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# Analysis of phylogenetic relations of durum, carthlicum and common wheats by means of comparison of alleles of gliadin-coding loci

**E. V. Metakovsky, A. M. Kudryavtsev, Z. A. Iakobashvili and A. Yu. Novoselskaya**

N.I. Vavilov Institute of General Genetics, Moscow, B-333, USSR

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**Summary.** Polymorphism and inheritance of wheat storage protein, gliadin, of *durum* (macaroni) and *carthlicum* wheats have been studied. Analysis of gliadin in 78 cultivars and in $F_2$ seeds of intercultivar crosses of *durum* wheat revealed three different chromosome 1A-encoded blocks of components similar to those found in common wheat (GLD1A2, GLD1A18, GLD1A19). Most of the *durum* cultivars studied had these three blocks; GLD1A2 was also frequent in common wheat. In contrast, all chromosome 1B-encoded blocks of *durum* clearly differed in component composition from those found in common wheat. Therefore, *durum* could not be an ancestor or a derivate of recent bread wheat. Analysis of gliadin in the collection of *carthlicum* wheat (14 accessions) revealed several suspected chromosome 1A, 1B, and 6A-controlled blocks, some of which were similar to those in common wheat, while others were different. Therefore, *carthlicum* is likely to be an ancestor or a derivate of some forms of bread wheat. There were also chromosome 1A and 6A-, but not 1B-encoded blocks which were identical in *durum* and *carthlicum* wheats. The results confirm that all three wheats share the same genome A, but emphasize the heterogeneity of genotypes among donors of this genome. Discovery of identical blocks in tetraploids and hexaploids indicates polyphyletic [from different genotypes of donor (s)] origin of these wheats.

**Key words:** Wheat relations – Gliadin alleles – *Durum* – *Carthlicum* – *T. aestivum*

## Introduction

Several approaches in investigating the origin and relationship of wheat species are used (see Kerby and Kuspira 1987 for review). Electrophoretic similarity of proteins is believed to be a sufficiently direct measure of gene homology and species affinity. "Biochemical" approach to electrophoretic spectra (i.e., comparison of patterns and relative electrophoretic mobility (REM) of individual bands) of several comparatively low-variable proteins made it possible to discuss relations of some species and to suggest certain accessions of common wheat (Johnson 1972; Jaaska 1978; Konarev et al. 1979; Nishikawa et al. 1980). However, some bands in spectra may consist of several different proteins, and even for homogeneous bands, similarity of REM cannot serve as a reliable indication of protein identity (homology) (Lagudah and Halloran 1988). Intraspecific genetic variability is very informative for the analysis of phylogenetic relationships (Lewontin 1967). We suggest that "genetical" approach, including comparison of sets of alleles of polymorphic protein-coding loci, is more suitable in establishing the kinship of wheats than analysis of electrophoretic spectra in terms of similarity-difference of REM of single components.

Gliadin is a highly heterogeneous protein: more than 30 bands are revealed by one-dimensional electrophoresis in a single seed of hexaploid wheat. Gliadin biosynthesis in common wheat (Shepherd 1968) and *durum* wheat (du Cros et al. 1983) is controlled by chromosomes of the first and sixth homeological groups. There is vast multiple allelism for gliadin-coding loci of common wheat (Sozinov and Poperelya 1979). Different alleles display themselves as groups (blocks) of electrophoretic components (few blocks are represented by a single component) in gliadin spectra. A catalogue of allelic variants of blocks of common wheat includes more than 10 (up to 25) blocks for each of the six gliadin-coding loci (Metakovsky et al. 1984a, unpublished results). Allelic variants of blocks controlled by the same locus differ in number,

charge, and molecular weight of protein components (Metakovsky et al. 1984b). Obviously, independent origin (through mutations) of two blocks with identical or similar component composition is improbable. Therefore, sharing of gliadin alleles by the species should unambiguously indicate their close affinity.

It has been shown, mainly by analysis of chromosome behaviour in hybrids, that *durum, carthlicum* and bread wheats have genomes A and B in common and, therefore, they are close relatives (Kihara 1954; Riley 1965). Moreover, monophyletic origin of tetraploid and hexaploid wheats with following divergence was suggested (Riley 1965; Sachs 1953). In the present work, we compared alleles of gliadin-coding loci of *T. durum* cultivars and *T. carthlicum* varieties with those found earlier in common wheat *T. aestivum*.

## Materials and methods

Original and collection seeds of 78 spring cultivars of *T. turgidum*, conv. *durum* (Desf) Mac Key were obtained from different sources, mostly from the N.I. Vavilov Institute of Plant Breeding, Leningrad. Four main varieties (14 accessions) of *T. turgidum* ssp *carthlicum* (Nevski) Mac Key which represent the collection of this wheat of the Agricultural Institute of Georgia, Tbilisi, have been studied. Varieties are: *rubiginosum* (4 accessions), *stramineum* (4), *fuliginosum* (3), and *dekaprelevichi* (3). Substitution lines of the cultivar Langdon were kindly provided by Dr. L. R. Joppa (USA).

Gliadins of 15–100 single seeds of each *durum* cultivar and 30 spikes (1–3 single seeds per spike) plus up to 100 single seeds of each *carthlicum* accession were analysed as described (Metakovsky et al. 1984a). All comparisons of spectra were performed in adjacent slots of one slab in repeated runs.

## Results

### *Genome A-encoded blocks in durum*

There are at least three chromosome 1A-controlled bands (one major component in $\gamma$-region and at least two minors in $\omega$-region) in the gliadin spectrum of Langdon obtained by our electrophoretic procedure (Fig. 1). The same three bands are present in several other *durums* studied, e.g., in Wells (Fig. 2, slots 8, 9). In the intercultivar cross Wells × Shark, these components inherited as a block: they are always either present or absent together in the spectra of $F_2$ seeds. Usual 3:1 (presence/absence) segregation was obtained (35:12; $\chi^2=0.01$; $p>0.9$). It was found earlier (unpublished results) that GLD 1A19 block of bread wheat (e.g., cultivar Ranniaya 73) has the same component composition (Fig. 2, slots 7, 8). We should note that GLD 1A19 block may include more minor components in *durum* as well as in bread wheat, some of them being located in the $\beta$-region of the spectrum. However, the analysis of inheritance of these bands with the help of one-dimensional electrophoresis is very uncertain, because this region is packed with many components controlled by different chromosoms (Metakovsky et al. 1984a, b).

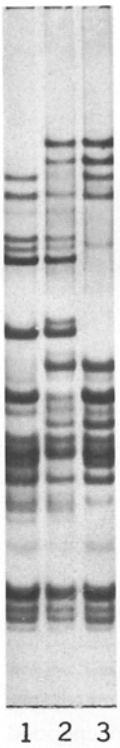


**Fig. 1.** Gliadin electrophoregrams of *durum* wheat cultivar Langdon *1* and its 1D (1A) *2* and 1D (1B) *3* disomic-substitution lines

Chromosome 1A-controlled block in bread wheat cultivar Bezostaya 1 was determined earlier (Akhmedov and Metakovsky 1987). In $F_2$ seeds of the cross Bezostaya 1 × Odesskaya 16, four patterns (Fig. 3, slots 2–5) of 1A-controlled components were found (two of them differ in intensity of bands only, according to gene doses in triploid endosperm) segregating in a 1:2:1 ratio (15:48:21; $\chi^2=2.46$, $p>0.25$). The allelic variant of chromosome 1A-controlled block discovered in winter bread wheat Odesskaya 16 (GLD 1A2) consists of one fast-moving $\gamma$-gliadin and two minors in $\omega$-region (Figs. 3 and 4). This block is present in many other unrelated cultivars of winter and spring bread wheat (E. V. Metakovsky, unpublished results). Thirty-three of all *durum* cultivars studied, including Orenburgskaya Ranniaya, have the same three distinctive components (Fig. 4, slots 2, 3, 4). These three bands in $F_2$ seeds of Orenburgskaya Ranniaya × Melanopus 7 intercultivar cross are again either present or absent together, i.e., they behave as a single character (block) in *durum* wheat also. There are four types of gliadin patterns in 112 $F_2$ seeds: first, GLD 1A2-like block is present (31 seeds,

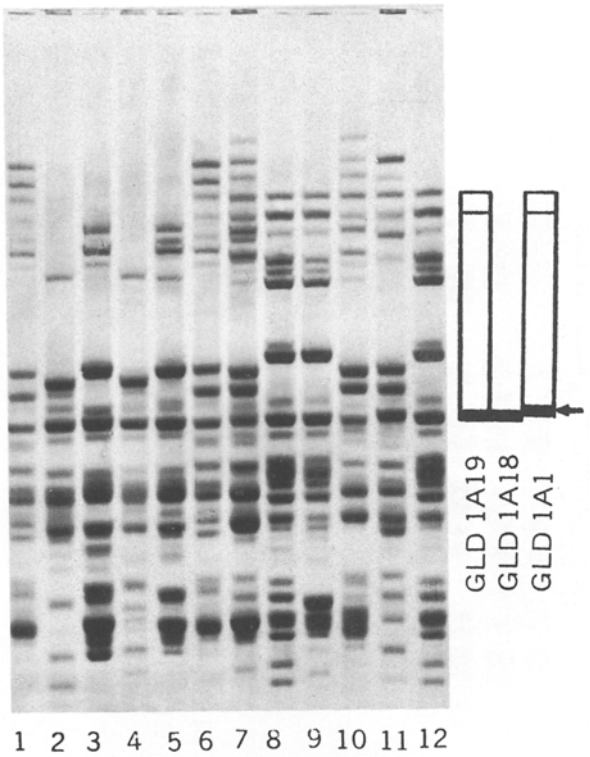


**Fig. 2.** Gliadin spectra of different wheats: *1, 6* – Kzyl Bas (*vulgare*); *2* – Melanopus 1932 (*durum*); *3* – var. fuliginosum (*carthlicum*); *4* – Melanopus 7 (*durum*); *5* – var. dekaprelevichi (*carthlicum*); *7, 10* – Ranniaya 73 (*vulgare*); *8, 12* – Wells (*durum*); *9* – Langdon (*durum*); *11* – Marquis (*vulgare*). Chromosome 1A-controlled variants of blocks are shown. Band $\gamma 50$ is marked by *arrow*. Note: two $\omega$-minors of GLD 1A19 are absent in cultivar Kzyl Bas. Actually, there are two other $\omega$-minors in this cultivar with electrophoretic mobility nearly identical to those in GLD 1A19. One of them (slow) is chromosome 1D-controlled, another (fast) is chromosome 1B-controlled

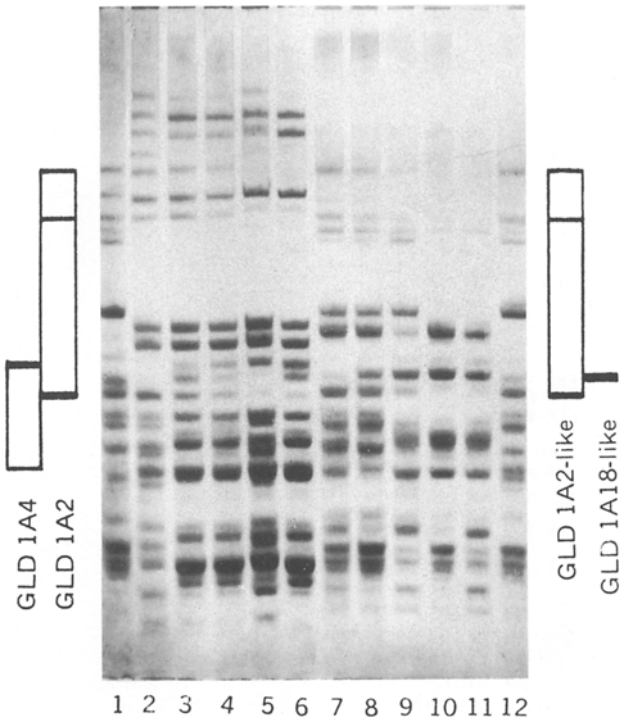


**Fig. 3.** Comparison of blocks controlled by chromosome 1A in some cultivars and in $F_2$ seeds: *1* – Kharkovskaya 7 (*durum*); *2* – Odesskaya 16 (*vulgare*); *3–5* – $F_2$ seeds of cross Bezostaya 1 × Odesskaya 16; *6* – Bezostaya 1 (*vulgare*); *7–10* – $F_2$ seeds of cross Orenburgskaya Ranniaya × Melanopus 7; *11* – Melanopus 7 (*durum*); *12* – Orenburgskaya Ranniaya (*durum*). Chromosome 1A-controlled blocks are shown. Note: in bread wheat, $\gamma$-gliadin of GLD 1A2 block overlaps with chromosome 1D-controlled minor

Fig. 3, slot 7); second, this block is absent, but a characteristic major component (from Melanopus) in the $\gamma$-region is present (25 seeds, slot 10); third and fourth, both this component and GLD 1A2-like block are present, but differ in intensity (25 and 31 seeds, slots 8 and 9, respectively). Segregation corresponds to a 1:1:1:1 ratio ($\chi^2 = 1.29$; $p > 0.5$) and undoubtedly indicates that GLD 1A2-like block of Orenburgskaya and the component of Melanopus are controlled by allelic variants of the same gliadin-coding locus. Melanopus 7′ component is identical to the major band of GLD 1A19 block (Fig. 2, slots, 4, 7). Thirty-one of all *durums* studied had this very characteristic component in $\gamma$-region. It was proved (Koval and Metakovsky 1985) that GLD 1A18 block of bread wheat consists only of one (the same) component (Fig. 2, slots 4, 6). Therefore, both allelic variants of blocks of *durum* discussed above are identical to those controlled by chromosome 1A of bread wheat. In addition, in the same cross of *durums*, the pair of blocks segregate independently of allelic components $\gamma 42$ and $\gamma 45$ ($\chi^2 = 8.82$ for ratio 1:2:1:2:4:2:1:2:1, $p > 0.2$) controlled by chromosome 1B (Joppa et al. 1982; du Cros et al. 1983). This confirms the assumed control of GLD 1A2-like and GLD 1A18-like blocks in *durum* by gliadin-coding locus of chromosome 1A.

Analysis of an intercultivar cross, Bezenchukskaya 105 × Kharkovskaya 7, confirmed joint inheritance of GLD 1A2-like components of Kharkovskaya 7, which is unrelated to cultivar Orenburgskaya (Fig. 4, slots 3, 4), and 3:1 segregation (presence/absence of the block) in $F_2$ seeds (52:19, $\chi^2 = 0.12$; $p > 0.5$). Cultivar Bezenchukskaya 105 (as well as cultivar Shark in combination Wells × Shark) was shown to have chromosome 1A-controlled block which is not found in common wheat (data not shown).

We have found earlier that $\alpha$-gliadins in many *durum* cultivars are similar or identical to some chromosome 6A-controlled blocks of common wheat and represent a

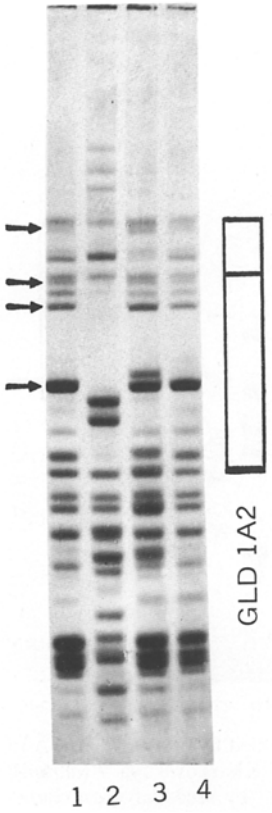


**Fig. 4.** Block GLD 1A2 in durum and bread wheat: *3* – Orenburgskaya Ranniaya (*durum*); *1, 4* – Kharkovskaya 7 (*durum*); *2* – Odesskaya 16 (*vulgare*). Block GLD 1A2 is shown. Chromosome 1B-encoded bands are marked by *arrows*

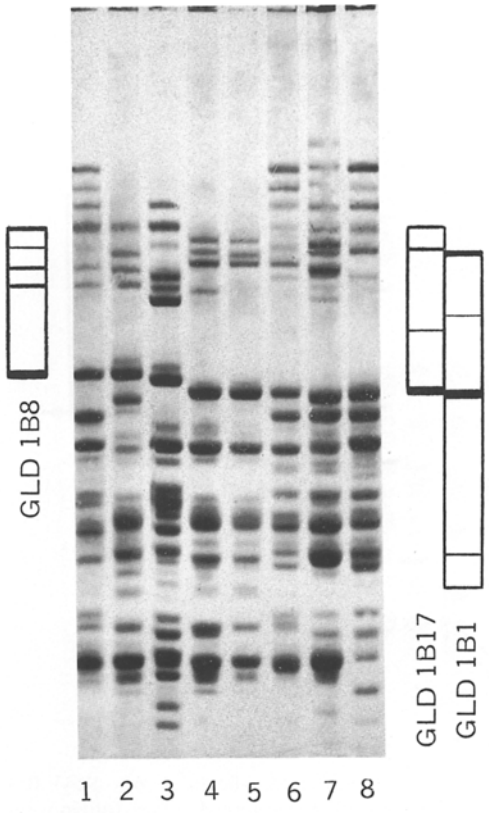


**Fig. 5.** Comparison of chromosome 1B-controlled blocks of different wheats: *1* – Rubin (*vulgare*); *2* – var. *rubiginosum* (*carthlicum*); *3* – Wells (*durum*); *4, 5* – var. *dekaprelevichi* (*carthlicum*); *6* – Kzyl Bas (*vulgare*); *7* – Ranniaya 73 (*vulgare*); *8* – Marquis (*vulgare*). Chromosome 1B-controlled blocks of bread wheat are shown

jointly inherited group (block) of components (Kudryavtsev et al. 1987). α-Gliadins in *durum* is under control of chromosome 6A (du Cros et al. 1983).

*Chromosome 1B-encoded blocks in durum*

All *durum* cultivars studied had either band γ42 or band γ45 in the single-seed gliadin spectra. Band γ42 is under control of chromosome 1B (Fig. 1, slots 1, 3) (Joppa et al. 1982; du Cros et al. 1983). In the cross Orenburgskaya Ranniaya × Melanopus 7 components γ42 and γ45 are controlled by allelic variants of the same locus (for 1:2:1 segregation $\chi^2 = 3.22$, $p > 0.2$). There are three components in the ω-region of Orenburgskaya which are controlled by genes linked to γ42-gene (Fig. 4). We did not find any other component in the Melanopus 7 gliadin spectrum which inherited together with band γ45. Similar inheritance of chromosome 1B-encoded components in *durum* was first shown by Damidaux et al. (1980).

Contrary to genome A-controlled gliadins, chromosome 1B-encoded blocks of *durum* cultivars show no resemblance to those of common wheat. None of chromosome 1B-controlled bands of bread wheat co-migrates with either γ42 or γ45 allelic components of *durums* (Figs. 2 and 5). The absence of γ42 in bread wheat cultivars was suggested earlier (Joppa et al. 1982).

*Blocks in carthlicum wheat*

Poor intravarietal gliadin polymorphism in *carthlicum* wheat was found. Each variety had its unique main spectrum, characterized by specific groups of bands. Accessions of the same variety and spikes of the same accession may differ only in the presence (and/or mobility) of some bands (e.g., Fig. 5, slots 4 and 5) or groups of bands. A total of 12 gliadin patterns were found.

Comparison of different spectra revealed several suspected genome A-encoded blocks in *carthlicum* wheat. Three varieties (*stramineum, rubiginosum,* and *dekaprelevichi*) undoubtedly have GLD 6A1-like α-gliadins (Fig. 6). In two accessions of the *fuliginosum* variety, the same variant of α-gliadins as in some *durum* wheat cultivars and as in bread wheat cultivar Solo is found (Fig. 7). It has been proved earlier that these α-gliadin compo-

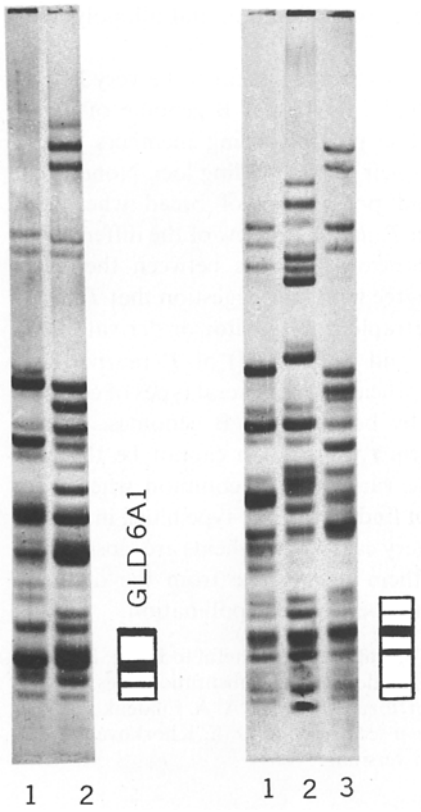


**Fig. 6.** GLD 6A1-like block in *T. carthlicum: 1* – var. *dekaprelevichi* (*carthlicum*); *2* – Bezostaya 1 (*vulgare*)

**Fig. 7.** Comparison of chromosome 6A-controlled block in three wheats: *1* – var. *fuliginosum* (*carthlicum*); *2* – Wells (*durum*); *3* – Solo (*vulgare*)

nents are inherited as a block in *durum* (Kudryavtsev et al. 1987) and in bread wheat (Koval and Metakovsky 1985). In Solo, which has *T. carthlicum* in its pedigree, this block is allelic to other chromosome 6A-controlled blocks of common wheat. The above arguments confirm that this group of gliadins of *carthlicum* wheat is a chromosome 6A-controlled block also. In two *carthlicum* varieties (*fuliginosum* and *dekaprelevichi*), a GLD 1A18-like component identical to those found in *T. aestivum* and *T. durum* is obviously present (Fig. 2, slots 1–6).

There are only two types of suspected chromosome 1B-controlled components in the $\gamma$-region of *T. carthlicum* spectra. One of them (present in *stramineum, fuliginosum,* and *dekaprelevichi*) co-migrates with the main component of chromosome 1B-controlled GLD 1B17 block of bread wheat (e.g., cultivar Kzyl Bas) (Fig. 5, slots 4–6). In variety *rubiginosum,* components identical to all those of GLD 1B8 block of *T. aestivum* (e.g., cultivar Rubin) are present (Fig. 5, slots 1, 2).

## Discussion

There is great genetical variability of morphological, physiological, and biochemical characters even within one wheat species. Therefore, to evaluate species relationships, it is necessary to compare their variabilities (i.e., sets of alleles). Comparison of sets of allelic variants of polymorphic proteins, especially wheat storage proteins (gliadins and HMW glutenins), provides a good tool for measuring species affinity.

To our knowledge, a similar approach exploiting storage proteins was used for the first time by Lawrence and Shepherd (1980), who found two similar alleles of chromosome 1D-encoded HMW glutenin in hexaploid wheat cultivars and in *Aegilops squarrosa*. They suggest that only a small proportion of this glutenin-coding locus variation of *Ae. squarrosa* is present in hexaploid wheats. Kasarda et al. (1984) found some resemblance between two-dimensional "extracted" pictures of gliadin components controlled by different genomes of common wheat (in fact, two-dimensional pictures of blocks) and corresponding gliadin patterns of several diploid species. Waines and Payne (1987) compared chromosome 1A-controlled HMW glutenin subunits in the extensive material of different species. They did find identical variants in bread wheat and some accessions of *T. urartu*. Lagudah and Halloran (1988) studied gliadin and HMW glutenin blocks in 79 *T. tauschii* accessions and found that only 6 of them had Gld $D^t$-1 and Glu $D^t$-1 alleles simultaneously identical to those in bread wheat. Therefore, these accessions might be considered as donors of genome D to bread wheat.

Besides storage proteins, isoenzymes can also be exploited for comparison intraspecies genetic variabilities. In recent work, inheritance of peroxidase isoenzymes in three tetraploid wheats was studied (Asins and Perez de la Vega 1985), then sets of isoenzymes of 13 different diploid and tetraploid wheats and *Aegilops* were compared, and intraspecies variability and genetic distances between these species were calculated (Asins and Carbonell 1986a, b). However, the absence of the information about inheritance of peroxidase isoenzymes in diploids, and possible difference in genetic control of isozymes with the same REM in different species (Asins and Perez de la Vega 1985), complicate the interpretation of the results.

Recognition and differentiation of allelic variants of blocks in the spectrum are easier and more unequivocal than of single bands. Of course, mutations and rare recombination events in a gliadin-coding locus may create new variants of blocks which should bear a great resemblance to the "parental" block. For example, GLD 1A18 might have originated from GLD 1A19 through recombination. Block GLD 1A1, very frequent in bread

wheat (e.g., cv Marquis), differs from GLD 1A19 only by slightly decreased electrophoretic mobility of major $\gamma$-gliadin (band $\gamma$50) (Fig. 2, slots 10, 11; Fig. 5 slots 7, 8). Clearly, GLD 1A1 originated from GLD 1A19 on the hexaploid level, because there is no such component (as band $\gamma$50 of Marquis) in *durum* and *carthlicum* wheats (Figs. 2 and 5). Therefore, one may suggest that GLD 1A19 is a very "old" block, and GLD 1A18 and GLD 1A1 are its younger derivatives. "Mutant" variants as well as the "old" blocks may be preserved in the course of long periods of time (Metakovsky and Sozinov 1987), presumably due to the relative selective neutrality of most mutations in storage-protein-coding loci. Our results with band $\gamma$50 are in contrast to the statement of Howes (1986) about the existence of band $\gamma$50 (as in cv Marquis) in *durum* wheat.

Completely different allelic variants of blocks (such as GLD 1A2 and GLD 1A19) are present in cultivars of both *durum* and bread wheats, and no available record indicates involvement of tetraploids in the ancestry of hexaploid cultivars studied, and vice versa. This indicates more than one act of "creation" of hexaploid wheat (Mac Key 1966). These acts should involve tetraploid progenitors (perhaps they belong to the same species) which differed one from another at least by allelic variants of gliadin-coding locus. These progenitors might have a rather long period of independent divergence – long enough for GLD 1A2 to be converted into GLD 1A19 (or vice versa) or for these two blocks to diverge from an unknown one. Maybe different alleles were obtained from diploid donor(s). During periods of divergence, homologous chromosomes of the progenitors may have become significantly different because of the accumulation of mutations as well as structural changes (Dvorák and McGuire 1981). These accumulated differences between homologs may influence many characters of bread wheat, including commercially important ones. Therefore, gliadin alleles may be very suitable markers of many important agronomic characters of bread wheat (Sozinov and Poperelya 1979).

Our results clearly confirm that all three wheats studied share one genome A. In addition, the results emphasize a considerable heterogeneity of genotypes among donors of this genome. For example, we found five distinct types of $\alpha$-gliandins in *durum* (Kudryavtsev et al. 1987), at least two types in *carthlicum* (this work), and several types of chromosome 6A-controlled blocks in bread wheat (Metakovsky et al. 1984a, b; unpublished results). None of these types can be converted into another by means of a few accidental mutations. Nevertheless, there are three similar types in *durum* and bread wheats, one type in *carthlicum* and bread wheats, and two types in *carthlicum* and *durum*. One may speculate that this heterogeneity has arisen at the diploid level and is maintained at tetraploid and hexaploid levels due to multiple acts of interspecies cross-pollination and allopolyploidization.

Also, donors of B-genome appear to be very heterogeneous. Undoubtedly, donors of B genome of *durum* and *carthlicum*, while possibly being members of one species, differed in their gliadin-coding loci. None of the suspected tetraploid progenitors of bread wheat was identical to modern *T. durum*, in view of the difference in chromosome 1B-controlled blocks between these two wheats. Our data agree with the suggestion that *T. carthlicum* could be a tetraploid progenitor or derivate (Mac Key 1966, Morris and Sears 1967) of *T. aestivum* ssp *vulgare*, since these wheats share several types of complex blocks controlled by both A and B genomes. On the other hand, modern *T. carthlicum* cannot be the only ancestor for all the variability of common wheat. For example, we did not find GLD 1A2-type block in *carthlicum* varieties. In every case, these wheats are closest relatives and one of them could arise from the other by multiple acts of interspecies cross-pollination.

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