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C-banding pattern and polymorphism of *Aegilops caudata* and chromosomal constitutions of the amphiploid *T. aestivum* – *Ae. caudata* and six derived chromosome addition lines

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Summary. C-banding patterns were analysed in 19 different accessions of *Aegilops caudata* (= *Ae. markgrafii*, = *Triticum dichasians*) (2n=14, genomically CC) from Turkey, Greece and the USSR, and a generalized C-banded karyotype was established. Chromosome specific C-bands are present in all C-genome chromosomes, allowing the identification of each of the seven chromosome pairs. While only minor variations in the C-banding pattern was observed within the accessions, a large amount of polymorphic variation was found between different accessions. C-banding analysis was carried out to identify *Ae. caudata* chromosomes in the amphiploid *Triticum aestivum* cv 'Alcedo' – *Ae. caudata* and in six derived chromosome addition lines. The results show that the amphiploid carries the complete *Ae. caudata* chromosome complement and that the addition lines I, II, III, IV, V and VIII carry the *Ae. caudata* chromosome pairs B, C, D, F, E and G, respectively. One of the two SAT chromosome pairs (A) is missing from the set. C-banding patterns of the added *Ae. caudata* chromosomes are identical to those present in the ancestor species, indicating that these chromosomes are not structurally rearranged. The results are discussed with respect to the homoeologous relationships of the *Ae. caudata* chromosomes.

Key words: C-banding – Polymorphic variation – *Aegilops caudata* – Chromosome addition lines

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Introduction

Species belonging to the genus *Aegilops* are an important source of genetic material for improving the genetic variability of cultivated bread wheat, *Triticum aestivum* (2n=6×=42, genomically AABBDD). *Aegilops caudata* (=*Ae. markgrafii*, = *T. dichasians*) is a diploid wild relative of wheat (2n=14, genomically CC) that is native to an region that extends from the eastern Mediterranean through Turkey to eastern parts of this country, southern parts of the USSR, northern Syria and northern Iraq. It carries resistance genes to several diseases (Eig 1936; Hammer 1985), especially against rust and powdery mildew (Blüthner 1984) and is involved as a genome donor in the parentage of *Ae. cylindrica* (=*T. cylindricum*) and *Ae. truncialis* (=*T. triunciale*). *Ae. caudata* has also played an important role in the evolution of diploid *Aegilops* species as a link between the primitive *Ae. speltoides* (subgenus *Sitopsis*) and species from subgenus *Aegilops* (Hammer 1987).

Giemsa C-banding allows the identification of all 21 chromosome pairs and most chromosome arms of hexaploid wheat (Endo 1986; Gill et al. 1991), and chromosome banding techniques have been widely used for identifying wheat-alien chromosome addition, substitution and translocation lines. Only limited information is available about the banding pattern of wild relatives of wheat (Gill and Kimber 1974; Natarajan and Sarma 1974; Iordansky et al. 1978; Gerlach 1977; Jewell 1979; Chen and Gill 1983; Jewell and Driscoll 1983; Teoh et al. 1983; Shang et al. 1989; Friebe and Heun 1989; Dhaliwal et al. 1990; Friebe et al. 1990), and so far only three reports describe the banding pattern of *Ae. caudata* (Gill 1981; Teoh and Hutchinson 1983; Schubert et al. 1987). However, almost nothing is known about the intraspecific polymorphic variation of its banding pattern,

which is essential for identifying *Ae. caudata* chromatin in manipulated wheat – *Ae. caudata* derivatives.

We have analysed the C-banding pattern and polymorphic variation of 19 different *Ae. caudata* accessions in order to establish a generalized C-banded karyotype of this species. Furthermore, C-banding analysis was used to identify *Ae. caudata* chromosomes in the amphiploid *T. aestivum-Ae. caudata* and in six derived disomic chromosome addition lines. The data presented are useful for analysing evolutionary relationships among polyploid *Aegilops* species and are crucial for a further directed chromosome engineering of this material aimed to produce rust and powdery mildew resistant wheat-*Ae. caudata* chromosome substitution and translocation lines.

Material and methods

The material analysed consists of 19 different accessions of *Ae. caudata* (Table 1), the hexaploid wheat cv 'Alcedo', the amphiploid *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740–69' and six derived *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740-69' chromosome addition lines. The production of this material has been described by Blüthner et al. (1988) and Schubert (1989).

Chromosome identification was carried out according to the C-banding technique described by Gill et al. (1991). Chromosome measurements were carried out on 20 complete C-banded mitotic metaphase cells in order ot establish a generalized C-banded karyotype of *Ae. caudata*. Since homoeologous relationships of *Ae. caudata* chromosomes have not been established yet, chromosomes were lettered from A to G, following the nomenclature system used by Teoh and Hutchinson (1983). Furthermore, meiotic chromosome pairing was analysed in Feulgen-stained PMC's of 'Alcedo', 'Chinese Spring', F_1 hybrids 'Alcedo' × 'Chinese Spring' and in F_1 hybrids between the 'Chinese Spring' monosomics 1B, 2B, 3B, 6B, 7B and 'Alcedo'. Microphotographs were taken with a Leitz Photomicroscope Dialux 22 using a Kodak Imagelink HQ microfilm 1461.

Table 1. Origins of the *Aegilops caudata* accessions analyzed in the present study

Accession no.	Origin
107/76[a]	USSR
108/85[a]	USSR
109/85[a]	USSR
110/78[a]	USSR
711/83[a]	Unknown
713/83[a]	Unknown
743/83[a]	Turkey
744/86[a]	Turkey
818/89[a]	Turkey (10 km NO Selčuk)
883/85[a]	Greece
884/85[a]	Greece
885/85[a]	Greece
TA1909[b]	Turkey
21[c]	Unknown
86TF01-18[d]	Unknown
86TF03-5[d]	Unknown
V 6[e]	Turkey (Perge)
V 1[e]	Turkey (10 km O Fethiye)
S 740-69[f]	Unknown

[a] Genebank Gatersleben, FRG
[b] Wheat Genetic Resource Center, Kansas State University, USA
[c] Obtained from R. Simeone, University of Bari, Italy
[d] Obtained from G. Kimber, University of Missouri Columbia, USA
[e] Collected by V. Schubert and A. Bauer, Martin-Luther University, Halle-Wittenberg, FRG
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Results and discussion

C-banding pattern and polymorphism of Ae. caudata

C-banded mitotic metaphases of plants from different accessions of *Ae. caudata* are shown in Fig. 1 and detailed C-banded karyotypes of 8 accessions showing the range of polymorphic variation are given in Fig. 2. *Ae. caudata* has a chromosome number of 2n = 14 and carries two SAT chromosome pairs of which one pair of satellites is very small and often not detectable by phase contrast analysis (Fig. 1 a). The chromosome complement consists of four pairs of more or less submetacentric chromosomes and three pairs of acrocentric ones. All chromosomes show a differential staining of the centromeric region and chromosome-specific C-bands that enable the identification of each chromosome of the complement.

Only minor variations in the C-banding pattern were found within and between plants of a given accession line (see Fig. 1 d, Fig. 2 H); however a large amount of variation was observed between the different accessions (Fig. 2). Polymorphic variation was found for C-band size as well as for C-band position. Figure 3 summarizes the results and shows a generalized C-banded karyotype of this species.

Chromosome A. Total chromosome length is 6.6 μm and the arm ratio (L/S) is 1.6. A secondary constriction and a satellite are present in the distal region of the short arm. Marker C-bands are present at the telomeres of both arms and on both sides of the secondary constriction. Additional C-bands may be present at several interstitial locations of both arms.

Chromosome B. The largest chromosome in the complement, showing a total length of 7.0 μm and an arm ratio of 2.9. Marker C-bands are present at the telomere of the short arm and adjacent to the centromere of the long arm. An additional C-band can be frequently seen in the middle of the short arm, and additional bands may be also present in several interstitial regions and at the telomere of the long arm.

Chromosome C. Identical in chromosome length (6.6 μm) to chromosome A, however is slightly more submetacentric (L/S: 1.8). This is the second SAT chromosome pair

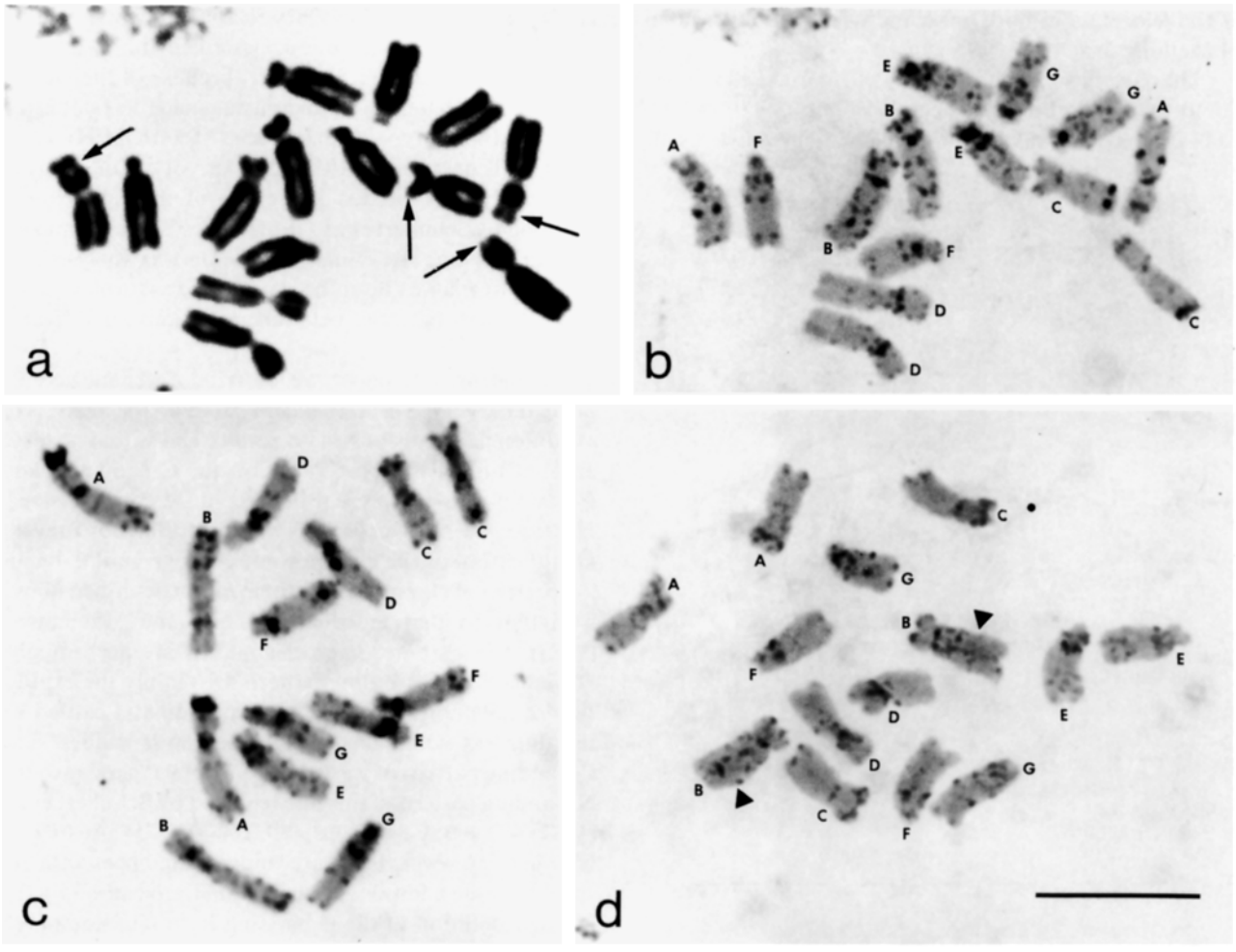


Fig. 1 a–d. C-banded mitotic metaphases of *Aegilops caudata* **a** 'S 740-69' (phase contrast), **b** 'S 740-69', **c** 110/78, **d** V 1. *Arrows* point to the secondary constrictions; *triangles* mark C-band polymorphism. *Bar* = 10 μm

of the complement. The satellite is located in the distal region of the short arm and is usually smaller and more difficult to detect than the one located in the short arm of chromosome A. Marker C-bands are present on both sides of the secondary constriction and at the telomere of the long arm, and several additional C-bands may be present in interstitial regions of both arms. The lack of diagnostic marker C-bands on both arms of chromosomes A and C makes it difficult to distinguish between these chromosomes in some of the accessions analyzed (see Fig. 2D, F, G).

Chromosome D. Similar in total chromosome length (6.6 μm) and arm ratio (1.9) to chromosomes A and C. No marker C-band was observed to be present in all the accessions analysed. However, usually one or two C-bands close to the centromere can be found either in the short or long arm of this chromosome, and further additional C-bands may be present at both telomeres and in the distal region of the long arm.

Chromosome E. The largest of the three acrocentric chromosome pairs (total chromosome length: 6.2 μm, L/S: 4.2). One marker band is present in the middle of the short arm, whereas the long arm carries two marker C-bands close to the centromere and another distally located marker band. Additional C-bands may be present at the telomeres of both arms and in interstitial regions of the long arm.

Chromosome F. Total chromosome length is 5.6 μm and the arm ratio is 7.0. Two marker C-bands are present close to the centromere, and another marker band is located in the distal region of the long arm. Additional C-bands may be present at the telomeres of both arms and in several interstitial regions of the long arm.

Chromosome G. The smallest (total chromosome length 5.3 μm) and most acrocentric chromosome pair of the complement (L/S: 7.8). Three marker bands, closely associated to each other, are present in the proximal region of the long arm, and additional C-bands may be present

at the telomeres of both arms and in interstitial regions of the long arm.

The chromosome morphology of *Ae. caudata* is similar to that described by Chennaveeraiah (1960) on the basis of conventional aceto-orcein staining analysis. Gill (1981), analyzing evolutionary relationships within *Triticeae* by C-band distribution, described the C-banding pattern of *Ae. caudata*. However, because of the lack of prominent C-bands, no attempt was made to establish a C-banded karyotype of this species. Teoh and Hutchinson (1983) described a C-banded karyotype of *Ae. caudata*, and an N-banded karyotype of this species was reported by Schubert et al. (1987). Since in these previous studies only one *Ae. caudata* accession was analysed, no data are available about the range of polymorphic variation of these patterns between accessions of different origins.

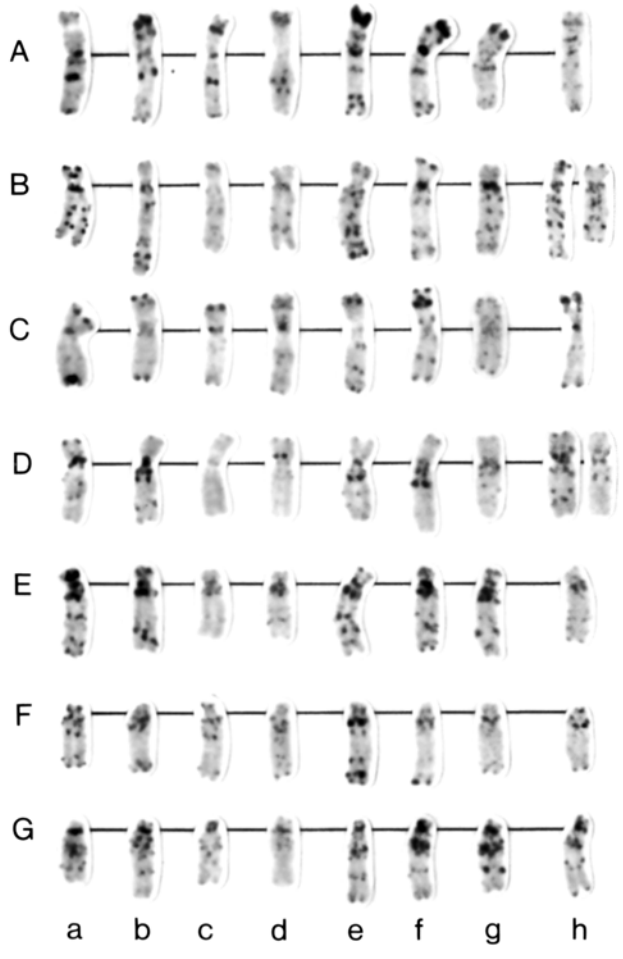


Fig. 2a–g. C-banded karyotypes of *Aegilops caudata*. **a** 'S 740-69' (unknown origin), **b** 21 (unknown origin), **c** 885/85 (Greece), **d** 884/85 (Greece), **e** 110/78 (USSR), **f** TA1909 (Turkey), **g** 743/83 (Turkey), **h** V 1 (Turkey)

In the present paper we describe a generalized C-banded karyotype of *Ae. caudata* based on the analysis of 19 different accessions. The results show that a large amount of polymorphic variation for C-band size and C-band position is present between different accessions. However, in most cases this variation did not prevent identification of the chromosomes. The overall C-banding pattern of *Ae. caudata* chromosomes described above is similar to that reported by Teoh and Hutchinson (1983), and chromosome designations are accordingly. Differences in C-banding pattern are mainly the expression of polymorphism for C-heterochromatin caused by the different accessions analysed in both studies. The C-banding pattern of accession S 740–69 is similar to the N-banding pattern of this line reported by Schubert et al. (1987) (C1 = B, C2 = C, C3 = D, C4 = E, C5 = A, C6 = F, C7 = G). However, there are minor differences with respect to some additional C-bands that are caused by the higher resolution of the C-banding technique compared to N-banding analysis.

Kihara et al. (1965) and Kihara (1981) reported that 1 of 11 accessions of *Ae. squarrosa* (= *T. tauschii*) tested carried reciprocal translocations when compared to other accessions. C-banding analysis also revealed the presence of a reciprocal translocation involving complete chromosome arms in 1 out of 15 different *Ae. squarrosa* accessions analysed (Friebe et al. unpublished results). Large structural rearrangements, which are detectable by

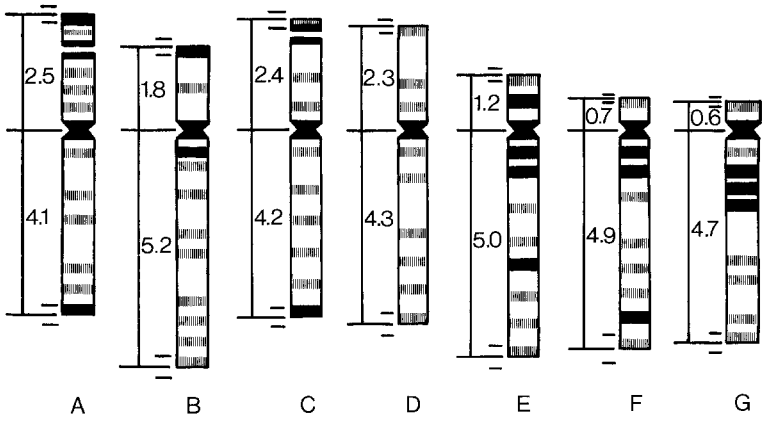


Fig. 3. Generalized C-banded karyotype of *Aegilops caudata*. Marker bands which are present in all accessions are shown in *black* and bands which are only present in some accessions are given in *hatching*. Chromosome arm length data given in μm are based on measurements of 20 complete C-banded cells. Standard deviations of chromosome measurement data are indicated by *small bars*

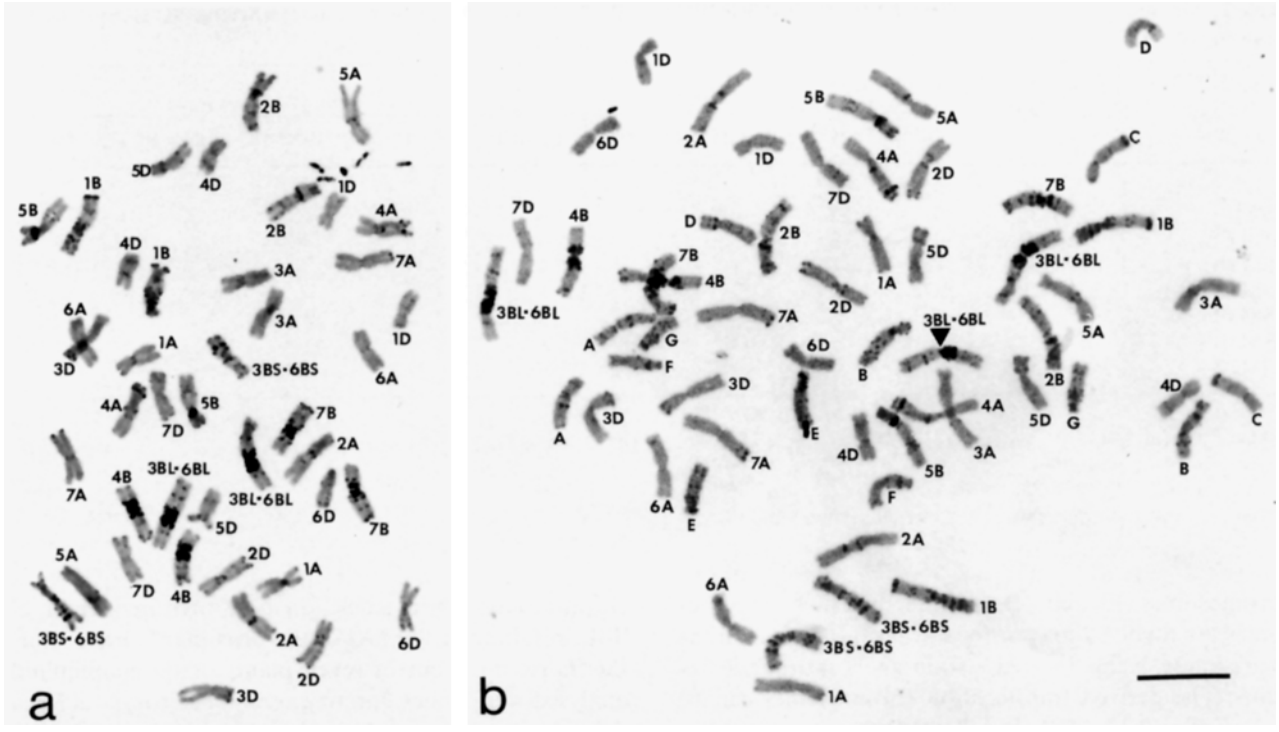
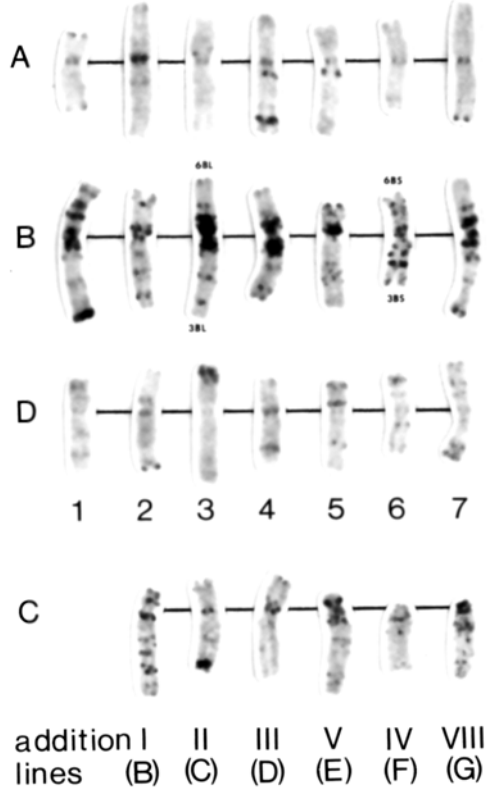


Fig. 4a, b. C-banded mitotic metaphases of *Triticum aestivum* cv 'Alcedo' (**a**) and the derived amphiploid *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740-69' trisomic for chromosome T3BL·6BL (**b**). *Triangle* marks a deletion in the proximal region of 3BL in one of the three T3BL·6BL chromosomes. *Bar* = 10 μm



C-banding analysis, were not found in any of the *Ae. caudata* accessions analysed in the present study. However, some of the polymorphic differences in C-banding pattern described above may be caused by small inversions and translocations, which are difficult to detect by C-banding analysis alone.

Cytological characterization of 'Alcedo' the amphiploid 'Alcedo'-Ae. caudata and derived chromosome addition lines

A C-banded mitotic metaphase of the recipient wheat cv 'Alcedo' is shown in Fig. 4a, and a detailed C-banded karyotype of this same cultivar is shown in Fig. 5. With the exception of chromosome 3B and 6B, the C-banding pattern of all of the other wheat chromosomes is similar to that of the hexaploid wheat cv 'Chinese Spring' (Gill et al. 1991), thus allowing the identification of each of the 21 chromosome pairs of wheat. The banding patterns of

Fig. 5. C-banded karyotype of *Triticum aestivum* cv 'Alcedo' and C-banding patterns of the added *Ae. caudata* chromosomes present in six derived *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740-69' chromosome addition lines

Table 2. Meiotic chromosome pairing at metaphase I in F_1 hybrids of 'Alcedo' (AL) with 'Chinese Spring' (CS) and the CS monosomic 1B, 2B, 3B, 6B and 7B

Cross	No. of plants	No. of PMC's	PMC's with								
			$20^{II}+2^{I}$	21^{II}	$19^{II}+1^{IV}$	$19^{II}+1^{III}+^{I}$	$20^{II}+1^{I}$	$18^{II}+1^{IV}+1^{I}$	$19^{II}+1^{III}$	$18^{II}+1^{III}+2^{I}$	Others
AL	1	30	–	28	2	–	–	–	–	–	–
CS	1	30	5	22	3	–	–	–	–	–	–
AL × CS	7	83	3	3	56	13	–	–	–	–	8[a]
CSM1B × AL	4	82	–	–	–	–	4	55	–	9	14[b]
CSM2B × AL	1	20	–	–	–	–	1	15	–	4	–
CSM3B × AL	3	57	–	–	–	–	15	1	22	7	12[c]
CSM6B × AL	3	57	–	–	–	–	8	–	42	6	1[d]
CSM7B × AL	3	40	–	–	–	–	5	20	–	5	10[e]

[a] $18^{II}+1^{IV}+2^{I}$
[b] $18^{II}+5^{I}$, $18^{II}+1^{III}+2^{I}$, $18^{II}+1^{IV}+1^{I}$, $17^{II}+1^{IV}+3^{I}$, $17^{II}+1^{III}+4^{I}$, $16^{II}+1^{III}+6^{I}$, $16^{II}+2^{III}+3^{I}$
[c] $19^{II}+3^{I}$, $17^{II}+1^{III}+4^{I}$
[d] $19^{II}+3^{I}$
[e] $19^{II}+3^{I}$, $17^{II}+1^{IV}+3^{I}$, $16^{II}+1^{IV}+5$, $16^{II}+1^{III}+6^{I}$

chromosomes 3B and 6B indicate that these chromosomes are involved in reciprocal translocations with the breakpoints being located within the centromeric regions. The derived translocation chromosomes can be described as T3BL·6BL and T3BS·6BS, respectively.

For confirming the presence of wheat-wheat translocations involving chromosomes 3B and 6B in 'Alcedo', meiotic chromosome pairing was analysed in F_1 hybrids of testcrosses of 'Alcedo' with 'Chinese Spring' and in F_1 hybrids between the CS monosomics 1B, 2B, 3B, 6B, 7B and 'Alcedo' (Table 2). The F_1 hybrid 'Alcedo' × 'Chinese Spring' frequently showed the configuration $19^{II}+1^{IV}$ or $19^{II}+1^{III}+1^{I}$, indicating that both wheat cultivars differ from each other by one wheat-wheat chromosome translocation. Furthermore, F_1 hybrids between 'Chinese Spring' mono-3B and mono-6B and 'Alcedo' frequently showed the critical pairing configuration $19^{II}+1^{III}$, thus confirming that the chromosomes involved in this translocation are 3B and 6B.

A C-banded mitotic metaphase of the octoploid amphiploid *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740–69' ($2n=8\times=56$, genomically AABBDDCC) is shown in Fig. 4b. All A-, B- and D-genome chromosomes of wheat and C-genome chromosomes of *Ae. caudata* can be identified by their characteristic C-banding patterns, which are identical to those of the corresponding chromosomes of the parent lines 'Alcedo' and 'S 740–69'. The amphiploid is also homozygous for T3BL·6BL and T3BS·6BS translocations and carries the complete chromosome complement of *Ae. caudata*. The C-banding patterns of *Ae. caudata* chromosomes indicate that these chromosomes are not structurally rearranged compared to the corresponding chromosomes of the donor species.

The metaphase plate shown in Fig. 4b derived from a plant that was trisomic for the translocation chromosome T3BL·6BL, and one of the three translocation chromosomes carries a deletion in the proximal region of 3BL, resulting in the loss of the proximal C-band. Furthermore, three out of seven plants of the amphiploid analysed were either homozygote or heterozygote for a deletion in the long arm of wheat chromosome 2A, and in one plant the *Ae. caudata* chromosome D was carrying a pericentric inversion, resulting in the relocation of the proximal C-band from DS to DL.

C-banding analysis was also used to identify *Ae. caudata* chromosomes in the dervied *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740–69' chromosome addition lines. Six different disomic addition lines, designated I, II, III, V, IV and VIII, were identified to be carrying the *Ae. caudata* chromosomes B, C, D, E, F and G, respectively. The C-banding patterns of the added *Ae. caudata* chromosomes (see Fig. 5) are identical to those of the corresponding chromosomes of the amphiploid and the *Ae. caudata* accession 'S 740–69' (see Fig. 2a), indicating that no structural rearrangements have occurred during the production of this material. So far, no addition line is available for the *Ae. caudata* SAT chromosome pair A. The presence of additional secondary constrictions at metaphase and increased numbers of nucleoli in interphase nuclei of the amphiploid and addition line II indicate that *Ae. caudata* SAT chromosomes are also active in organizing nucleoli when transferred into a wheat background.

C-banding analysis of the wheat chromosome complement in the *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740–69' chromosome addition lines showed that all of the plants of line IV analysed were homozygous for normal wheat chromosomes 3B and 6B and that one plant of line V was heterozygous for chromosomes 3B, 6B, T3BL·6BL and T3BS·6BS. Differences in the C-banding pattern compared to the 'Alcedo' type were also found in other addition lines. The majority of these modifications

are similar to variations also found in other cultivars of wheat, indicating that they are probably not the result of chromosomal rearrangements that occurred during the production of the chromosome addition lines but the expression of C-band polymorphism present among wheat cultivars. These results indicate that the addition lines are not in a pure 'Alcedo' background and that other cultivars of wheat were also involved in the production of this material.

Endo and Katayama (1978) reported the presence of a selectively retained *Ae. caudata* chromosome in wheat-*Ae. caudata* derivatives. Gametocidal chromosomes showing preferential transmission and causing chromosome aberrations are known to be present in many species of the genus *Aegilops*, including *Ae. caudata* and the derived polyploids *Ae. triuncialis* and *Ae. cylindrica* (for review see Endo 1990). The gametocidal C-genome chromosome is acrocentric and related to homoeologous group 3 (Endo 1990). This chromosome corresponds to one of the three acrocentric chromosomes designated E, F or G present in the addition lines V, IV and VIII. However, neither one of these lines nor the addition lines I, II and III showed unusual cytological behavior. Only chromosome C is characterized by a preferential transmission compared to the other *Ae. caudata* chromosomes studied up until now (Schubert 1989).

Schubert (1989) and Blüthner et al. (1988) reported a high chromosomal instability of the amphiploid *T. aestivum* cv 'Alcedo'-*Ae. caudata* 'S 740–69' and in their derived backcross derivatives. This has resulted in the selection of many 42-chromosomic lines that diverge from the 'Alcedo' type and that show features of the *Ae. caudata* parent. It was assumed that this instability may be caused by gametocidal *Ae. caudata* chromosomes. However, neither the analysis of meiotic chromosome pairing in the six *T. aestivum* cv 'Alcedo' -*Ae. caudata* 'S 740–69' chromosome addition lines (Schubert 1989) nor the present C-banding analysis of the material analysed in the present study has revealed any evidence in support of this assumption. Further analysis of the 42-chromosomic 'Alcedo'-*Ae. caudata* derivatives are neccessary in order to establish their chromosomal constitutions.

The present analysis shows that addition line II is carrying the *Ae. caudata* SAT chromosome C and that the other SAT chromosome of the *Ae. caudata* complement is not present in any of the addition lines analyzed. Within the *Triticeae* SAT chromosomes are known to belong to homoeologous groups 1, 5 and 6. Preliminary studies on *T. aestivum-Ae. caudata* substituion and translocation lines showed that the short arm of the *Ae. caudata* chromosome C compensates for the loss of wheat chromosome arm 5DS in a derived TCS·5DL translocation line. Since compensation is known to occur only between chromosomes belonging to the same homoeologous group, this indicates a close relationship of the *Ae. caudata* chromosome C to group 5. Furthermore, chromosome C carries an isozyme marker (leaf NADP-dependent aromatic alcohol dehydrogenase) (Schmidt et al. unpublished results) known to be present on group 5 chromosomes which is further evidence that chromosome C is homoeologue to group 5.

Schmidt et al. (unpublished results) also showed that a group 1-specific isozyme marker (leaf peroxidase) derived from *Ae. caudata* is only present in the amphiploid and not in any of the derived six chromosome addition lines. Thus, the *Ae. caudata* SAT chromosome A which was shown to be missing in the set of addition lines may be related to group 1. Homoeology of chromosome A to group 1 is also indicated by the C-banding analysis of a *T. aestivum-Ae. caudata* (1C) 1D substitution line described by Muramatsu (1959) (Friebe et al. unpublished results). The results confirm that the *Ae. caudata* SAT chromosome of this line substitutes for the loss of wheat chromosome 1D and that the overall C-banding pattern of chromosome 1C is very similar to that of the *Ae. caudata* designated A in the present study.

Furthermore, isozyme analysis of the addition lines III carrying the *Ae. caudata* chromosome D indicates homoeology of this chromosome to group 6, and chromosome F present in the addition line IV shows homoeology only to group 3 (Schmidt et al. unpublished results). In the same study no isozyme marker was found for the addition line V carrying chromosome E, and chromosome B and G present in addition lines I and VIII show a relationship to group 4 and 5 and to group 4 and 3, respectively. Further, analysis of the compensation abilities of *Ae. caudata* chromosomes in substitution and translocation lines are necessary in order to establish unambiguously the homoeology of all *Ae. caudata* chromosomes.

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