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Linear Differentiation of Cereal Chromosomes

II. Polyploid Wheats

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Summary. The BSG test was used in a comparative study of the linear chromosome differentiation and the idiograms of *T. macha* ssp. *tubalicum* v. 'letschchumicum' Dek. et Men., *T. georgicum* Dek., *T. timopheevi* Zhuk., *T. carthlicum* Nevski, *T. dicoccum* Schrank. v. 'rufum', *T. durum* Desf. v. 'Arnautka' were compiled.

The karyotype of each polyploid wheat species consists of two groups of chromosomes. The first is formed by ten pairs of "constant" chromosomes occurring almost in all species and the second by all the rest of the "variable" chromosomes that are either fully specific for the species in question or occur only in a few species. *T. timopheevi* largely differs from other species of polyploid wheats in the high level and specific localization of structural heterochromatin on chromosomes. The rols of introgression in wheat evolution and the necessity of establishing a General Cytological Nomenclature of Cereal Chromosomes are discussed.

Key words: Heterochromatin - "Constant" and "Variable" Chromosomes - Introgression

Introduction

The differential Giemsa staining technique (Sumner 1972; Vosa 1973) permits identification and structural analysis of individual wheat chromosomes (Zurabishvili et al. 1974; Gill and Kimber 1974b; Iordansky et al. 1977). Therefore it was reasonable to undertake a karyological study of diverse tetraploid and hexaploid wheats in an attempt to obtain new data on their phylogeny and genome composition.

Earlier we studied the linear chromosome differentiation of the supposed ancestors of common wheat.

This paper deals with the analysis of chromosomes of some endemic forms of polyploid wheats of the Caucasus as well as *T. dicoccum* and *T. durum*.

Materials and Methods

The seeds of *T. georgicum* Dek. K-6, *T. timopheevi* Zhuk. K-7 and *T. macha* ssp. *tubalicum* v. 'letschchumicum' Dek. et Men. K-II were obtained from Prof. L.L. Dekaprelevich (the Georgian Agricultural Institute, Tbilisi), *T. carthlicum* Nevski from Prof. P.A. Gandilyan (the Armenian Agricultural Institute, Yerevan); *T. durum* Desf. v. 'Arnautka' and *T. dicoccum* Schrank. v. 'rufum K-38915' from the collection of the N.I. Vavilov Plant Breeding Institute (Leningrad).

The preparations and idiograms were made as previously described (Iordansky et al. 1977). The chromosomes of each species were compared with the karyotype of *T. aestivum* L., var. 'Diamant' used as a standard. Thus, the first two rows of the karyotypes contain chromosomes similar to the corresponding chromosomes of the 'Diamant' variety, whereas the lower rows include specific chromosomes.

Results

T. macha. Each chromosome of this hexaploid species has an individual pattern of structural heterochromatin distribution which, together with the specific linear parameters, permits their reliable identification (Fig. 1 Nine chromosomes (1 to 3, 5, 8 to 12) are similar to the chromosomes of *T. aestivum* L., var. 'Diamant' which suggests their homeology. The same chromosomes as well as chromosome 14 exhibit similarity to those of the 'Chinese Spring' variety. The similarity of the above chromosomes of *T. macha* with *T. aestivum* L. var. 'Diamant' is not always full and in some regions, such as 2q13, 3p22, 8q13, marked structural interspecific differences are observed. Eight (6 to 17 and 19) out of the other 12 chromosomes have a distinctly specific pattern of heterochromatin distribution different from that of the 'Diamant' chromosomes. The amount of heterochromatin in chromosomes 4, 18, 20 and 21 is insignificant, thus although they can be

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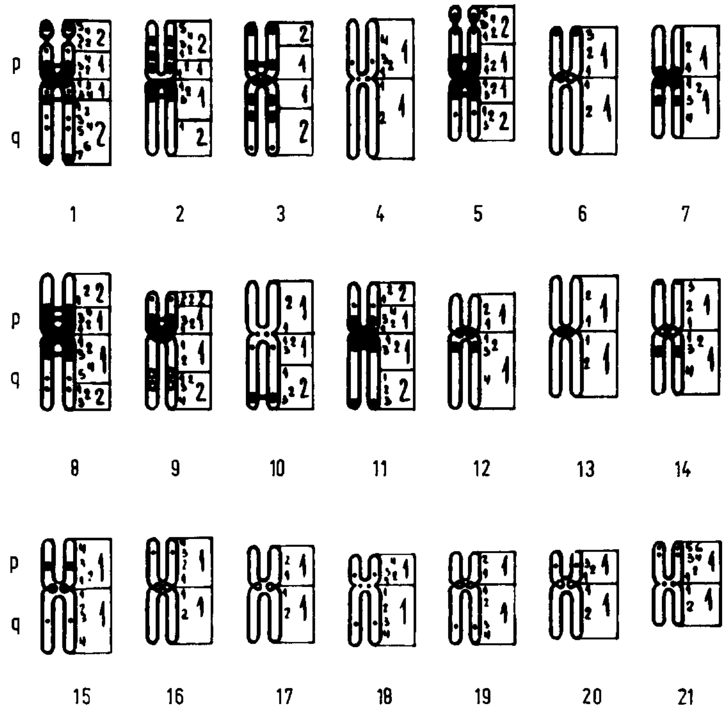
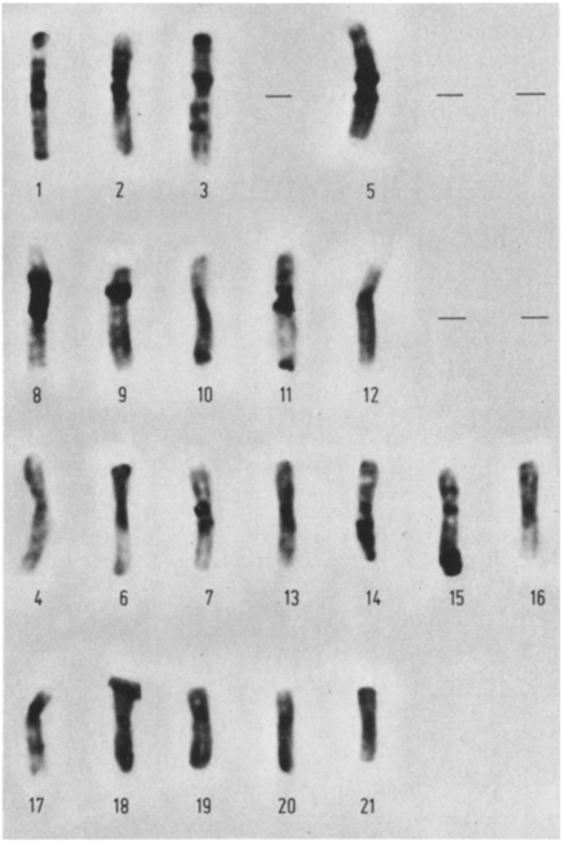
Fig.1.a) Idiogram of the differentially stained chromosomes of *T. macha* b) Differentially stained chromosomes Karyotype of *T. macha*





identified within the *T. macha* karyotype, it is impossible to establish their similarity or dissimilarity with the chromosomes 13 to 19 of the variety 'Diamant' by their comparison. Underscoring the similarity of 10 chromosomes of *T. macha* and 'Chinese Spring' it should be noted that on the whole the latter's chromosomes contain considerably more heterochromatin. The similarity is particularly high in the pattern of heterochromatin distribution of homeologues 1 to 3.

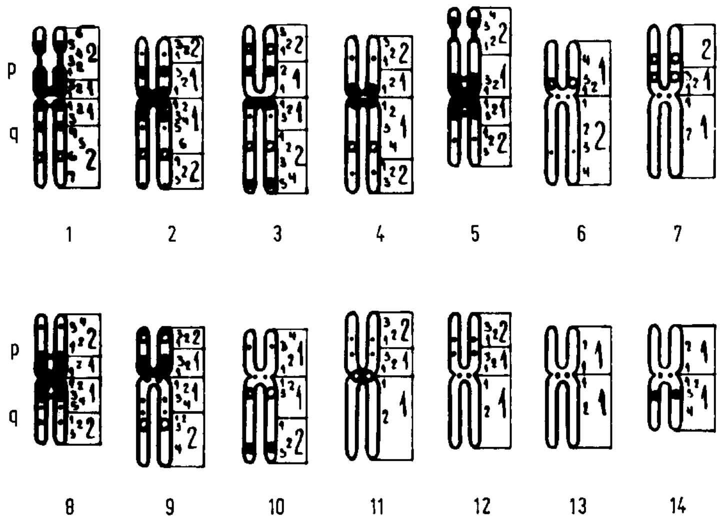
The comparison of the rest of the specific chromosomes of *T. macha* with the chromosomes of 'Chinese Spring' has not revealed any examples of similarity between the pairs.

T. georgicum. The linear differentiation of the seven chromosomes (Fig.2), abundant in heterochromatin (1 to 3, 5, 8 to 10) proved to be rather similar to that of the corresponding chromosomes of *T. aestivum*, var. 'Diamant' (Iordansky et al. 1977). Some differences between the *T. georgicum* and *T. aestivum* homeologues are most obvious when the idiograms are compared; they lie in the regions 1q23, 2p11 and 3q11. Differences between some other regions are less significant and dot not prevent establishing interspecific homeology of the above chromosomes. The other seven chromosomes, of which chromosomes 4 and 14 are distinguished by the densely stained intercalary regions, do not show any noticeable similarity with those of *T. aestivum*, var. 'Diamant'. The comparison with the karyotype of *T. aestivum*, var. 'Chinese Spring' reveals similarity between chromosomes 1 to 3, 5 and 8 to 10, although not so great as with respective chromosomes of the 'Diamant' variety. This can be accounted for by the higher heterochromatin amount in the 'Chinese Spring' karyotype.

Among the chromosomes specific to *T. georgicum*, chromosomes 6 and 14 manifest similarity with respective chromosomes of 'Chinese Spring'.

A number of *T. georgicum* chromosomes are also similar to those of *T. macha*, in the first place, the above seven chromosomes (1 to 3, 5, 8 to 10) are similar to those of *T. aestivum* and chromosome 14 is morphologically similar to chromosome 14 of *T. macha*.

Fig.2.a) Idiogram of the differentially stained chromosomes of *T. georgicum* b) Differentially stained chromosomes
Karyotype of *T. georgicum*



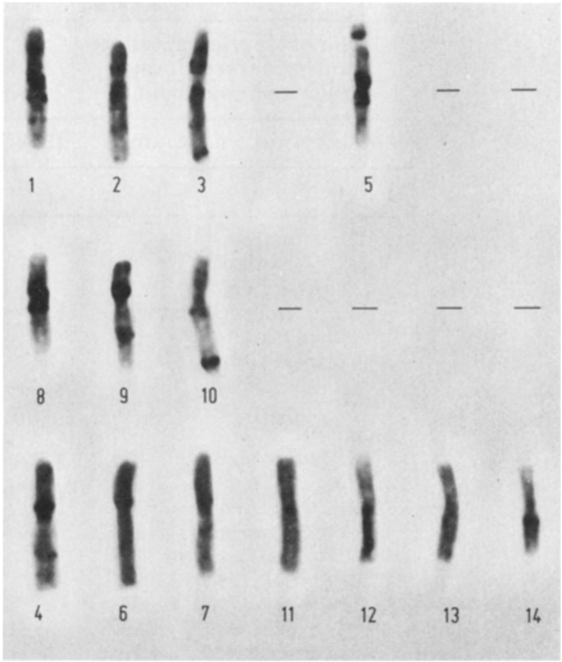
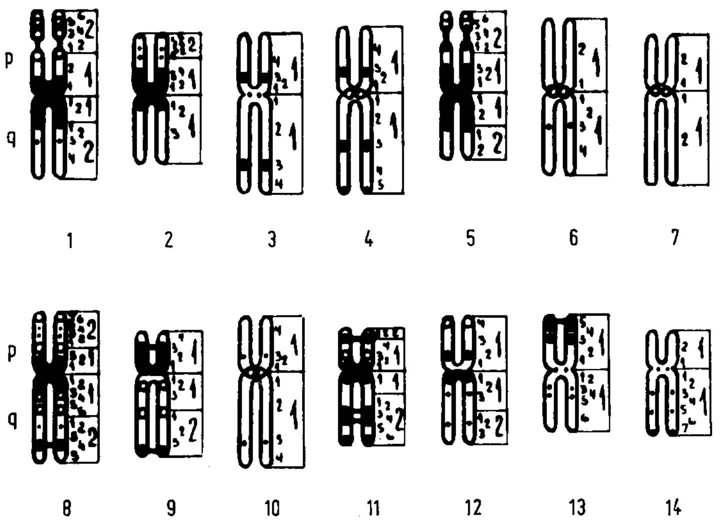
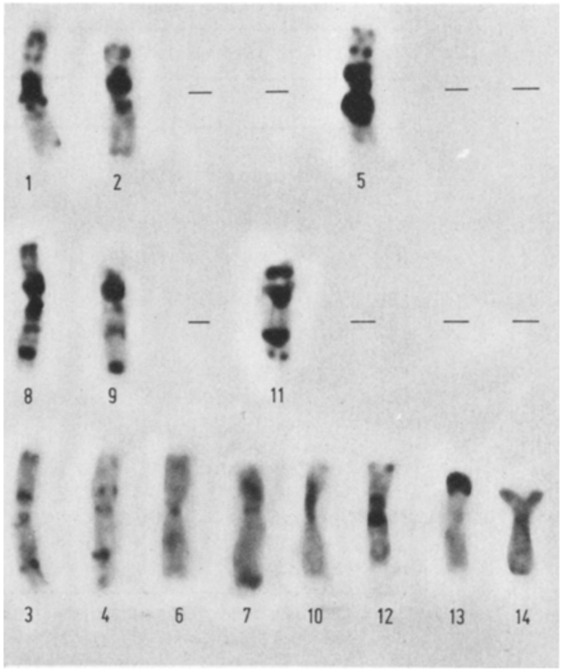


Fig.3.a) Idiogram of the differentially stained chromosomes of *T. timopheevi* b) Differentially stained chromosomes
Karyotype of *T. timopheevi*





Homeology between chromosomes 7, 11 and 12 of *T. georgicum* and 4, 13 and 16 of *T. macha*, respectively, is not ruled out.

T. timopheevi. The differential stain of the karyotype differs noticeably from that of the endemic species described above and from *T. aestivum*, var. 'Diamant' in very large blocks of heterochromatin occurring in several chromosomes and having different localization compared with known wheat chromosomes (Fig.3). As a result, it is more difficult to establish the homeology but easier to identify chromosomes within the karyotype.

Table 1. Comparison of chromosome types in the species and varieties studied

1	General cytological nomenclature of cereal chromosomes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2	Genetic nomenclature	1B	2B			6B			4A	5B	6A		3B*									
3	Species	*T. aestivum* v. 'Diamant'																				
4	*T. aestivum* v. 'Diamant'	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
5	*T. aestivum* v. 'Chinese Spring'	1	2	3		5			8	9	10	11	12									
6	*T. macha*	1	2	3		5			8	9	10	11	12									
7	*T. georgicum*	1	2	3		5			8	9	10											
8	*T. timopheevi*	1	2	3		5			8	9		11										
9	*T. dicoccum*	1	2	3		5			8	9	10	11	12									
10	*T. durum*	1	2	3		5			8	9	10	11	12									
11	*T. carthlicum*	1	2	3		5			8	9	10	11	12									
12	*Ae. speltoides*																					
13	*Ae. squarrosa*																					
14	*Secale cereale* v. 'Zhitkinskaya'																					
15	*Triticale* 'F-1239'	1	2	3		5				9	10	11	12									
16	*Triticale* 'AD 196'		2			5			8	9	10	11	12									
17	*T. aestivum* 'Aurora'		2	3		5			8	9	10	11	12	13				17				21

1	General cytological nomenclature of cereal chromosomes	50		51	52	53	54	55	56	57	58				59	60	61	62	63	64	65	66
2	Genetic nomenclature																					
3	Species	*T. timopheevi*						*T. dicoccum*				*T. durum*			*Ae. speltoides*							
4	*T. aestivum* v. 'Diamant'	4	6	7	10	12	14	4	6	7	13	4	6	13	1	2	3	4	5	6	7	2
5	*T. aestivum* v. 'Chinese Spring'																					
6	*T. macha*																					
7	*T. georgicum*																					
8	*T. timopheevi*																					
9	*T. dicoccum*																					
10	*T. durum*									7												
11	*T. carthlicum*									7												
12	*Ae. speltoides*																					
13	*Ae. squarrosa*																					
14	*Secale cereale* v. 'Zhitkinskaya'																					
15	*Triticale* 'F-1239'									8*												
16	*Triticale* 'AD 196'									3												
17	*T. aestivum* v. 'Aurora'																					

The chromosomes of each species are compared in succession with the chromosomes of all previous
ple, out of 14 pairs of *T. georgicum*, chromosomes 7 (1,2,3,5,8,9 and 10) are similar to the cor-
14 of the 'Chinese Spring' variety. Among the remaining 5 chromosomes one (4) is similar to chro-
and 13) do not show similarity with either chromosome of the species studied. The horizontal line I
Kimber, 1974a,b). The vertical lines contain numbers of morphologically similar chromosomes.
cal Nomenclature of Cereal Chromosomes (I horizontal line).
* - the similarity of this chromosome with the corresponding chromosome in the 4th horizontal line

Nevertheless, we may speak, with some probability, about the homeology between six chromosomes of *T. timopheevi* (1,2,5,8,9,11) and those of *T. aestivum*, var. 'Diamant', the probability being the highest with respect to chromosome 5.

The other nine *T. timopheevi* chromosomes are unique if compared to the 'Diamant' karyotype. The similarity pattern of the first six chromosomes with

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45		46	47	48	49
			7D	1D*			4B*			4D*																		
T. aestivum v. 'Chinese Spring'												*T. macha*											*T. georgicum*					
4	6	7	13	14	15	16	17	18	19	20	21	4	6	7	13	15	16	17	18	19	20	21	4	6	7	11	12	13
				14																								
	6*			14																								
					13										6*								3					
				14																								
				14					13*					4*														
	6*			14					13*					4											6*			
	1			7*			3*									4												
				14												6												
		7*							14*							1							6					
							19*			18*						4												

	67	68		69	70	71	72	73	74	75	76	77		78	79	80				81	82	83	84	85	86	87	88	89	90	91	92
				1R	2R*	3R	4R	5R	6R	7R																					
Ae. squarrosa				*S. cereale*							'F-1239'					'AD-196'						*T. aestivum* v. 'Aurora'									
3	5	6	7	I	II	III	IV	V	VI	VII	4	7	8	13	11	4	7	13	14	15	III	1	6	7	13	14	15	16	18	19	20
				I		III	IV	V	VI	VII																					
				I	II		IV	V	VI			13*																			

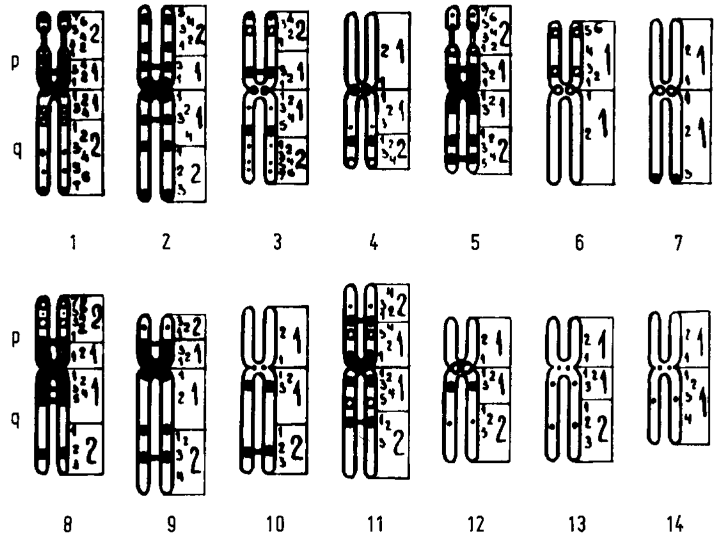
species. In the horizontal line 4 only those chromosomes are marked that were not detected earlier. For exam-
responding ones in the 'Diamant' variety of common wheat and 2 (6 and 14) are similar to chromosomes 6 and
mosome 3 of *T. timopheevi* and the other (7) to chromosome 6 of *T. dicoccum*. Three chromosomes (11, 12
is an entire enumeration of original chromosomes of all species. Line 2 is a genetic nomenclature (Gill and
The chromosomes whose morphological specificity gives rise to doubt are not included in the General Cytologi-

gives rise to doubt.

those of 'Chinese Spring' is nearly the same as with 'Diamant'; among the specific chromosomes of *T. timopheevi* only chromosome 13 shows similarity with chromosome 16 of 'Chinese Spring'.

Chromosomes 3, 4, 7, 10, 12 to 14 of *T. timopheevi* exhibit no similarity with those of *T. macha*. One can suppose with some certainty the homeology between chromosome 6 of *T. timopheevi* and chromosome 13

Fig.4.a) Idiogram of the differentially stained chromosomes of *T. dicoccum* b) Differentially stained chromosomes
Karyotype of *T. dicoccum*



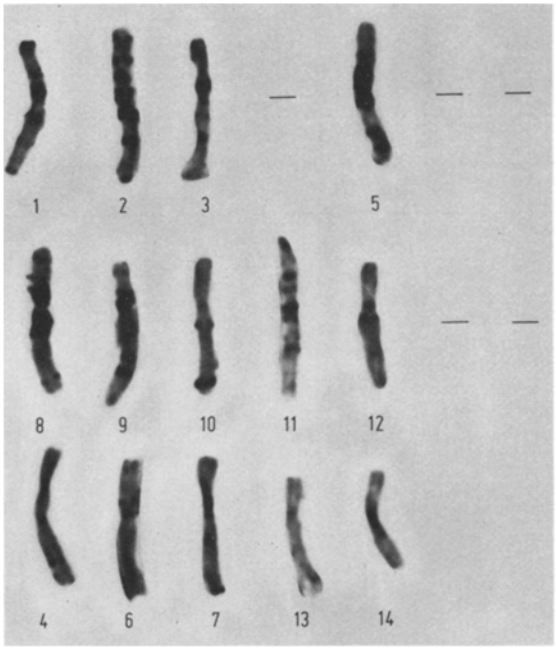
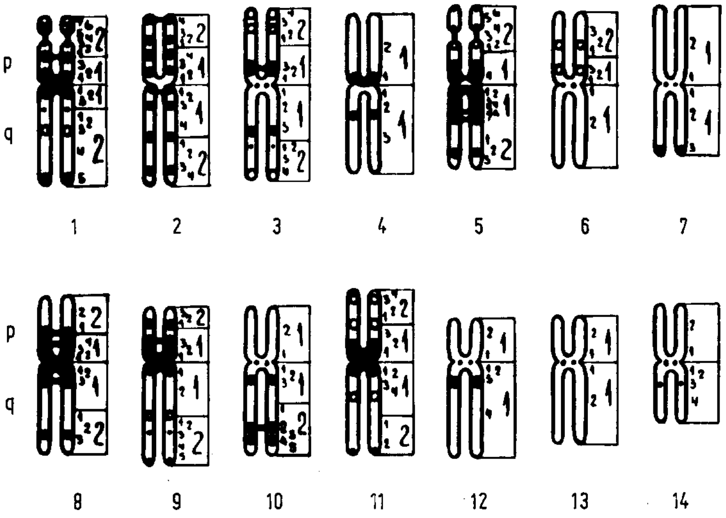
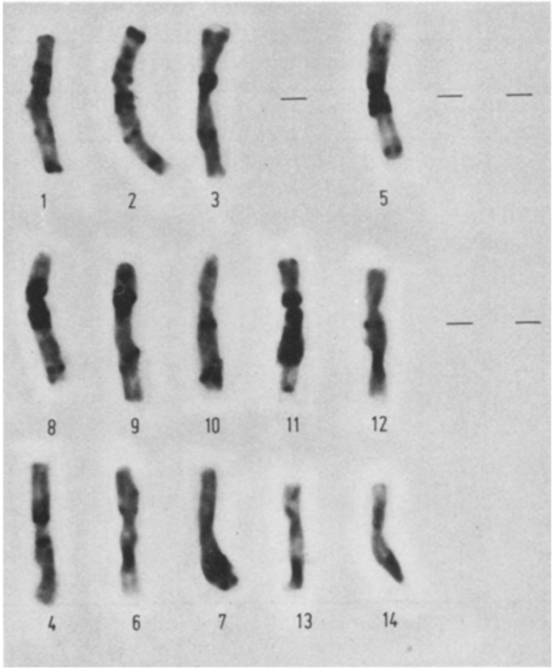


Fig.5.a) Idiogram of the differentially stained chromosomes of *T. carthlicum* b) Differentially stained chromosomes
Karyotype of *T. carthlicum*



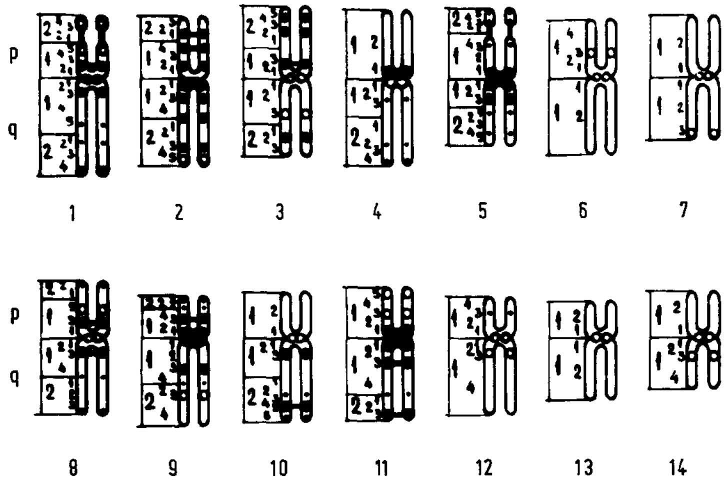


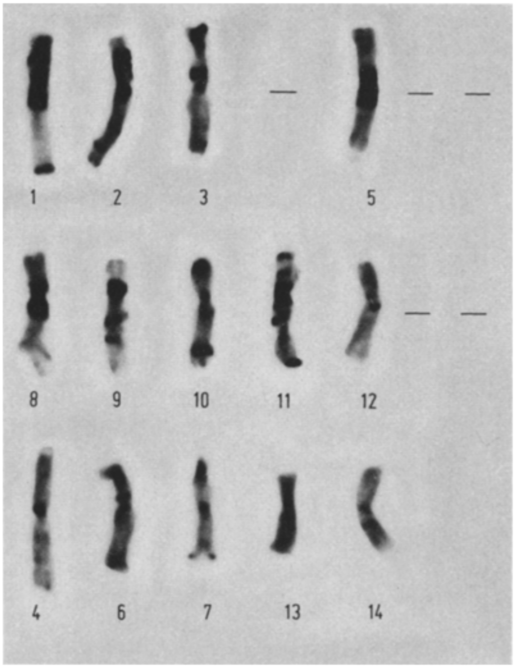
of *T. macha*. The similarity of *T. timopheevi* chromosomes with those of other species are shown in Table 1.

T. dicoccum. In terms of total heterochromatin the chromosomes of this species lie half way between *T. timopheevi* and *T. aestivum* of the 'Chinese Spring' variety (Fig.4). Nine chromosome pairs (1 to 3, 5, 8 to 12) are similar to those of the 'Diamant' variety. Chromosome 14 is similar to that of 'Chinese Spring' and *T. georgicum*, and only four chromosomes (4,6, 7,13) proved to be unique in *T. dicoccum*. Other cases of interspecific similarity are shown in Table 1.

T. carthlicum and *T. durum*. The karyotypic similarity of these species is so high that their chromosomes can be rightfully analysed together (Figs.5,6).

Fig.6.a) Idiogram of the differentially stained chromosomes of *T. durum* b) Differentially stained chromosomes Karyotype of *T. durum*





Few noticeable differences are observed in the regions 1q13, 2p24, 4q12, 5q77, 8q22 and 9p22 and also in chromosome 6.

Nine chromosomes of these species (1 to 3, 5, 8 to 12) show certain similarities with those of *T. aestivum*, var. 'Diamant' and 'Chinese Spring' and two *T. durum* chromosomes (6,14) are similar to the respective chromosomes of 'Chinese Spring'. Chromosome 6 of *T. carthlicum* is similar to that of *T. georgicum*. Chromosome 7 of these species is similar to that of *T. dicoccum*. Thus compared with the karyotypes of the other species studied, *T. carthlicum* and *T. durum* contain only two (4 and 13) unique chromosomes.

Interphase nuclei. The structure of the interphase nuclei in the BSG stained preparations reflects clearly the differences between wheat varieties in the heterochromatin content in the chromosomes (Fig.7). Thus in *T. timopheevi*, particularly rich in heterochromatin, the nuclei differ greatly from those of *T. macha*, *T. georgicum*, *T. carthlicum* and *T. durum* in the large number of big, densely stained chromocentres; in the size of the chromocentres, *T. dicoccum* nuclei occupy an intermediate position between those of *T. timopheevi* and the latter four species.

Discussion

With the material analysed a complete karyological picture of the genus *Triticum* cannot be built up. This would require knowledge of the linear differentiation of chromosomes not only of many species but also of a great number of varieties and forms which might be expected to have a wide diversity of structurally unique chromosomes and variants of known chromosomes. Without this we cannot reconstruct the general scheme of the phylogenetic relationships between *Triticum* species, although the methods of analysis of linear chromosome differentiation in themselves are highly promising.

At the same time the results of studies of the differentially stained karyotypes of 11 species and varieties of *Triticum* and *Aegilops* (together with those published earlier-Iordansky et al. 1977) indicate some specific features of the evolution of polyploid wheat chromosomes.

First of all, there is no morphological similarity between the chromosomes of the supposed diploid ancestors of wheats (*T. monococcum*, *Ae. speltoides*, *Ae. squarrosa*) and of the polyploid species studied. As seen from the comparison of the karyotypes, the chro-

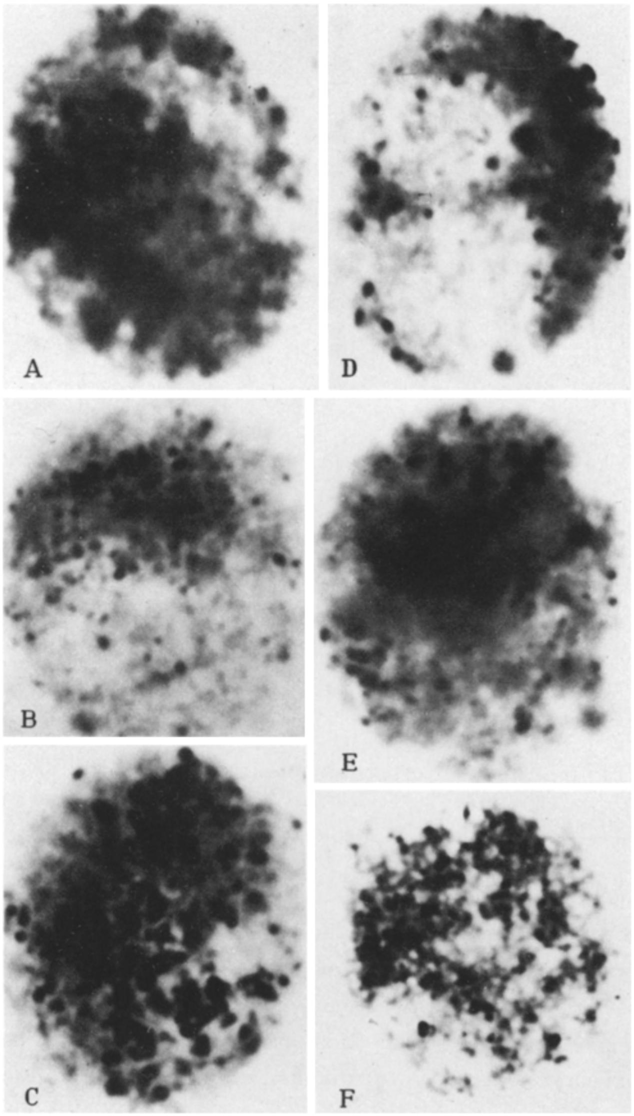


Fig.7. Differentially stained interphase nuclei
A - *T. macha;* B - *T. georgicum;* C - *T. timopheevi;* D - *T. dicoccum;* E - *T. carthlicum;* F - *T. durum*

mosomes of polyploid species, poor in heterochromatin, may tentatively be ascribed to A genome and the rest to B and D genomes proceeding from general consideration (without identification and karyotyping) of the differentially stained metaphase plates (Natarajan and Sarma 1974). Only four chromosomes of *Ae. squarrosa* are the exception; three of these exhibit similarity with *T. aestivum*, var. 'Chinese Spring' and one with *T. macha* (Table 1).

This marked difference between diploids and polyploids may be due to both divergence in the chromosome structure (Kostov 1940) and introgression (Iordansky et al. 1977). The fact that many forms within each diploid species of *Triticum* and *Aegilops* have not beeen analysed yet may also be relevant.

Another specific feature of polyploid wheat karyotypes studied is differing heterochromatin content. It is highest in *T. timopheevi* and *T. aestivum*, var. 'Chinese Spring' and somewhat lower in *T. dicoccum*.

In *T. timopheevi* the chromosomes rich in heterochromatin (1,2,5,8,9,11 and 13) have a specific unique distribution of densely stained regions so it is rather difficult to establish their morphologic homeology, the karyotype as a whole being quite original. Since chromosomes of *T. monococcum* (A genome) are poor in heterochromatin, they may be supposed to belong to the second genome whose distinction from the B genome of a majority of other polyploid wheats has been reported by many authors (Lilienfeld and Kihara 1934; Svetozarova 1939; Kostov 1940; Sachs 1953). Our preliminary data are indicative of considerable similarity of the *T. timopheevi* karyotype only with that of *T. araraticum*, which is borne out by earlier studies (Svetozarova 1939; Menabde and Yeritsyan 1942; Mac Key 1966).

In view of the unique structure of *T. timopheevi* chromosomes, we support the opinion that this species had its individual genesis and formed a secondary branch of wheat evolution not involved in the development of common wheat (Zhukovsky 1964; Dekaprelevich 1971). At the same time, the concept of the autopolyploid origin of *T. timopheevi* from *T. monococcum* seems unrealistic (Tumanyan 1939). Sears (1975) is presumably right to suggest that the weak synapsis in *T. timopheevi* and *T. aestivum* chromosomes can be due to their structural differences and not to the presence in the former of genes favouring asynapsis, as was supposed by Wagenaar (1966).

It can also be remembered that, according to Kostov (1940) and Love (1941), A genome of *T. timopheevi* differs from that of contemporary *T. monococcum* and polyploid wheats. A comparison of the differentially stained karyotypes supports this viewpoint.

The sharp difference between the chromosomes of *T. aestivum*, var. 'Chinese Spring' and 'Diamant' and 'Aurora' (Iordansky et al. 1977) may be interpreted in terms of the concept of N.I. Vavilov (1958) according to which the Chinese varieties of common wheat may be regarded, in view of their morpho-physiological peculiarities, as a subspecies of *T. aestivum*. Conceivably, the Chinese varieties branched off from the European group very long ago and better conserved the chromosomes of diploid ancestors in thier karyotype, which accounts for the similarity of the three chromosomes of *Ae. squarrosa* and 'Chinese Spring'.

We find it difficult to explain the presence of a large amount of constitutive heterochromatin in the *T. dicoccum* genome. Mac Key (1968) is included to consider *T. dicoccum* as an ancestor of all other cultivated emmers (Mac Key 1968), of which we have studied only three. If he is right then it should be expected that at least some chromosomes of *T. georgicum*, *T. carthlicum* or *T. durum* would be similar to those of *T. dicoccum* in the total high amount of heterochromatin. Yet this is not the case, the only similarity being manifested by several chromosomes is in the localization of the densely stained regions. Taking into account only the total heterochromatin content, it seems that *T. dicoccum* is more closely related to *T. timopheevi* than to the above species. Unfortunately, the general laws of heterochromatin evolution and its adaptive role remain largely unexplored (Chuksanova 1971) and cannot help in this study.

A third specific feature of the evolution of wheat karyotypes studied is revealed by the general comparison of the chromosome structure (Table 1). It turned out that the karyotype of each polyploid wheat species and variety consists of two rather clearcut groups of chromosomes.

The first one includes ten chromosomes common to almost all polyploid species. In spite of some structural differences their morphological homology is still undoubted. The second one covers all remaining chromosomes that are either fully specific to a species or variety or occur in few species. We shall call the chromosomes of the first group "constant" and the chromosomes of the second one "variable."

This specific feature of polyploid wheat karyotypes dictates the necessity of constructing the General Cytological Nomenclature of Cereal Chromosomes (GC NCC) to cover all identified chromosomes of original structure in wheats and other cereals crossed with them, no matter what species or variety they were first found in.

Such a nomenclature is exemplified in the first horizontal line of Table 1 containing as many as 75 chromosomes, against 21 in Sears' genetic nomenclature (1954). It is also seen from Table 1, that, accoring to GCNCC, chromosomes 1, 2, 3, 5, 8, 9, 10, 11, 12 and 26 may be classed as "constant".

Despite the work of Gill and Kimber (1974b), the relationship between the genetic nomenclature and GCNCC is far from being clear yet. In the coming years a much wider scope of investigations of differential staining may be expected, and an increase of the number of structurally original chromosomes of wheats and related cereals up to 300 to 500 will ensue. Of particular interest will be the investigations of monosomics of common wheat varieties, for they will allow identification of structural variants of each of the 21 genetically original chromosomes and will possibly open the way for subdividing all "variable" chromosomes into eleven groups, genetically homeologic but morphologically different.

Apparently, homeology between chromosomes within each haploid genome and between chromosomes of different genomes of polyploid species has provided for considerable interspecific chromosome substitution in the course of continuous introgression in *Triticum* and *Aegilops*. Chromosome dilution of genomes occurs at all levels of ploidy but is most intensive in cultivated polyploid forms. Karyotype divergence of diploid and polyploid species caused by introgression has been so extensive that a search for wild diploid ancestors of contemporary wheats in the existing flora would be quite hopeless. At a polyploid level the divergence has not been so crucial. Ten "constant" chromosomes of most polyploid species are, evidently, of the same origin, belonging to the polyploid wheat prekaryotype, and six "constant" chromosomes of *T. timopheevi* (and *T. araraticum?*) have retained the features of another ancient prekaryotype related but not identical to the first one. Currently, on the basis of chromosome analysis, we can accept as a rough scheme a biphyletic origin of tetraploid wheats, which, in general terms, is consistent with the ideas of Mac Key (1966, 1968).

Unlike the "constant", the "variable" chromosomes reflect unknown stages of the introgressive karyotype evolution of wheat species and varieties and in the future they may give the key to understanding their phylogeny. It is noteworthy that there is almost full similarity of "variable" chromosomes in *T. carthlicum* and *T. durum* karyotypes which may be only due to the common origin.

It may be anticipated that wider investigations into linear differentiation of cereal chromosomes and the construction of their standard nomenclature will enhance considerably our knowledge of the phylogeny of wheats and other cultivated plants.

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