

C-banded Wheat Chromosomes in Wheat and Triticale

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Summary. The C-banding patterns of wheat chromosomes in 7 hexaploid triticale and 7 wheat genotypes are described and compared. All 14 wheat chromosome pairs were individually identified in the triticales and a tetraploid wheat, and all the B and two A genome chromosome pairs in the hexaploid wheat genotypes. Little variation was found between genotypes in the distribution of C-bands but considerable variation was found in their size, total number and total length.

Key words: C-banding – Wheat – Triticale – Heterochromatin

Introduction

Variation in the size and pattern of C-bands occurs in rye chromosomes in *Secale cereale* (Weimarck 1975; Lelley et al. 1978; Naranjo and Lacadena 1980) and in triticale (Darvey and Gustafson 1975; Seal and Bennett 1981). Little is known, however, about the extent of such variation in the wheat chromosomes of *Triticum aestivum* and triticale. The C-banded karyotype of hexaploid wheat (cv. 'Diamant') was described in detail by Zurabishvili et al. in 1974. Since then the C-banding patterns of *T. aestivum* cv. 'Chinese Spring' (Gill and Kimber 1974; Iordansky et al. 1978a) and cv. 'Aurora' (Iordansky et al. 1978b), two hexaploid triticales (Iordansky et al. 1978b) and three tetraploid triticales (Gustafson and Krolow 1978) have been published. Using N-banding, Gerlach (1977) was able to identify 9 pairs of wheat chromosomes in wheat cv. 'Chinese Spring'. Wheat chromosomes involved in translocations have been identified by C-banding (Gill and Kimber 1977) and by N-banding (Jewell 1978).

In the present work the C-banding patterns of wheat chromosomes in 7 triticales and 7 wheat genotypes are described and compared. Variation in C-banding patterns is of practical importance in two respects. It enables cytogeneticists to recognise and

select firstly, for chromosomes carrying desirable genes and secondly, for chromosomes bearing larger or smaller amounts of heterochromatin (Bennett and Gustafson 1982). The amount of C-banded heterochromatin in rye chromosomes in triticale has been shown to affect endosperm development and grain quality (Bennett 1977). Selection for reduced amounts of rye heterochromatin in conjunction with selection for increased amounts of wheat heterochromatin may further improve the nuclear stability of triticales (Gustafson and Bennett 1982).

Materials and Methods

The genotypes studied are listed in Table 1. Wheat chromosomes were C-banded using the technique described by Seal and Bennett (1981) except that 20% v/v Leishman or Wright stain was used instead of Giemsa. A minimum of 10 metaphases from each of 5 plants were examined for each genotype. The term 'C-band' is used to describe a pair of laterally adjacent stained dots (which may appear fused as a single dot or band) one belonging to each of the two chromatids comprising each metaphase chromosome. Thus, two adjacent 'bands' consist of two pairs of dots longitudinally juxtaposed. The variation between genotypes described below was assumed to reflect karyotypic differences rather than differences in staining quality between slides. Variation between preparations from the same plant was small and confined to differences in general intensity of staining rather than differences in banding pattern. Only obvious and consistent differences are described here. Long and short arms of chromosomes are referred to by the letters L and S respectively.

All B genome chromosomes and chromosomes 4A and 7A were identified by comparison with their N-banding patterns in 'Chinese Spring' described by Gerlach (1977). Other A genome chromosomes were identified in tetraploid wheat and triticale by comparing their total lengths and arm ratios with those for 'Chinese Spring' telophase II (Sears 1954). Owing to similarities in size, arm ratio and banding pattern, A and D genome chromosomes in hexaploid wheat (except 4A and 7A) could not be individually identified. The D genome chromosomes bear the least heterochromatin and even though individual banding patterns in 'Chinese Spring' can be distinguished using telocentric stocks, identification as whole

Table 1. Genotypes used in the present study

<i>Triticale, Triticosecale</i> Wittmack (2n=6x=42, AABBRR)	1. 'Cocorit' × UC90 rye 6A530
	2. cv. 'Rosner'
	3. URSS-3310 × M2A, LT 1336-76 CIMMYT WTCB (7) 1978
	4. 6TB-059, Alabama WTSN (12) 1977
	5. KISS-URSS 2310, CIMMYT WTCB (35) 1977
	6. 6TA 876, CIMMYT WTCB (7) 1978
	7. II 75 - 23 b 367
<i>T. durum</i> L. (2n=4x=28, AABB)	8. cv. 'Cocorit'
<i>T. aestivum</i> L. (2n=6x=42, AABBDD)	9. cv. 'Chinese Spring' (King II rye addition line 4R/7R, Cambridge stock).
	10. cv. 'Holdfast' (King II rye addition set)
	11. cv. 'Mironovskaya 808'
	12. cv. 'Besostaya I'
	13. cv. 'Cappelle-Desprez'
	14. cv. 'Viking' (hairy-necked)

chromosomes is difficult (Gill and Kimber 1974). Extensive telocentric stocks are unavailable for most other varieties. The banding patterns of rye chromosomes in triticales 6TA 876, KISS-URSS 2310 and 6TB-059 were discussed by Seal and Bennett (1981).

'Hairy-necked Viking' wheat has a wheat/rye translocation, a small segment of 5RL being inserted into 4A (Riley et al. 1971). 'Cappelle-Desprez' wheat has a 5B/7B translocation (Riley et al. 1967).

Results

General Observations

The C-banding patterns of A genome chromosomes are shown in Figs. 1 and 2 and those of the B genome chromosomes in Figs. 3 and 4. The bands in both genomes were concentrated in the centromeric and the distal and terminal regions. The mid-regions of both long and short arms generally had fewer and smaller bands. From 48 to 67 bands were found in the A and B genomes of the triticales and the tetraploid wheat of which about three-quarters were found on B genome chromosomes. In terms of total chromosome length, C-bands accounted for 10 to 14% of the A genome (triticale), 30 to 40% of the B genome (wheat and triticale) and 20 to 27% of the A and B genomes combined (triticale). The total length and the variation in total length and distribution of C-bands in A and B genome chromosomes were similar in both wheat and triticale. Within each genome, differences between homologous chromosomes (Figs. 1-4, between columns) were small, whereas differences between heterologous chromosomes (Figs. 1-4, between rows) were large,

thus facilitating identification of individual chromosomes. The banding patterns of homoeologous chromosomes from the A and B genomes were dissimilar (e.g. compare 1A with 1B, Figs. 1-4). The C-banding patterns of the B genome chromosomes and chromosomes 4A and 7A closely matched their N-banding patterns (Gerlach 1977). Nevertheless, many homologous chromosomes differed in detail between genotypes with respect to band distribution, size or staining intensity.

The A Genome (Figs. 1, 2)

1A: This was the only chromosome in the A and B genomes which in all genotypes showed no C-bands with the present technique (apart from a faint terminal band on 1AL in 'Rosner' triticale).

2A: 2AS had a band close to the centromere. A second fainter band in a proximal position on 2AL was visible in some genotypes.

3A: Bands were found at from one to four sites on this chromosome. The band on 3AS next to the centromere was usually the largest and most intensely stained. A proximal band on 3AL was present in most genotypes but varied in size between genotypes, being prominent in Rosner triticale. A subterminal band was found on 3AL in 'Cocorit' wheat and 'Cocorit' × UC90 triticale. A terminal band was present in 5 genotypes including 'Cocorit' wheat. However, in the triticale derived from 'Cocorit' wheat and UC90 rye this band was absent. The patterns could be accounted for by the translocation of the 3AL terminal band in 'Cocorit' wheat to the telomere of 3BL in 'Cocorit' × UC90 triticale. Whether the events producing this variation occurred before or after the formation of the triticale is unclear but the difference was maintained in all 5 plants of each genotype examined. There was considerable variation between genotypes in the total length of C-banded regions in chromosome 3A (Figs. 1, 2).

4A: This chromosome had more C-banded chromatin than any other in the A genome due to the presence of large C-banded regions on either side of the centromere. An examination of pro-metaphase chromosomes showed that these regions consisted of aggregations of smaller C-bands. The size of these regions varied little between genotypes (Figs. 1, 2). Small terminal bands were present on 4AS in 5 genotypes and on 4AL in three genotypes. A subterminal band of variable size between genotypes, was found on 4AL in 6 genotypes. Triticale KISS-URSS 2310 had bands at all these sites while 5 other genotypes showed only the centromeric bands.

5A: Chromosome 5A had a single band in a proximal position on the long arm which did not vary between genotypes.

6A: The smallest chromosome, 6A, was metacentric and had a band located proximally in one arm. In the same arm a smaller subterminal band was sometimes

found. In triticales KISS-URSS 2310 and 6TB 059 the smallest chromosome was metacentric with only one faint subterminal band.

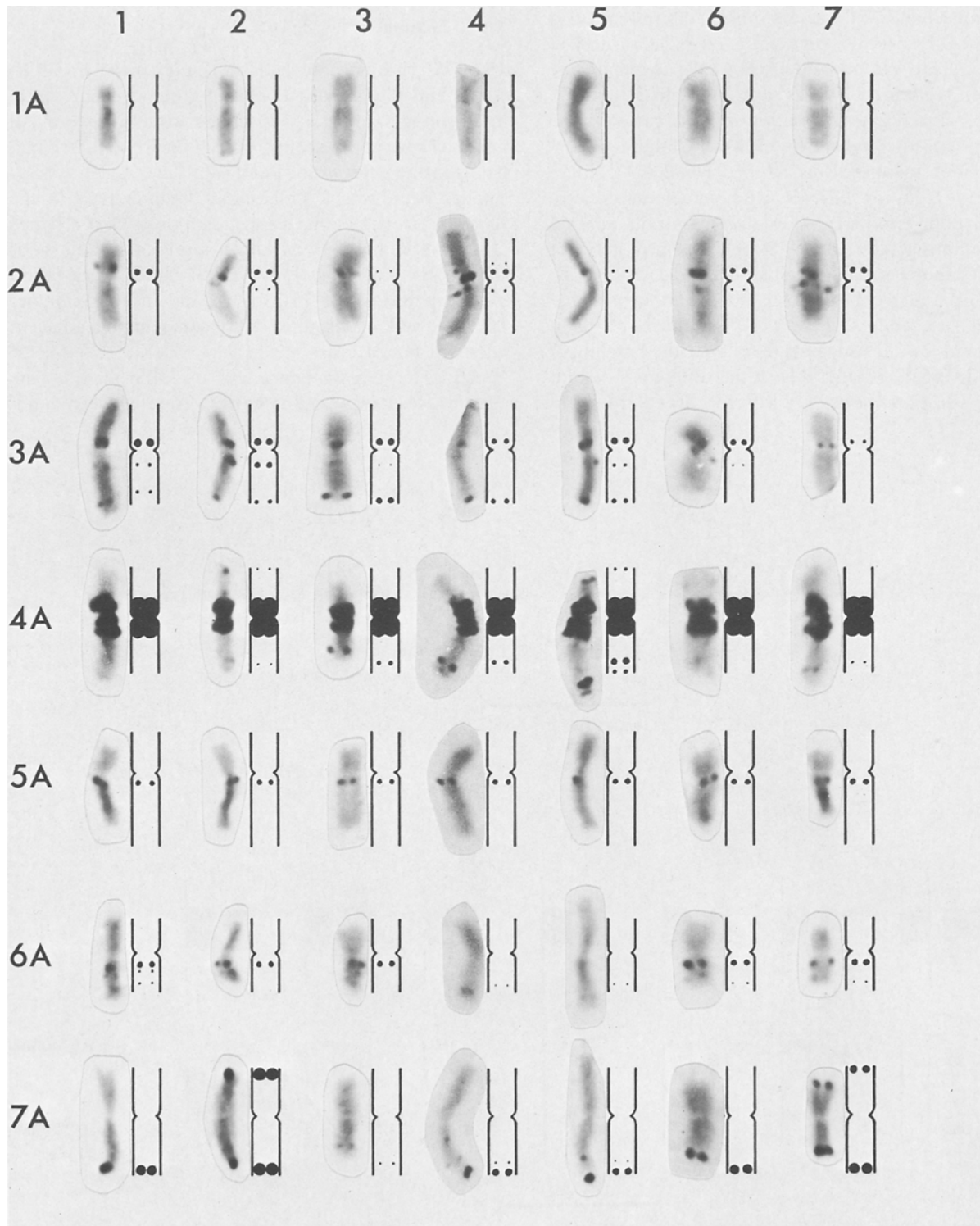


Fig. 1. C-banded A genome chromosomes of triticales. 1 'Cocorit' x UC90; 2 'Rosner'; 3 URSS-3310; 4 6TB-059; 5 KISS-URSS 2310; 6 6TA 876; 7 H 75-23b 367. Bar = 10 μ

7A: This large metacentric chromosome usually had one or two telomeric bands which varied in size between genotypes. The triticales 'Rosner' and II 75-23b had particularly large bands at both telomeres. Triticale URSS-3310 had a single subterminal band but no terminal bands on 7A. A similar subterminal band was present in 5 other genotypes. 7A in hairy-necked 'Viking' wheat was unbanded. Thus the length of the C-banded regions on 7A was quite variable (Figs. 1, 2). There was intravarietal variation for this chromosome in 'Chinese Spring' wheat. In euploid 'Chinese Spring' material one telomere was banded while in 'Chinese Spring'/rye addition line 4R/7R both telomeres were banded. Both telomeres showed N-bands in euploid 'Chinese Spring' (Gerlach 1977). In telocentric stocks of 7A of 'Chinese Spring' originally derived from E. R. Sears, Gill and Kimber (1974) found only a proximal band on 7AS while Gerlach (1977) found N-bands at both telomeres. This suggests that either the banding of 7A has diverged considerably in the different stocks or that this chromosome or part of it has been substituted

by that of another variety by introgression. Terminal deletions are known to have occurred in some telocentric stocks (Gill and Kimber 1974).

The B Genome (Figs. 3, 4)

1B: This chromosome had the largest number of C-bands and the greatest length of C-banded chromatin in all genotypes but varied little between genotypes. All genotypes except triticales II 75-23b 367 had a terminal band on the short arm satellite. In several genotypes a smaller band was found on the satellite next to the secondary constriction. An aggregation of 5 or 6 bands around its centromere was always present. About midway along 1BL one or two small bands were found except in triticales II 75-23b 367 and in all genotypes 1BL showed a terminal band or pair of adjacent telomeric bands.

2B: The largest band was on 2BS next to the centromere. Its size and intensity varied between geno-

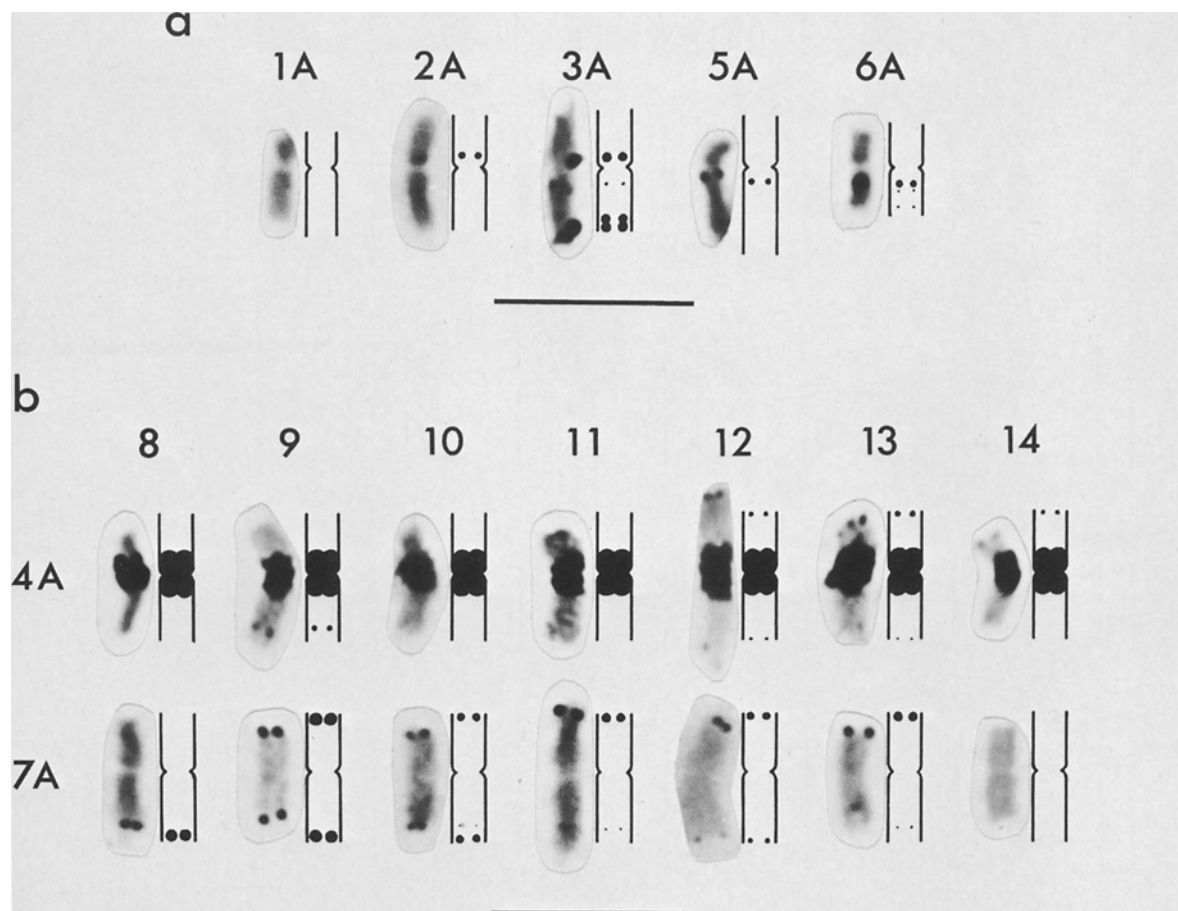


Fig. 2a and b. a C-banded A genome chromosomes of 'Cocorit' wheat. b C-banded chromosomes 4A and 7A of wheat. 8 'Cocorit'; 9 'Chinese Spring'; 10 'Holdfast'; 11 'Mironovskaya 808'; 12 'Besostaya I'; 13 'Cappelle-Desprez'; 14 'Hairy-necked Viking'. Bars = 10 μ

types, being greatest in 'Chinese Spring', 'Cappelle-Desprez' and 'Cocorit' wheat and triticales 'Cocorit' × UC90 and II 75-23b 367. Small bands in the distal

region of 2BS also showed variation in size and number between genotypes (compare triticales II 75-23b 367 and URSS 3310, Fig. 3). A small band usually occurred

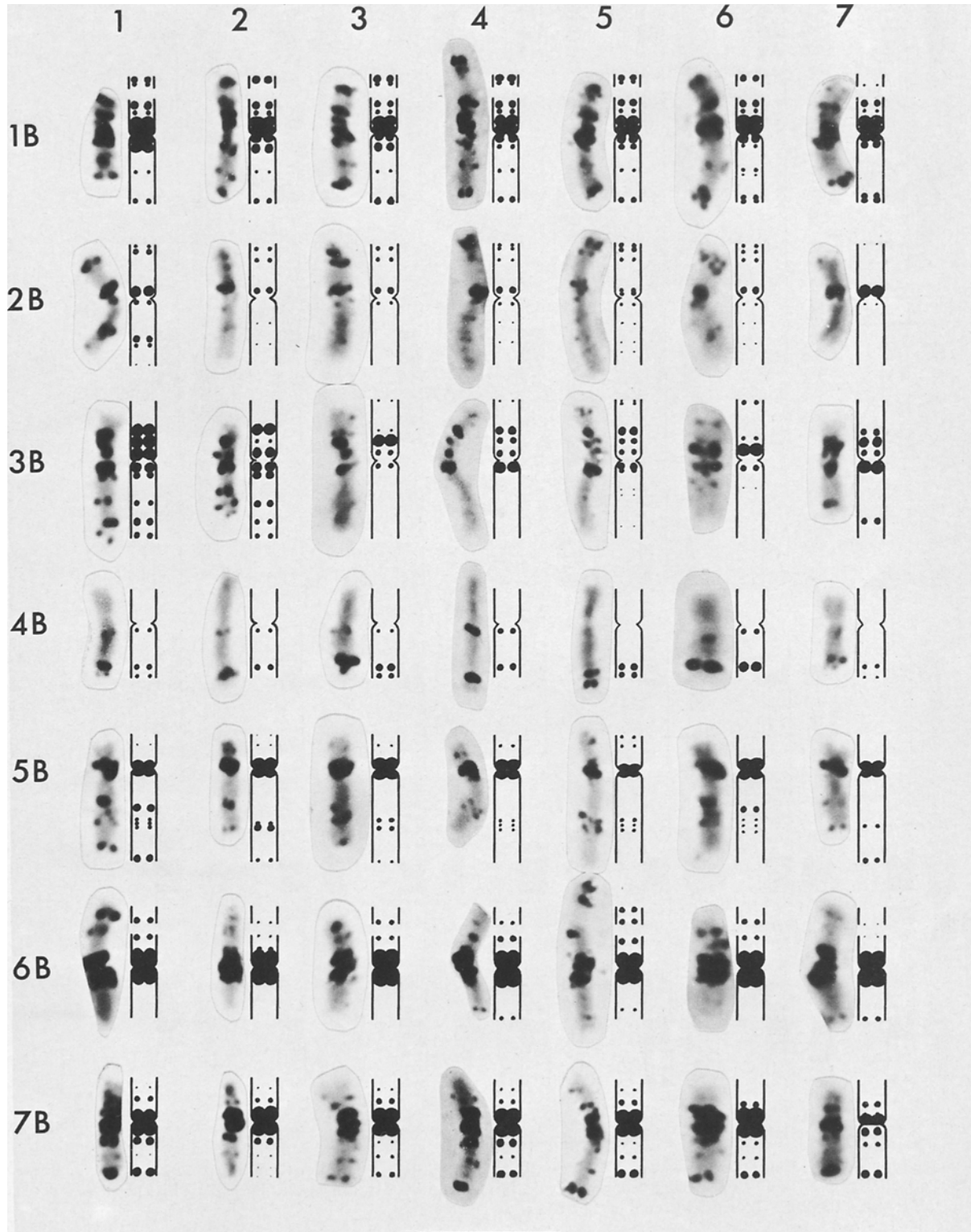


Fig. 3. C-banded B genome chromosomes of triticale. 1 'Cocorit' × UC90; 2 'Rosner'; 3 URSS-3310; 4 6TB-059; 5 KISS-URSS 2310; 6 6TA 876; 7 II 75-23b 367. Bar = 10 μ

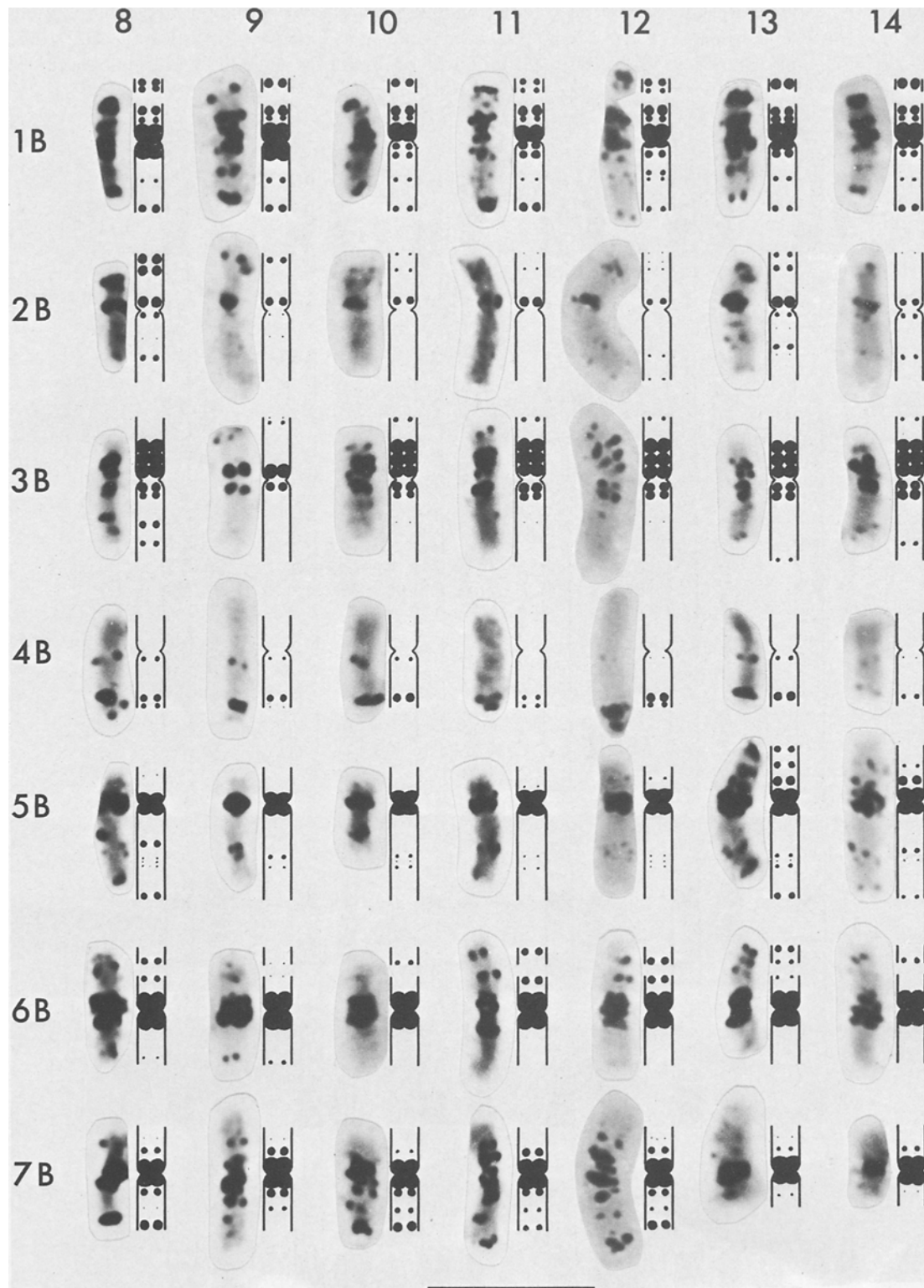


Fig. 4. C-banded B genome chromosomes of wheat. 8 'Cocorit'; 9 'Chinese Spring'; 10 'Holdfast'; 11 'Mironovskaya 808'; 12 'Besostaya I'; 13 'Cappelle-Desprez'; 14 'Hairy-necked Viking'. 13 and 14 have a 5B/7B translocation. The 5BL/7BL chromosomes are shown in the 5B row and the 5BS/7BS chromosomes in the 7B row

on 2BL next to the centromere and a variable number of small, faint bands were seen around the central region of 2BL. However, in 'Cappelle-Desprez' and 'Cocorit' wheat, and 'Cocorit' × UC90 triticale, 2BL had a large band in this region.

3B: This chromosome varied most between genotypes. In most genotypes there were one or two small distal bands and two or three adjacent bands in the proximal half of 3BS. In 'Chinese Spring' a single large band was present in this region. In 5 triticales and in all the hexaploid wheat genotypes in the present study, 3BL had two adjacent bands or a single large band close to the centromere, sometimes accompanied by a few smaller bands further from the centromere. This pattern was found in the hexaploid wheats 'Chinese Spring', 'Diamant' and 'Aurora' by Iordansky et al. (1978a, 1978b – their chromosome 2). Three genotypes had two or three additional large bands in the distal half of 3BL. Triticales 'Rosner' and 'Cocorit' × UC90 had all three 'extra' bands, one about mid-way along 3BL, one subterminal and one terminal in position. In the durum wheat, 'Cocorit', the central and subterminal bands were present. Chromosomes with similar patterns were found by Zurabishvili et al. (1978) in *T. durum* cv. 'Arnautka', *T. dicoccum* and *T. carthlicum* and may therefore be a common feature of tetraploid wheats. The difference between 'Cocorit' wheat and 'Cocorit' × UC90 triticale regarding the terminal band on 3BL may be due to a translocation involving 3AL (see above).

4B: Bands were found only in 4BL at three sites, one proximal, one subterminal and one terminal. The subterminal band was present in all genotypes and was often the largest. The terminal band was minute in triticale II 75-23b 367 and 'Chinese Spring' wheat and absent from three triticales and hairy-necked 'Viking' wheat. The proximal band, which was generally small, was minute in 'Besostaya I' wheat and absent from 'Mironovskaya 808' wheat and two triticales. The two bands on 4B in hairy-necked 'Viking' wheat were faintly stained.

5B: The largest C-bands on 5B in all genotypes were on either side of the centromere. These showed variation in size and staining intensity. The centromeric region of 5B in 'Chinese Spring' wheat was the most intensely stained region of all chromosomes. A small subterminal band was seen on 5BS in many genotypes. The central region of 5BL had from one to three pairs of C-bands. 'Cocorit' wheat and triticales 'Cocorit' × UC90 and 6TA 876 had an additional large C-band just proximal to this region. A terminal band on 5BL was found in some genotypes.

6B: In all genotypes chromosome 6B had an aggregation of large C-bands around the centromere. There were three other banding sites on 6BS, one on

either side of the secondary constriction and a terminal site. 6B in triticale KISS-URSS 2310 had large bands at all three sites while triticale II 75-23b 367 had only two minute bands in this region. Apart from the proximal bands 6BL generally had few or no C-bands. A minute subterminal band was found in some genotypes and a terminal band was found in 'Chinese Spring' wheat and two triticales.

7B: 7B also had an aggregation of C-bands in the centromeric region but the most distal of these were often separate from the main group (e.g. see 'Rosner' triticale or 'Chinese Spring' wheat, Figs. 3, 4). There were no terminal bands on 7BS but a subterminal band was found in some genotypes. In most genotypes a single small band was seen just distal to the mid-point of 7BL and a large terminal band was present in all genotypes except 'Rosner' triticale and 'Chinese Spring' and hairy-necked 'Viking' wheat.

Translocation Chromosomes

The present results confirm the presence of a 5B/7B translocation in 'Cappelle-Desprez' (Riley et al. 1967). A similar translocation was found in hairy-necked 'Viking' (Fig. 4). In both genotypes the translocation break-point is near the centromere. However, 'Viking' lacks the large terminal bands found on the 5BL/7BL chromosome in 'Cappelle-Desprez'. Whether these differences are present in the French varieties from which both 'Cappelle-Desprez' and 'Viking' are derived or whether they have arisen during the subsequent selection of the two genotypes is unknown. The banding pattern of 4A in hairy-necked 'Viking' was very similar to that of other genotypes (Fig. 2) despite the insertion of a segment of rye chromosome 5RL (Riley et al. 1971). The translocated segment could not be identified. Several hexaploid wheat varieties, including 'Cappelle-Desprez' and 'Holdfast' (Riley et al. 1967), are known to have 3B/3D translocations. None were identified in the present study since 3D could not be identified using the present technique. However, such translocations may contribute to the observed intervarietal variation in the banding pattern of 3B in wheat and triticale (Figs. 3, 4).

Discussion

Overall, little variation was found between genotypes in the distribution of C-bands in the A and B genome chromosomes. In contrast, Iordansky et al. (1978b) found high morphological diversity among triticales and polyploid wheats which they attributed to intensive introgression. At best they identified 10 pairs of chromosomes with similar banding patterns in the genotypes studied, the remainder having no morphological

similarity between genotypes. The present results show, however, that their division of wheat and triticale chromosomes into 'constant' and 'variable' groups with respect to their banding patterns was unnecessary. The A genome chromosomes identified in the present study showed no more variation between genotypes than the B genome chromosomes. If extensive variation in banding patterns in wheat chromosomes does exist then presumably it must be confined to the D genome, although other observations suggest this is unlikely. Except for 7A, 7B and the general absence of centromeric bands, the banding patterns were similar to those of Gill and Kimber (1974) for 'Chinese Spring'.

Iordansky et al. (1978a) and Zurabishvili et al. (1978) noted in wheat considerable intervarietal variation in the total amount of heterochromatin identified by C-banding, this being particularly great in Chinese Spring. They suggested a progressive loss of heterochromatin during the development of advanced from primitive wheats. The present results also show variation in the heterochromatic content of chromosomes of polyploid wheats and triticale (e.g. compare 'Cappelle-Desprez' with hairy-necked 'Viking', Figs. 2, 4). However, they show that 'Chinese Spring' does not have an exceptionally large amount of heterochromatin among polyploid wheats (Figs. 2, 4). Although chromosomes 1A, 2A, 3A, 5A, 6A and the D genome chromosomes were excluded from the present study, together they contribute little to the total heterochromatic content in all genotypes. The difference in total length of C-banded regions in the A and B genomes of triticale can account entirely for the difference in chromosome length between these genomes in 'Chinese Spring' wheat (Sears 1954).

Chromosomes 4A and 4B were exceptional compared with other chromosomes of their respective genomes. 4A had at least 4 times the heterochromatin of other A genome chromosomes and 4B had the lowest heterochromatic content among B genome chromosomes. 4A is unusual among A genome chromosomes in terms of its N-banding pattern (Gerlach 1977), satellite DNA content (Dennis et al. 1980), failure to pair with chromosomes of *T. urartu* (Chapman et al. 1976) and unique complement of fertility factors (Sears 1966). These peculiarities have cast doubt upon whether this chromosome shares a common origin with the other A genome chromosomes (Driscoll 1981).

Although no two heterologous chromosomes had similar banding patterns, some heterologous chromosome arms did. 1BL and 7BL had matching banding patterns in all genotypes except 'Rosner' triticale and 'Chinese Spring' wheat. 2BL and 3BL, 4AL and 6BL, and 6BS and 7BS also showed some correspondence in banding pattern. Whether such similarities have any

significance is unknown, but it has been suggested that they may have structural or functional significance in terms of the spatial organisation of heterologous chromosomes in the nucleus (Bennett 1982).

The variation found in C-banding patterns may be useful in determining the chromosomal location of cross-over events in A and B genome chromosomes in hybrids between the various genotypes. Such studies may also permit a comparison of the genetic map of these chromosomes with their physical dimensions (Linde-Laursen 1979). In structural terms, the banding patterns probably reflect differences in the amount and distribution of certain highly repetitive DNA sequences. The general pattern of C-bands closely coincides with the distribution of such sequences in the wheat genomes (Dennis et al. 1980; Hutchinson and Lonsdale 1982). This variation may enable selection for changes in the DNA content of the wheat as well as the rye genomes in triticales in efforts to improve nuclear stability (Seal and Bennett 1981).

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Literature

- Bennett, M.D. (1977): Heterochromatin, aberrant endosperm nuclei and grain shrivelling in wheat-rye genotypes. *Heredity* **39**, 411–419
- Bennett, M.D. (1982): The nucleotypic basis of the spatial ordering of chromosomes in eukaryotes and the implications of the order for genome evolution and phenotypic variation. In: *Systematics assoc. Special Vol. 20: Genome Evolution* (eds. Dover, G.A.; Flavell, R.B.) pp. 234–241 London: Acad. Press
- Bennett, M.D.; Gustafson, J.P. (1982): The effect of telomeric heterochromatin from *Secale cereale* L. on triticale (\times Triticosecale Wittmack). 2: The presence or absence of blocks of heterochromatin in isogenic backgrounds (in press)
- Chapman, V.; Miller, T.E.; Riley, R. (1976): Equivalence of the A genome of bread wheat with that of *Triticum urartu*. *Genet. Res.* **27**, 69–76
- Darvey, N.L.; Gustafson, J.P. (1975): Identification of rye chromosomes in wheat-rye addition lines and triticale by heterochromatin bands. *Crop Sci.* **15**, 239–243
- Dennis, E.S.; Gerlach, W.L.; Peacock, W.J. (1980): Identical polypyrimidine-polypurine satellite DNAs in wheat and barley. *Heredity* **44**, 349–366
- Driscoll, C.J. (1981): Perspectives in chromosome manipulation. *Phil. Trans. R. Soc. (Lond.) B* **292**, 535–546
- Gerlach, W.L. (1977): N-banded karyotypes of wheat species. *Chromosoma* **62**, 49–56
- Gill, B.S.; Kimber, G. (1974): Giemsa C-banding and the evolution of wheat. *Proc. Nat. Acad. Sci. (USA)* **71**, 4086–4090
- Gill, B.S.; Kimber, G. (1977): Recognition of translocations and alien chromosome transfers in wheat by the Giemsa C-banding technique. *Crop Sci.* **17**, 264–266

- Gustafson, J.P.; Bennett, M.D. (1982): The effect of telomeric heterochromatin from *Secale cereale* L. on triticale (\times Triticosecale Wittmack). 1: The influence of the loss of several blocks of telomeric heterochromatin on early endosperm development and kernel characteristics at maturity. (in press)
- Gustafson, J.P.; Krolow, K.D. (1978): A tentative identification of chromosomes present in tetraploid triticale based on heterochromatic banding patterns. *Can. J. Genet. Cytol.* **20**, 199–204
- Hutchinson, J.; Lonsdale, D.M. (1982): The chromosomal distribution of cloned highly repetitive sequences from hexaploid wheat. (in press)
- Iordansky, A.B.; Zurabishvili, T.B.; Badaev, N.S. (1978 a): Linear differentiation of cereal chromosomes. 1: Common wheat and its supposed ancestors. *Theor. Appl. Genet.* **51**, 145–152
- Iordansky, A.B.; Zurabishvili, T.G.; Badaev, N.S. (1978 b): Linear differentiation of cereal chromosomes. 3: Rye, triticale and 'Aurora' variety. *Theor. Appl. Genet.* **51**, 281–288
- Jewell, D.C. (1979): Recognition of alien material and chromosome re-arrangements in wheat using N-banding. In: *Proc. 5th Int. Wheat Genetics Symp.*, p. 1208–1212. New Delhi: Indian Soc. Genetics and Plant Breeding
- Lelley, T.; Josefek, K.; Kaltsikes, P.J. (1978): Polymorphism in the Giemsa C-banding pattern of rye chromosomes. *Can. J. Genet. Cytol.* **20**, 307–312
- Linde-Laursen, I. (1979): Giemsa C-banding of barley chromosomes 3: Segregation and linkage of C-bands on chromosomes 3, 6 and 7. *Hereditas* **91**, 73–77
- Naranjo, T.; Lacadena, J.R. (1980): Interaction between wheat chromosomes and rye telomeric heterochromatin on meiotic pairing of chromosome pair 1R of rye in wheat-rye derivatives. *Chromosoma* **81**, 249–261
- Riley, R.; Chapman, V.; Miller, T.E. (1971): Hairy-necked Viking. *Ann. Rep. Plant Breeding Inst. Cambridge* 1970, 98
- Riley, R.; Coucoli, H.; Chapman, V. (1967): Chromosomal interchanges and the phylogeny of wheat. *Heredity* **22**, 233–247
- Seal, A.G.; Bennett, M.D. (1981): The rye genome in winter hexaploid triticales. *Can. J. Genet. Cytol.* **23**, 647–653
- Sears, E.R. (1954): The aneuploids of common wheat. *Missouri Agr. Exp. Stn. Res. Bull.* **572**, 1–59
- Sears, E.R. (1966): Nullisomic-tetrasomic combinations in hexaploid wheat. In: *Chromosome manipulations and plant genetics* (eds. Riley, R.; Lewis, K.R.), pp. 29–45. Edinburgh: Oliver and Boyd
- Weimarck, A. (1975): Heterochromatin polymorphism in the rye karyotype as detected by the Giemsa C-banding technique. *Hereditas* **79**, 293–300
- Zurabishvili, T.G.; Iordanskii, A.B.; Badaev, N.S. (1974): Polykaryogram analysis and investigation of differential staining of *Triticum aestivum* L. chromosomes. Translated from *Doklady Akad. Nauk SSSR* **218**, 207–210
- Zurabishvili, T.G.; Iordansky, A.B.; Badaev, N.S. (1978): Linear differentiation of cereal chromosomes II. Polyploid wheats. *Theor. Appl. Genet.* **51**, 201–210

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