loss of part of chromosome *5D*, a *4A/5DL* translocation replacing chromosome pair *4B* of wheat.

Key words: *Triticum aestivum* – *Triticum monococcum* – blue aleurone color – Chromosome substitution/translocation

Introduction

Since Kattermann (1932a, b, c) reported a strain of common wheat characterized by blue aleurone color of the grain, plant breeders and geneticists have been interested in using this trait as a genetic marker. The "Blaukorn" strain found by Kattermann (1932a, b, c) was believed to have arisen from a cross between a speltoid plant of the local Bavarian wheat cv. "Moosburger begrannter Dickkopf" and a plant of a wild tetraploid species, *Aegilops ovata* L. (2n = 28) produced in 1923 at the Bayerische Landesanstalt Weihenstephan, Germany. In the F_3 generation of this hybrid, several lines were selected that had blue-green or greyish-blue seeds (Kattermann 1932a), but a grain structure resembling that of common wheat. Forty years later, Zeller and Baier (1973) described a Weihenstephan wheat strain "W 70a86" possessing blue aleurone color and a hairy peduncle. They found a complete rye chromosome *5R* pair carrying the hairy neck gene substituted for wheat chromosome pair *4B* (new nomenclature after the Seventh International Wheat Genetics Symposium, 1988). However, the chromosome determining the grain color could not be identified.

From earlier studies it is known that species of *Agropyron*, such as *Ag. elongatum* and *Ag. trichophorum* and their hybrids with *Triticum* species, possess blue aleurone color (Tschermak-Seysenegg 1938; Suneson and Pope 1946). Investigations by Knott (1958) in the blue-grained common wheat strain "Blue Dark" revealed that the wheat chromsome *4D* pair was replaced by an unknown chromosome pair from *Agropyron elongatum* (Zeller 1976). A similar substitution was found by Larson and Atkinson (1970, 1973) using derivatives of a hybrid between *T. aestivum* and *Ag. elongatum* (2n = 70) and in the "Blaukorn" strain "Xiao Yan" from China (Li et al. 1983; Cermeño and Zeller 1986; Mu et al. 1986). One case of a spontaneous translocation in which the β-arm of wheat chromosome *4B* was replaced by an *Ag. elongatum* chromosome arm carrying the blue aleurone gene was identified by Soliman et al. (1980) and Jan et al. 1981). Škorpík et al. (1983) also described a wheat strain characterized by blue aleurone color.

More recently, blue aleurone coloration was reported in a *T. aestivum* × *Ag. junceum* amphiploid (Alonso and Kimber 1980; Forster et al. 1987). From this amphiploid, several disomic wheat-alien chromosome addition lines have been developed (B. P. Forster, T. E. Miller, G. Kimber, and S. M. Reader, unpublished results). One of these shows blue grain coloration. Furthermore, an alien chromosome from *Ag. trichophorum* was reported to possess a gene that confers blue grain color when added as a telesome to the common wheat genome (Whelan 1989).

The "blue aleurone" trait of the European *Triticum* strains in the present study may represent a gene mutation, the transfer of a gene or a chromosome segment from an alien source, or the transfer of a complete chromosome from an alien species into common wheat. The objective of the study was to investigate the distribution and origin of the chromosome conferring blue aleurone color in wheat, by creating appropriate crosses between blue-grained strains and aneuploid wheat lines and by studying chromosome pairing associations in the hybrids.

Materials and methods

The Weihenstephan wheat strain "W 70a86", previously described by Zeller and Baier (1973) and designated as Blaukorn "W 70a86" (W70), was backcrossed to Chinese Spring wheat three times. One line, "Blue Chinese Spring" (Blue CS), with blue aleurone color but lacking the hairy peduncle trait, was selected from the backcross progenies. Tschermak's Blaukörniger Winterweizen (Blaukorn "Tschermak") was kindly provided by the Experimental Station Fuchsenbigl of the Austrian Bundesanstalt für Pflanzenbau und Samenprüfung, Haringsee, which had originally obtained it from the germ plasm bank of the Landwirtschaftlich-Chemische Bundesversuchsanstalt, Linz, Austria.

Three blue-grained wheat strains were obtained from Dr. Lehmann, Gatersleben, GDR. One of these strains, *T. aestivum* var. *tschermakiano-barbarossa*, Speltoidform No. 375/49, originally came from the Institut für Pflanzenbau und Pflanzenzüchtung, Weihenstephan. It is awned, speltoid, and was designated Blaukorn "Weihenstephan." The second Gatersleben wheat strain is called *T. aestivum* var. *tschermakianum* Mansf., "Tschermak's Blaukörniger Sommerweizen." This strain, also awned, originally belonged to Prof. E. Schiemann's wheat collection in Berlin-Dahlem. It was designated Blaukorn "Berlin." The third strain from the Gatersleben collection was a blue aleurone wheat from the Main Botanical Garden, Moscow. This Russian strain is awnless and was designated Blaukorn "Moskau."

Blaukorn "Probstdorf" was obtained from the Breeding Station Probstdorf, Austria. It is a blue-grained awnless wheat strain with the following ancestry: (Tschermak's Blaukörniger Winterweizen × LP 10189) × (Maris Huntsman × Probstdorfer Gigant).

In addition, a seed sample of "colored wheat," a gift from Prof. E. Tschermak, Vienna, to Dr. K. Mostovoj, Provincial Research Institute, Brünn, Czechoslovakia, was provided by Dr. Škorpik, Research Institute for Crop Production, Prague-Ruzyne, Czechoslovakia. This strain was designated Blaukorn "Brünn." Two other blue-grained wheat accessions were used: a disomic substitution line "Xiao Yan, blue wheat" kindly supplied by Dr. Li, Xian, China, in which wheat chromosome *4D* was replaced by an *Ag. elongatum* chromosome, and "Blue Dark," also a (*4D*) *Ag. elongatum* chromosome substitution, which was kindly provided by Dr. Knott, Saskatoon, Canada.

A series of aneuploid, alien substitution and addition lines were used in crosses with this material as described in the "Results." Cytological analyses were carried out by using traditional (Feulgen), differential C-banding (Giraldez et al. 1979) and Ag-NOR silver staining (Lacadena et al. 1984) techniques.

Results and discussion

Identification and distribution of substituted wheat chromosomes and cytological characterization of the alien chromosome pair in European blue-grained wheat strains

All European Blaukorn strains described in "Materials and methods" were crossed with the wheat cultivars "Holdfast" or "Chinese Spring", and the chromosome pairing of the resulting hybrids was studied. The F_1 hybrids always showed a minimum of two univalent chromosomes at metaphase I of meiosis, suggesting that in the Blaukorn strains one wheat chromosome pair had been replaced by a complete pair of alien chromosomes.

In order to identify the substituted wheat chromosome, the different Chinese Spring double ditelosomic (DDT) lines, with the exception of *7D*, were crossed with Blaukorn strains. The results of the critical crosses are presented in Table 1. In the hybrids of DDT line 4A × Blaukorn strain "Tschermak," a minimum meiotic pairing of $20'' + 1' + 2t'$ was observed, whereas all other DDT-F_1 hybrids formed a ditelosomic trivalent ($t1t'''$). For

Table 1. Chromosome pairing in PMCs of $2n = 41 + t + t$ F_1 hybrids between CS double ditelosomic lines (DDT) *4A*, *4B*, and *4D* and blue-grained strains "Weihenstephan" (W), "Berlin" (Be) "Tschermak" (T), "Moskau" (M), "Brünn" (Br), and "Blue CS" (BCS)

F_1 hybrids		No. of plants	Metaphase I chromosome configurations No. of cells				
			$2'$ $19''$ $t1t'''$	$t1t'''$ $2'$ $17''$ 1^{IV}	$1'$ $2t'$ $20''$	$3'$ $2t'$ $19''$	$18''$ $1'$ $2t'$ 1^{IV}
DDT-*4A*	× W	4	–	–	20	5	1
	× Be	3	–	–	194	10	6
	× T	8	–	–	123	33	11
	× M	5	32	–	–	–	–
	× BCS	3	112	–	–	–	–
DDT-*4B*	× W	3	18	–	–	2	–
	× Be	1	–	1	–	–	–
	× T	4	35	1	–	3	–
	× M	5	–	–	60	5	–
	× Br	1	–	–	9	–	–
	× BCS	2	–	–	132	–	–
DDT-*4D*	× W	1	5	–	–	–	–
	× Be	1	23	3	–	–	–
	× T	3	40	10	–	1	1
	× M	2	15	3	–	–	–
	× BCS	4	321	–	–	–	–

chromosome *7D*, a hybrid between CS ditelo-*7D* was crossed with strain "Tschermak," and maximum pairing of $19'' + 2' + t1''$ and $17'' + 2' + t1'' + 1^{IV}$, was detected.

Similar results were obtained in crosses of CS DDT lines with Blaukorn strains "Berlin" and "Weihenstephan" (Table 1), indicating that in these Blaukorn strains chromosome pair *4A* was also replaced by an alien chromosome pair, and confirming the preliminary results of Cermeño and Zeller (1988). In the cross with DT-*7D*, a heteromorphic bivalent (t1") almost always was observed. The frequent occurrence of a quadrivalent configuration in the F_1 hybrids between CS DDT lines, strain "Tschermak," indicates a chromosomal translocation relative to Chinese Spring. One cell in the cross between DDT-*5B* and "Tschermak" formed $17'' + 2' + t1t''' + 1^{VI}$ (hexavalent), indicating two translocations involving three pairs of chromosomes. The occurrence of quadrivalent configurations involving a telosomic chromosome in the hybrids with DDT lines *1A*, *2A*, and *2D* (data not shown) implicates the involvement of at least chromosomes *1A*, *2A*, and *2D* in the translocation complex.

Configurations of $20'' + 1' + 2t'$ in meiocytes of F_1 hybrids of Chinese Spring DDT line *4B* × Blaukorn "Moskau" indicates a *4B* chromosome substitution (Table 1, Fig. 1). Likewise, in hybrids between Chinese Spring and Blaukorn "Brünn" a minimum of two univalents *4B* and the alien chromosome always occurred. From these results it can be concluded that Blaukorn "Moskau" and "Brünn" possess the same chromosome substitution.

The alien chromosome presented similar (submetacetric) morphology in all cases analyzed, and its C-banding pattern shows only a very slight centrometric or pericentromeric band. To clarify the identity of the alien chromosomes, intercrosses between the different strains were made and the meiotic pairing of the hybrids was studied. Hybrids between Blaukorn "Moskau" and "Brünn" (*4B* substitutions) and between (*4A* substitutions) "Berlin," "Probstdorf," "Tschermak," and "Weihenstephan" exhibited cells with 21 bivalents. The F_1 between the *4A* and *4B* substitution lines showed cells possessing 20 bivalents plus chromosomes *4A* and *4B* as univalents. One open bivalent was always observed, except in crosses between (*4A*) lines "Weihenstephan" and "Probstdorf," in which 21 ring bivalents could be observed (frequency: 3.23%). By applying the C-banding technique, it could be concluded that such open bivalent(s) always consisted of wheat chromosomes, sometimes belonging to the B genome, which were easily recognizable. In Fig. 2, a PMC of a hybrid between (*4A*) strain "Tschermak" and (*4B*) strain "Moskau" is depicted showing 20 ring bivalents, including the alien chromosome pair and two univalents (*4A*+*4B*). The present results indicate that the alien chromosomes in the (*4A*) and (*4B*) European Blaukorn strains are completely homologous.

Search for the origin of the alien chromosome pair controlling blue aleurone color

In the first report on the Weihenstephan Blaukorn strain, it was claimed that *Aegilops ovata* (2n=28, genome formula: UUM^0M^0) was responsible for the blue aleurone color (Kattermann 1932a). Mettin et al. (1977) have established a set of six disomic wheat-*Ae. ovata* addition lines. None of these addition lines have blue aleurone color (D. Mettin, personal communication). Two of them, lines II and VI, were crossed with Blaukorn strain (*4B*) "Moskau." The meiotic pairing showed a minimum of three univalents (*4A*, Blaukorn alien, and *Ae. ovata* chromosome II or VI), indicating no homology between the Blaukorn and the *Ae. ovata* chromosomes analyzed.

Kattermann (1932a) expressed doubts as to the involvement of *Ae. ovata* chromatin in controlling the blue aleurone color in Blaukorn. He assumed that the ability to produce anthocyanin may trace back to common rye, since this species may be characterized by purple seed color. For this reason, all seven disomic and several ditelosomic wheat-rye addition lines of the Chinese Spring-

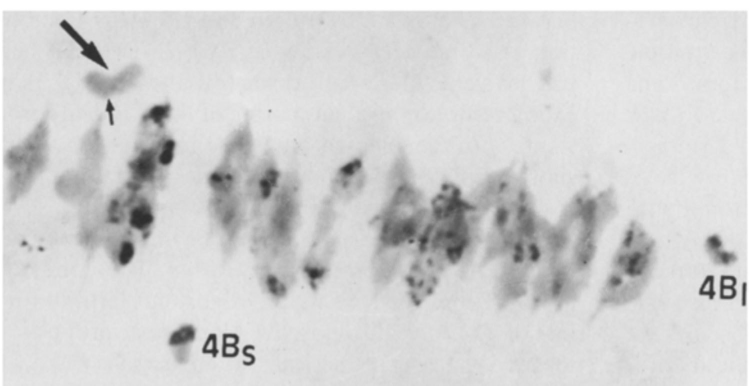

Fig. 1. C-banded meiotic MI PMC of a hybrid between CS line DDT-*4B* and Blaukorn strain "Moskau", showing 20 ring bivalents, one complete alien chromosome (*arrows*), and telosomes *4BL* and *4BS* as univalents

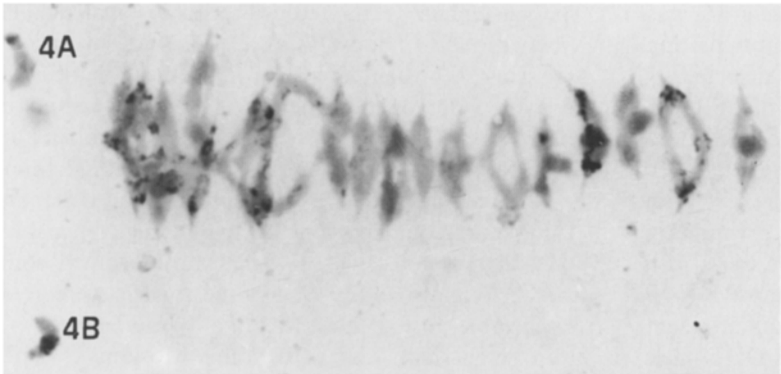

Fig. 2. C-banded meiotic MI PMCs of a hybrid between strains "Tschermak" and "Moskau", showing 20 ring bivalents and wheat chromosome univalents *4A* and *4B*

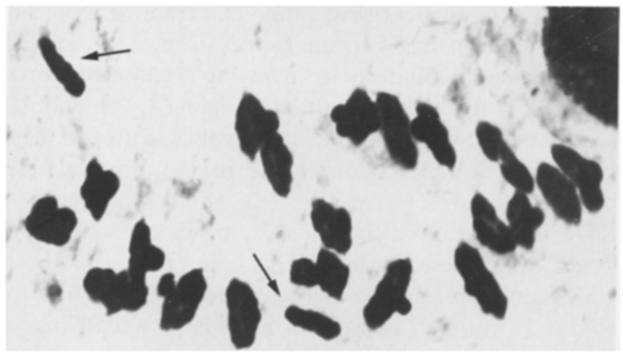

Fig. 3. Feulgen-stained MI PMC of a hybrid between wheat strain "Berlin" and CS-*T. urartu* substitution line (*4B*) $4A^u$, showing 20 ring bivalents and two univalents (*4A*, *4B*). The univalents are marked by *arrows*

Imperial and the Holdfast-King II wheat-rye chromosome addition sets were crossed to Blaukorn strain "Tschermak." However, no added rye chromosome paired with the alien chromosome conferring blue aleurone. Additionally, wheat-alien chromosome addition lines of *Ae. variabilis,* and *Ae. umbellulata* and substitution lines of *Ae. longissima* and *Ae. sharonensis* were crossed to Blaukorn strains. In all hybrids analyzed, no homology between the Blaukorn and the added or the substitution chromosomes was found.

The European Blaukorn strains were also crossed with blue-grained *Agropyron* substitution, translocation and addition lines. The meiotic chromosome pairing again revealed no homology between the alien chromosome in the European Blaukorn strains and those of *Ag. elongatum, Ag. intermedium,* and *Ag. junceum.*

Triticum urartu, a diploid wild wheat species, is believed to be the donor of the AA genome of cultivated wheats (Chapman et al. 1976; Konarev et al. 1979; Kasarda 1980; Dvorák et al. 1988; Galili et al. 1988). However, it has been shown that only six A genome chromosome pairs are present in hexaploid bread wheat and tetraploid emmer wheat. Chromosome *4A* (now designated *4B*) most probably is not from an A genome donor, but from an as yet unknown species, possibly the G genome of *T. timopheevii* (Miller et al. 1981; Dvorák 1983; Gill and Chen 1987; Naranjo et al. 1988; Naranjo 1990; Dvorák et al. 1990). The former wheat chromosome *4B* (now designated $4A^a$) appears to have multiple structural rearrangements in comparison to chromosome *4A* of *T. monococcum*, and therefore is not able to pair with its homoeologue in *T. monococcum* and *T. urartu*, respectively (Naranjo 1990; Dvorák et al. 1990).

Wazuddin and Driscoll (1986) obtained disomic substitution lines of *Triticum urartu* chromosome 4 for wheat chromosomes *4A* and *4B* and Dvorák et al. (1990) obtained disomic substitution lines of *T. monococcum* ssp. *aegilopoides* chromosome 4 for wheat chromosomes *4A* and *4B*. Similarly, Miller et al. (1987) produced three substitution lines in which each chromosome of homoeologous group 4 in Chinese Spring wheat was replaced by the homoeologous chromosome *4A* of *T. urartu*. The latter substitution line Chinese Spring (*4B*)$4A^u$ and the ditelosomic addition line CS/$4A^u$ were crossed to Blaukorn strain "Berlin," and the meiotic chromosome pairing of the F_1 plants was analyzed. Table 2 shows that, in the cross CS/$4A^u$ ditelo addition × Blaukorn "Berlin," the *T. urartu* telesome predominantly paired as a heteromorphic bivalent, presumably with the complete alien chromosome in the Blaukorn strain. Likewise, in the hybrid between "Berlin" substitution and CS (*4B*)$4A^u$ substitution, most meiocytes exhibited $20''+2'$. Two cells had 20 ring bivalents plus 2 univalents (*4A* and *4B*; Fig. 3), indicating complete bivalent pairing of the *T. urartu* chromosome, with the alien chromosome in Blaukorn "Berlin" substituting for wheat chromosome *4A* (Table 2).

It is notable that Joppa and Maan (1982) also were able to produce a *T. durum* – *T. boeoticum* (genome formula: AA) chromosome substitution. The donor chromosome compensated well in vigor and fertility for the loss of *T. durum* chromosome *4B*. A great proportion of the seeds had purple pericarp. It appears very likely that the alien chromosome from *T. boeoticum* in the *T. durum*

Table 2. Chromosome pairing in PMCs of Chinese Spring/*4A*ᵘ di-telosomic addition line and Chinese Spring *(4B)4A*ᵘ substitution line with Blaukorn strain "Berlin" and "Blue Chinese Spring"

F_1 hybrids	No. of plants	Metaphase I chromosome configurations No. of cells							
		20″ +t1″ +t′	20″ +2′ +t′	19″ +4′ +t′	21″	18″ $+1^{IV}$ +2′	20″ +2′	19″ +4′	18″ +6′
CS/*4A*ᵘ DT addition × Blauk. Berlin	4	55	88	7	–	–	–	–	–
Blauk. Berlin × CS *(4B)4A*ᵘ substitution	5	–	–	–	–	7	206	60	7
Blue CS × CS/*4A*ᵘ DT addition	2	3	7	–	–	–	–	–	–
Blue CS × CS *(4B)4A*ᵘ substitution	6	–	–	–	29	–	27	–	–

substitution is homologous to the alien chromosomes in the European Blaukorn strains and the Chinese *(4B)*-*T. urartu* substitution. In fact, the blue aleurone color is known in diploid wheat species having the A genome. By screening small collections of 59 *T. boeoticum*, 62 *T. monococcum*, and 50 *T. urartu* accessions, it was found that 36, 2, and 0% respectively, showed this character. Kuspira et al. (1989) also found blue grain color in several diploid *T. boeoticum* accessions.

Cytological characterization of Blaukorn line Weihenstephan "W 70a86" and its derivative "Blue Chinese Spring"

The Weihenstephan wheat strain Blaukorn 'W 70a86" (W70) exhibits the hairy neck character conferred by rye chromosome *5R*. Earlier investigations on meiotic pairing in hybrids between monosomic lines of Chinese Spring and W70 showed it to be a *(4B)5R* substitution (Zeller and Baier 1973). By applying the C-banding technique to some of these hybrids, in addition to the *4B*, *5R*, and the corresponding monosomic univalents, a bivalent consisting of a normal and a modified chromosome *5D* lacking the major part of the short arm could be identified. Feulgen-stained meiotic chromosome pairing of F_1 hybrids between double ditelosomic (DDT) CS line *5D* and W70 also exhibited a heteromorphic bivalent involving the telosome *5DL*, the translocated alien chromosome, and a *5DS* univalent at a frequency of 92%. Silver staining of the nucleolus organizing regions of W70 and the CS monosomic F_1 hybrid (*5D* missing) between mono-*5D* and W70 confirmed that the satellite region of chromosome *5D* is lacking in Blaukorn W70. In wheat, chromosome arms *1BS 6BS*, and *5DS* are involved in organizing the nucleoli.

In order to probe the partial homology of the alien chromatin in W70 with the chromosome conferring blue aleurone color in the European lines, meiotic pairing in crosses between W70 and *(4B)* "Moskau" was studied. Some cells containing only chromosome *5R* as a univalent were found. This demonstrated partial homology of the European alien chromosome with a W70 chromosome segment.

It is not known whether the missing segment of the alien chromosome conferring blue aleurone color is involved in a translocation with a further wheat chromosome or whether it has been eliminated. Since the involvement of a chromosome segment belonging to homoeologous group 4 in the translocation with *5D* appeared likely, W70 was crossed with CS DDT lines *4A* and *4D*. Whereas hybrids with *4D* predominantly showed t1t‴ trivalent configurations in 23 meiocytes, in the DDT-*4A* crosses 28 cells presented heteromorphic bivalents (t1″) and only three cells had t1t‴ trivalents. Further studies are required to confirm whether or not this indicates the presence of a further alien chromosome segment in chromosome *4A*.

In a backcross program of W70 to disomic Chinese Spring (BC_3 generation), initiated to separate the hairy neck character from the blue grain trait, a blue-grained derivative possessing a smooth peduncle was selected. This line, Blue Chinese Spring ("Blue CS"), turned out to be an alien chromosome substitution. To identify the substituted chromosome of this strain, Chinese Spring DDT-*4A*, *4B*, and -*4D* lines were crossed with strain "Blue CS," and the meiotic chromosome pairing was analyzed. The hybrids with DDT-*4A* and -*4D* showed configurations containing t1t‴ trivalents, which indicate the presence of complete wheat chromosomes *4A* and *4D*, whereas in the crosses with DDT-*4B*, a minimum of two telosomic and one complete univalent was found (Table 1). In the F_1 between "Blue CS" and other *(4B)* European Blaukorn strains, no univalents occurred. However, in hybrids with *(4A)* Blaukorn strains, a minimum of two univalents *(4A+4B)* could be observed. From these results a *(4B)* chromosome substitution in "Blue CS" can be presumed.

In order to study the identity of the alien chromosome in "Blue CS," intercrosses between this line and the different *(4A)* and *(4B)* European blue-grained substitu-

Table 3. Frequency of chromosomal configurations of PMCs at metaphase I in F_1 hybrids between "Blue Chinese Spring" (BCS), several blue-grained (*4A*) strains ("Tschermak" = T, "Berlin" = B, "Weihenstephan" = W, "Probstdorfer" = P), (*4B*) Blaukorn "Brünn" (Br), and (*4B*) Blaukorn "Moskau" (M)

F_1 hybrids	No. of plants	Total cells	Chromosomal configurations No. of cells				
			21″ (rings)	20″ (rings) 1″ rod	20″ (rings) 2′ (*4A*, *4B*)	19″ (rings) 1″ rod 2′ (*4A*, *4B*)	Other configurations
BCS × Br	7	591	8	71	–	–	522
BCS × M	4	120	–	21	–	–	99
BCS × T	3	227	–	–	12	93	122
BCS × B	1	47	–	–	–	3	44
BCS × W	6	233	–	–	5	65	153
BCS × P	4	127	–	–	1	37	89

Table 4. Meiotic pairing (C-banding analysis) of the critical chromosomes in F_1 hybrids between Blaukorn "W 70a86" (W70) and "Blue Chinese Spring" (BCS)

No. of plants	Chromosomal configurations			
	5R′ 1‴ (*5D* BCS/ *5D* Transl. W70/ BCS alien)	*5R*′ 1′ BCS alien 1″ (*5D* Transl. W70/*5D* BSC)	*5R*′ *5D*′ BCS 1″ (*5D* Transl. W70/BCS alien)	*5R*′ *5D*′ 1′ *5D* Transl. W70 1′ BCS alien
5	88	990	541	239

tion lines were made. The data are shown in Table 3.The cytological analysis revealed that in hybrids with the (*4B*) strain Blaukorn "Brünn," the only open bivalents were clearly recognizable as wheat bivalents, and in 1.6% of the cells 21 rings could be observed. Similar results were obtained in the crosses with the (*4A*) substitution lines in which for three different lines, PMCs with 20 closed bivalents plus chromosomes *4A* and *4B* as univalents were detected. This clearly shows complete homology of the alien chromosome from "Blue CS" with those of the blue-grained European strains studied.

By applying the Giemsa C-banding technique, additional cytological studies were carried out on F_1 hybrids of W70 × "Blue CS." From the meiotic pairing analysis (Table 4), partial homology between the alien chromosome in W70 and "Blue CS". From the meiotic pairing analysis (Table 4), partial homology between the alien chromosome in W70 and "Blue CS" became evident. In conclusion, besides the *5R* chromosome, Blaukorn W70 possesses a translocated alien chromosome consisting of a piece of chromosome *5D* and a segment of the alien chromosome conferring blue aleurone.

The origin of "Blue Chinese Spring" remains obscure. Although there is no cytological evidence, it is assumed that the Weihenstephan Blaukorn line W 70a86 used for the backcrossing procedure to Chinese Spring to separate the hairy neck character from the blue grain trait was heterozygous for a complete *4A*/alien chromosome substitution and a *5D*/alien translocation, and homozygous for (*4B*)*5R* chromosome substitution. In the BC_4 progeny, the line possessing the homozygous *4A*/alien chromosome substitution, "Blue Chinese Spring," was selected. Subsequently, this line was crossed with the Chinese/*T. urartu* ditelosomic addition line (2n = 42 + 2t) and substitution line (*4B*)*4A*ᵘ. One PMC (meiotic metaphase I) of the hybrid between "Blue Chinese Spring" and line (*4B*)*4A*ᵘ showed 21 ring bivalents (Fig. 4). This chromosomal behavior and the data in Table 2 confirm the homology of the "Blue CS" and CS(*4B*)*4A*ᵘ alien chromosomes. In conclusion, "Blue CS" and the European Blaukorn strains possess an alien chromosome that is homologous to chromosome 4 from the AA genome of Einkorn wheats. However, this is not present in common tetraploid and hexaploid wheats.

The occurrence of blue-grained tetraploid and hexaploid wheat strains possessing a pair of complete *4A* chromosomes from the AA genome enables geneticists and breeders to use genes located on this chromosome of cultivated *T. monococcum* and wild *T. boeoticum* wheats, as well as of *T. urartu*. Up to now, only a few genes are known on chromosome *4A*: the gene for aleurone color, a gene for insufficient production of gibberellic acid (Jop-

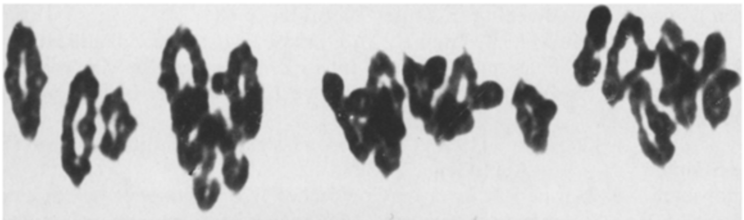

Fig. 4. Feulgen-stained MI PMC of a hybrid between "Blue Chinese Spring" and the substitution line CS (*4B*) *4A*^{u}, showing 21 ring bivalents

pa and Maan 1982), and a gene for leaf pubescence (Maystrenko 1976; Kuspira et al. 1989). It appears likely that new genes for disease resistance, plant height, and other traits located on this chromosome can be found and utilized in durum and common wheat breeding programs.

As a final note, we would like to emphasize that several Blaukorn strains have been attributed to Prof. E. Tschermak. It must be pointed out that G. Kattermann was the first to report such a blue-grained wheat strain. He had sent material from Weihenstephan to Prof. Tschermak in Vienna, Austria (Tschermak-Seysenegg 1936). It is assumed that originally individual wheat lines possessing either blue aleurone color (Kattermann 1932b) or the hairy neck character (Kattermann 1938) existed. Intercrossing of these two lines and subsequent selection of a strain possessing both characters might have given rise to Weihenstephan strain W 70a86.

In addition, it is assumed that the original Blaukorn strain described by Kattermann was a *(4B)4A Triticum aestivum/T. monococcum* or */T. boeoticum* substitution. Already in 1914 Tschermak had reported hybrids between *T. durum* lines and *T. monococcum* showing poor seed set. He did not use the wild diploid *T. boeoticum* at that time. The diploid *T. urartu* was only discovered in Armenia by M. G. Tumanjan in 1938 (Jakubziner 1958). Thus, it is unlikely that a chromosome *4A* from this species is present in the European Blaukorn strains. However, it is possible that later on, by intercrossing with other common wheat strains, a chromosomal shift occurred with wheat chromosome *4A* in the (*4B*) Blaukorn substitutions leading to the (*4A*) Blaukorn strains "Brünn" and "Moskau." A blue-grained (*4D*)-*T. monococcum* substitution has not yet been found.

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