Pl. Syst. Evol. 192: 165 – 176 (1994)

—Plant—
Systematics
and
Evolution

Comparison of the Giemsa C-banded and N-banded karyotypes of two *Elymus* species, *E. dentatus* and *E. glaucescens* (*Poaceae: Triticeae*)

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Received April 4, 1994

Key words: *Poaceae, Triticeae, Elymus dentatus, E. glaucescens.* – Karyotype, Giemsa C-banding, N-banding, genome differentiation.

Abstract: The karyotypes of *Elymus dentatus* from Kashmir and *E. glaucescens* from Tierra del Fuego, both carrying genomes **S** and **H**, were investigated by C- and N-banding. Both taxa had 2n = 4x = 28. The karyotype of *E. dentatus* was symmetrical with large chromosomes. It had 18 metacentric, four submetacentric and six satellited chromosomes. The karyotype of *E. glaucescens* resembled that of *E. dentatus*, but a satellited chromosome pair was replaced by a morphologically similar, non-satellited pair. The C-banding patterns of both species had from one to five conspicuous and a few inconspicuous bands per chromosome. N-banding differentiated the chromosomes of the constituent genomes by producing bands in the **H** genome only. The **S** genomes of both species were similar with five metacentric and two satellited chromosomes having most conspicuous C-bands at telomeric and distal positions. They resembled the **S** genome of the genus *Pseudoroegneria*. The **H** genomes had four similar metacentric and two submetacentric chromosomes. The seventh **H** genome chromosome of *E. dentatus* was satellited, that of *E. glaucescens* non-satellited, but otherwise morphologically similar. The C-bands were distributed at no preferential positions. The **H** genome of *E. dentatus* resembles the **H** genomes of some diploid *Hordeum* taxa.

Giemsa C- and N-banding patterns of chromosomes at somatic metaphase supplemented by chromosome morphology are widely used to identify chromosomes, to separate taxa, and to study relationships. In the large, non-monophyletic genus *Elymus* L. (Kellogg 1989, Seberg & al. 1991) which comprises approximately 150 allopolyploid species, the C-banded karyotypes have only been studied in three of the about 45 tetraploid **SH** genome-carrying species. The three species are: the North American *E. canadensis* L. (Park & al. 1990), the North American-North Asian *E. trachycaulus* (Link) Gould ex Shinners (Morris & Gill 1987), and the North-Central Asian *E. sibiricus* L. (Agafonov 1991). These three species represent only a small fraction and a limited part of the distribution range of the **SH** genome carrying *Elymus* species, which otherwise occur in the temperate parts of the Americas, Eurasia, and New Zealand.

The only species that has hitherto been subjected to N-banding is *E. trachycaulus*. The technique proved to differentiate the chromosomes of genome **S** supposed to be derived from the genus *Pseudoroegneria* (NEVSKI) LÖVE from those of genome **H** supposed to be derived from the genus *Hordeum* L. (syn. *Critesion* RAFIN.) (MORRIS & GILL 1987). In addition to the few species studied in depth by banding techniques, the karyotypes of a few additional species have been investigated using conventional cytological approaches (SCHULZ-SCHAEFFER & JURASITS 1962, HUNZIKER 1966, RUNEMARK & HENEEN 1968, DUBCOVSKY & al. 1989).

The present investigation was initiated to enlarge our knowledge of the karyotype variation found among the **SH** genome-carrying *Elymus* species. For this purpose, the C- and N-banded karyotypes of two species from geographically widely separated marginal areas, viz. *E. dentatus* (HOOK. f.) TZVELEV from Kashmir, Pakistan, and *E. glaucescens* SEBERG from Tierra del Fuego, Argentina, were compared with the previously published karyotypes. The species of the genus *Elymus* are of considerable interest agronomically. Some of them are important forage grasses, and they are members of the secondary gene pool of wheat (BOTHMER & al. 1992).

Material and methods

Plants. The material was derived from seeds of accession H 4092 of *E. dentatus* collected in Kashmir, Pakistan, by R. VON BOTHMER, September 13, 1983 (SALOMON & al. 1988), and of accession H 6102 of *E. glaucescens* (for synonyms, see SEBERG 1989) collected on Tierra del Fuego, Argentina, by O. SEBERG, January 31, 1987. H 4092 had been multiplied before use. The plants used for cytological studies were grown in pots in a greenhouse at Risø National Laboratory. Nomenclature of species follows LÖVE (1984) and BOTHMER & al. (1991).

Cytology. Giemsa C- and N-banding of root tip chromosomes at somatic metaphase and $AgNO_3$ staining of interphases to visualize nucleoli followed LINDE-LAURSEN (1975, 1984), LINDE-LAURSEN & al. (1980), and LINDE-LAURSEN & BOTHMER (1984a). In the idiograms, the chromosomes are grouped according to supposed genomic similarity. Within the groups they are arranged in three types, i.e., metacentric, submetacentric, and satellited (SAT)-chromosomes (cf. LEVAN & al. 1965).

Results

E. dentatus. All plants of *E. dentatus* H 4092 had invariably 2n = 4x = 28 (Table 1) in agreement with a previous observation by SALOMON & al. (1988). The chromosomes were long. Their length varied from 8.3 to 12.6 µm with an average of 11.2 µm. The quotient (ratio) longest/shortest chromosome was 1.5 (Table 1). The symmetrical karyotype consisted of nine pairs of metacentrics, two pairs of submetacentrics, and three pairs of SAT-chromosomes. The latter included two metacentric pairs with satellites approximately equal in length to the subtending short and long arms, respectively, and a submetacentric pair with small satellites on the short arms (Figs. 1, 2a). The presence of six SAT-chromosomes was supported by observations of a maximum of six standard-sized nucleoli in interphases (Table 1).

The C-banding patterns of the chromosomes of *E. dentatus* (Figs. 1, 2a) were characterized by from very small to larger bands. A few bands were double. The number of conspicuous bands varied from one to five per chromosome. The banding patterns of the single chromosomes varied from patterns with one or a few bands localized at telomeric and distal positions to patterns with bands distributed at no

Table 1. Chromosome number, maximum number of submetacentrics (SM), SAT-chromosomes (SAT) and nucleoli (N), chromosome length, ratio longest/shortest chromosome (L/S), and amount of constitutive heterochromatin in the two *Elymus* species investigated

Species	Acc. no.	2n	SM	SAT	N	Mean chromosome length and range (μm)	L/S	Constitutive heterochromatin (%)
E. dentatus	H 4092	28	4	6	6	11.2 (8.3–12.6)	1.5	8.3
S genome		14		4		10.9 (8.3–12.3)	1.5	6.5
H genome		14	4	2		11.6 (10.3–12.6)	1.2	10.0
E. glaucescens	H 6102	28	4	4	4	14.6 (10.7–17.1)	1.6	9.5
S genome		14		4		14.4 (10.7–16.7)	1.6	6.8
H genome		14	4			14.8 (12.1–16.3)	1.3	11.8

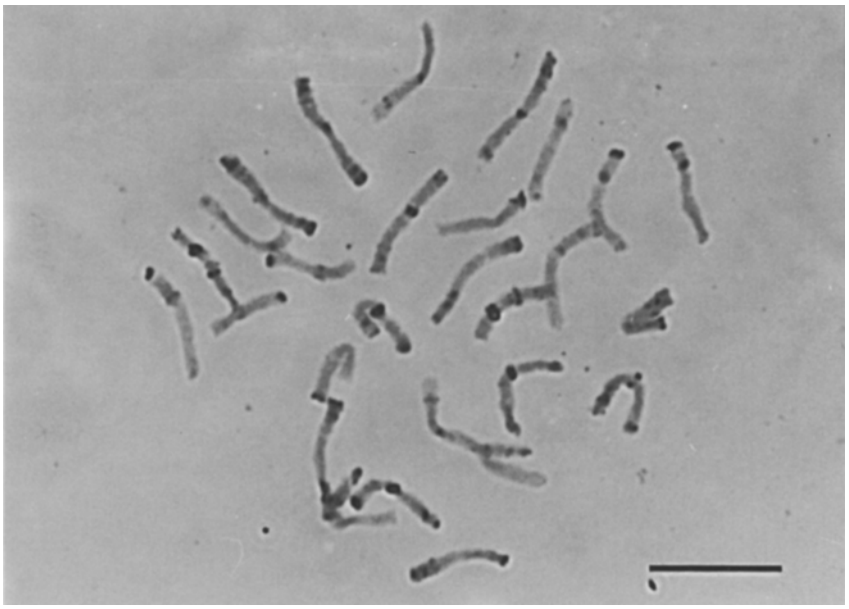

Fig. 1. C-banded somatic metaphase of *Elymus dentatus* H 4092, 2n = 28. – Bar: 10 μm

preferential positions. Eleven chromosomes had conspicuous bands at one or both telomeres. The two SAT-chromosome pairs with comparatively large satellites had bands at the nucleolar constrictions in the short arms and in the satellites, respectively. These bands showed at duller magenta colour than other C-bands indicating a different constitution. The small satellites were entirely heterochromatic. Banding patterns and chromosome morphology identified homologous and differentiated non-homologous chromosomes. The banding patterns gave no indication of homoeology. The absence of C-band heteromorphy agrees with the predominantly self-fertilizing nature of *E. dentatus*. The chromocentres of Giemsa-stained interphases varied in size from very small to more conspicuous ones in agreement with the size

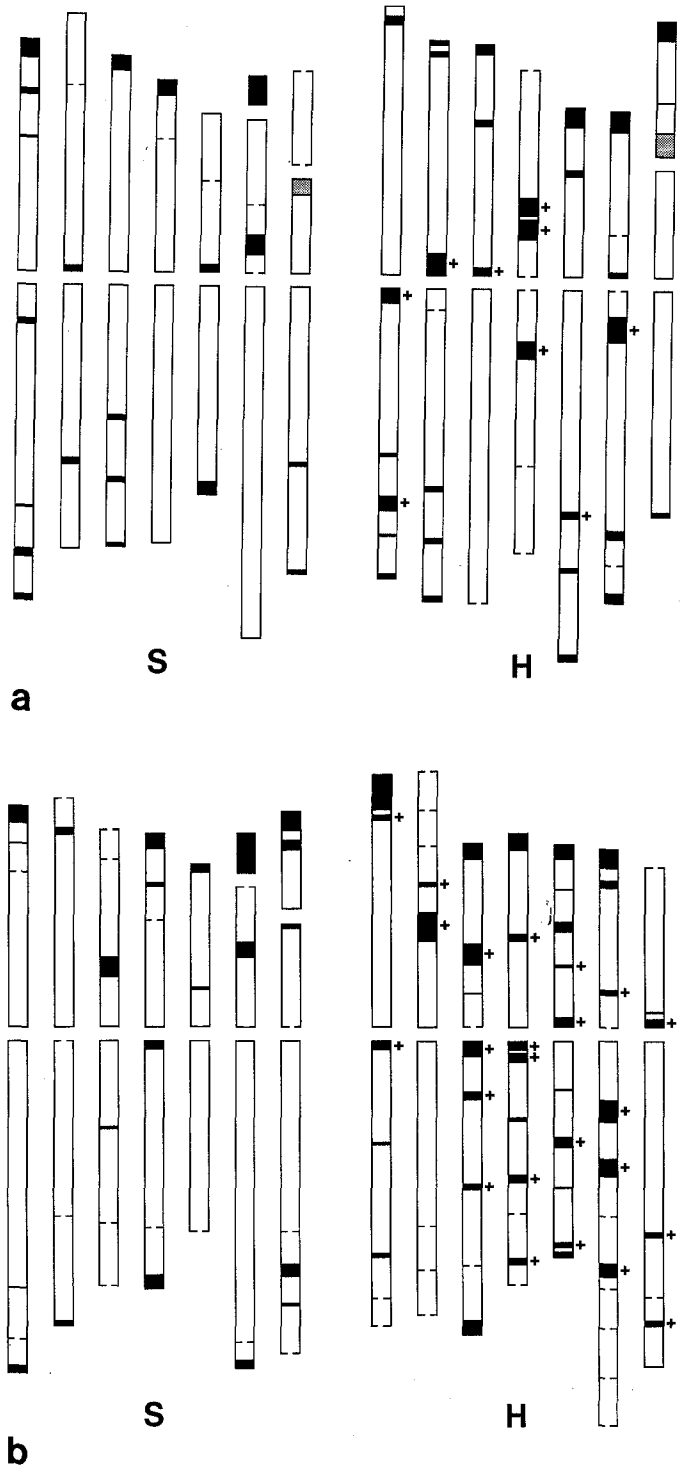

Fig. 2. Idiograms of the chromosomes of *Elymus dentatus* and *E. glaucescens* showing relative sizes and positions of C-bands (solid regions; broken lines indicate very small, inconsistently observed bands). *a E. dentatus* H 4092, n = 14; *b E. glaucescens* H 6102, n = 14. – **S** and **H** indicate genomic relationship of the chromosomes. Conspicuous bands observed at similar positions as C-bands in **H** genomes after N-banding indicated by +

of the C-bands. The length of the C-banded area on the chromosomes constituted 8.3% of total chromosome length (Table 1).

N-banding produced conspicuous bands in six chromosome pairs only, four metacentric and the two submetacentric pairs. In the six pairs, the N-bands were located at the same positions as the C-bands except that no telomeric bands were produced. In spite of this, the similarity in the banding patterns reliably made homologous chromosomes identifiable with the two banding techniques. The remaining eight chromosome pairs showed no or very weak N-bands with some variation between cells. In agreement with observations in *E. trachycaulus* it can be concluded that the six chromosome pairs having both C+ and N+ heterochromatin belong to genome **H** (MORRIS & GILL 1987). Of the eight pairs producing no bands after N-banding, the metacentric pair with nucleolar constrictions in the long arms most probably belong to genome **H.** No diploid *Pseudoroegneria* species investigated cytologically has more than two SAT-chromosome pairs, and the chromosome type has not been observed in any *Pseudoroegneria* karyotype (DVOŘÁK & al. 1984, ENDO & GILL 1984, HSIAO & al. 1986, PARK & al. 1990). Further, the type is found in most *Hordeum* species of the Americas and in *H. brevisubulatum* (TRIN.) LINK subsp. *brevisubulatum* from East Asia (LINDE-LAURSEN & al. 1992). The failure to produce N-bands in this SAT-chromosome pair at the same positions as the conspicuous bands produced at the nucleolar constrictions by C-banding corresponds to similar observations in the SAT-chromosomes of *H. vulgare* L. (e.g., LINDE-LAURSEN 1981, SINGH & TSUCHIYA 1982). The seven remaining unbanded chromosome pairs belong to genome **S** (cf. MORRIS & GILL 1987). The development of a number of very weak bands in some N-banded cells at the positions of conspicuous C-bands supported by chromosome morphology rendered it possible to identify each of the seven chromosome pairs with its C-banded homologue.

The differentiation of the **S** and **H** genomes of *E. dentatus* through the differential reaction of the chromosomes to C- and N-banding made it possible to study the karyotypic characteristics of each genome. Five metacentric and the two SAT-chromosome pairs with the satellites in their short arms belong to the **S** genome (Fig. 2 a). The remaining four metacentric, the two submetacentric, and the metacentric SAT-chromosome pair with the satellites in the long arms belong to the **H** genome. The C-banding patterns of the **S** genome chromosomes were characterized by mainly telomeric and distal bands, whereas those of the **H** genome chromosomes had the bands at no preferential positions. The average length of the chromosomes of the two genomes differed somewhat, 10.9 µm for the **S** genome vs. 11.6 µm for the **H** genome (Table 1), but the ratios longest/shortest chromosome were different. The ratio was 1.5 for the **S** genome and 1.2 for the **H** genome. The difference was primarily caused by the comparative shortness of the smallest metacentric chromosome of the **S** genome. The **H** genome had more and larger C-bands at centromeric and intercalary positions than the **S** genome (Fig. 2 a). This resulted in a larger area (10.0%) on the chromosomes of the **H** genome covered by C-bands than on the chromosomes of the **S** genome (6.5%) (Table 1).

E. glaucescens. All plants of *E. glaucescens* had 2n = 4x = 28 as expected (Table 1; Figs. 2 b, 3) (HUNZIKER 1966; DUBCOVSKY & al. 1989, 1992). The chromosome complement had an overall similarity with that of *E. dentatus* (Figs. 1, 2 a). The chromosomes were long. Their length varied from 10.7 to 17.1 µm with

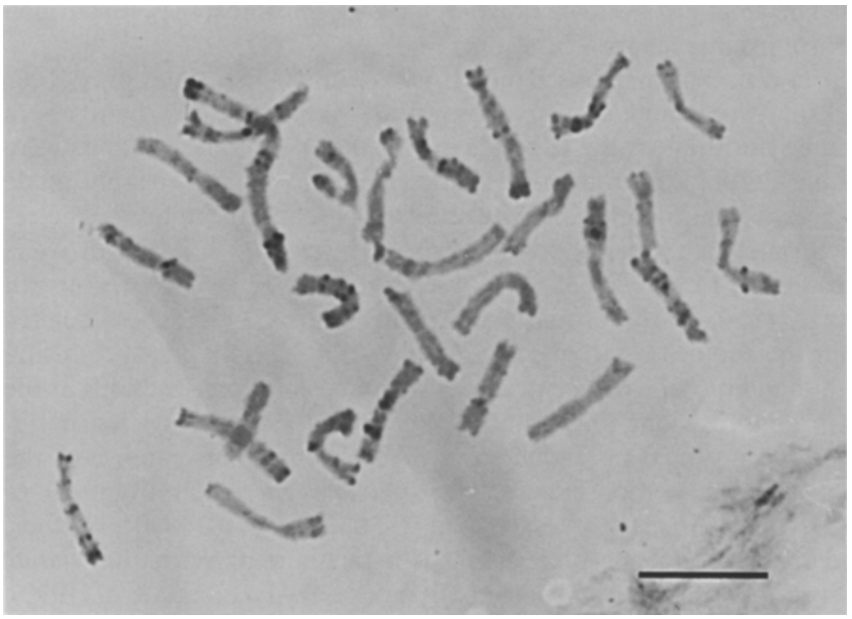

Fig. 3. C-banded somatic metaphase of *Elymus glaucescens* H 6102, 2n = 28. – Bar: 10 µm

a mean length of 14.6 µm (Table 1). The ratio longest/shortest chromosome at 1.6 was very similar to that of *E. dentatus* at 1.5. The symmetrical karyotype was similar to that of *E. dentatus* (Fig. 2 a) except that the metacentric chromosome pair with satellites in the long arms was replaced by a pair of metacentrics without satellites (Fig. 2 b). The karyotype was similar to those presented by HUNZIKER (1966) and DUBCOVSKY & al. (1989). The presence of four chromosomes with nucleolar constrictions was supported by observations of a maximum of four standard-sized nucleoli in silver nitrate-stained interphases. Four nucleoli had previously been reported by DUBCOVSKY & al. (1992). The C-banding patterns of the chromosomes of *E. glaucescens* (Figs. 2 b, 3) were also very similar to those of *E. dentatus*, but the chromosomes with intercalary bands had generally a higher number of conspicuous bands at these positions. This resulted in a slightly larger area (9.5%) covered by C-bands on the chromosomes of *E. glaucescens* (Table 1) than in *E. dentatus* (8.3%). The small satellites were entirely heterochromatic. Ten chromosome pairs had conspicuous bands at the telomeres. In contrast to the conspicuous bands at the nucleolar constrictions of the SAT-chromosomes of *E. dentatus*, the SAT-chromosomes of *E. glaucescens* had only small or very small bands at these locations. Similarities in banding patterns and chromosome morphology rendered it possible to identify homologues and differentiate non-homologues. There was no indication of homoeology. The absence of band heteromorphy supports that *E. glaucescens*, like *E. dentatus*, is generally inbreeding. The chromocentres were from small to very small corresponding to the size of the C-bands.

N-banding produced deeply stained, conspicuous bands in seven chromosome pairs, five metacentric pairs and the two submetacentric ones, at intercalary and centromeric positions. At these positions, the N-bands were located similarly to the conspicuous C-bands rendering it possible to identify homologues. The tech-

nique produced no or very weak bands in the remaining seven pairs, five metacentric and the two SAT-chromosome pairs.

As in *E. dentatus*, the differential reaction of the chromosomes of *E. glaucescens* to N-banding made it possible to study the karyotypes of genomes **S** and **H** separately (cf. Fig. 2 b). The seven chromosome pairs producing deeply stained bands after both C- and N-banding belong to the **H** genome, whereas the seven pairs reacting with clearly identified bands only to C-banding belong to the **S** genome (cf. MORRIS & GILL 1987). The chromosomes of the two genomes were rather equal in length, but the ratio longest/shortest **S** genome chromosome at 1.6 was greater than that of the **H** genome chromosomes at 1.3 on account of the relative shortness of the shortest metacentric **S** genome pair like in *E. dentatus* (Table 1). The C-banding patterns of the **S** genome chromosomes were characterised by mainly having telomeric and distal bands, whereas the patterns of the **H** genome chromosomes were characterized by having the conspicuous bands distributed at no preferential positions (Fig. 2 b). A more heavy banding of the **H** genome chromosomes was reflected in a larger banded area (11.8%) of the total length of the **H** genome chromosomes, than of the **S** genome chromosomes (6.8%, Table 1).

Discussion

The populations of *E. dentatus* and *E. glaucescens* were tetraploid with $2n = 4x = 28$. This chromosome number was previously established in *E. glaucescens* (HUNZIKER 1966; DUBCOVSKY & al. 1989, 1992) and in the *E. dentatus* population H 4092 (SALOMON & al. 1988). However, other studies on *E. dentatus* report $2n = 6x = 42$ (PARKASH 1979, LÖVE 1984). The observation of two different chromosome numbers indicates that what has hitherto been named *E. dentatus* may in fact be two different species. The problem needs further investigation.

MORRIS & GILL (1987) used C- and N-banding in their characterization of the chromosome complement of the **SH** genome carrying *E. trachycaulus*. The seven chromosomes belonging to the **H** genome showed strongly stained, conspicuous, diagnostic bands at centromeric, intercalary and telomeric positions after C-banding, whereas N-banding produced bands at centromeric and a few intercalary positions only. A failure of N-banding to produce telomeric bands in a **H** genome was previously observed in the **I(H)** genome carrying *H. vulgare* L. (cf. LINDE-LAURSEN 1981). In contrast, six of the seven chromosomes belonging to the **S** genome showed clearly stained, mostly telomeric or subtelomeric bands only after C-banding. N-banding produced weakly stained bands at the centromeric regions in three chromosomes only. The seventh chromosome showed no bands at all. Our observations showed a very similar differentiation of the chromosomes of *E. dentatus* and *E. glaucescens* into two sets of seven chromosomes each, supporting their grouping with the **SH** genome carrying *Elymus* species (SALOMON 1994). The chromosomes of the **S** genomes of *E. dentatus* and *E. glaucescens* were morphologically similar comprising five metacentric and two SAT-chromosomes, the latter including a submetacentric with a small satellite and a metacentric with a rather large satellite in the short arms. Only the latter SAT-chromosome was observed in *E. trachycaulus* by MORRIS & GILL (1987), designated S 1. However, DUBCOVSKY & al. (1992) observed four nucleoli in this species indicating two pairs of chromosomes with nucleolus forming activity. The failure of MORRIS & GILL (1987) to identify the

unobserved SAT-chromosome type may be the presence of only a minute satellite in this chromosome in their material. Six chromosomes of the **H** genomes of *E. dentatus* and *E. glaucescens*, four metacentrics and two submetacentrics, were likewise similar, whereas the seventh chromosome of *E. dentatus*, the metacentric with a rather large satellite in the long arm, was represented by a metacentric without a satellite in *E. glaucescens*. A similar constitution without a SAT-chromosome of the **H** genome was also found in *E. trachycaulus* (MORRIS & GILL 1987) indicating complete suppression of the **H** genome NORs in the two species in contrast to the active **H** genome NOR of the Asian *E. dentatus*.

The karyotype of *E. glaucescens* has been reported in five other populations of *E. glaucescens*, in three populations of *E. angulatus* PRESL, in *E. caninus* (L.) L., and in *E. lanceolatus* (SCRIBN. & SMITH) GOULD (SCHULZ-SCHAEFFER & JURASITS 1962, HUNZIKER 1966, RUNEMARK & HENEEN 1968, DUBCOVSKY & al. 1989). However, in one population of *E. angulatus* [syn. *E. breviaristatus* (HITCHC.) LÖVE, nomen illeg.], HUNZIKER (1966) found only metacentric chromosomes besides the four satellited ones. In *E. caninus*, SCHULZ-SCHAEFFER & JURASITS (1962) did not observe the submetacentric SAT-chromosome type. The karyotype of *E. sibiricus* was studied by AGAFONOV (1991), and it was largely similar to the *E. glaucescens* type, but a metacentric chromosome pair was replaced by a submetacentric pair. The karyotype of *E. trachycaulus* with a single SAT-chromosome pair similar to the metacentric pair of *E. glaucescens* was previously established in *E. alaskanus* (SCRIBN. & MERR.) LÖVE and, as mentioned, in a population of *E. caninus* (SCHULZ-SCHAEFFER & JURASITS 1962). A karyotype, also with one SAT-chromosome pair only, but of a different type, has been published for the North American *E. canadensis* (PARK & al. 1990). The SAT-chromosome pair was metacentric and carried small satellites. The type may have been formed through a pericentric inversion in the submetacentric SAT-chromosome type. However, DUBCOVSKY & al. (1992) observed four nucleoli in *E. canadensis* indicating the existence of four chromosomes with nucleolus forming activity. Considered together, the observations suggest that the basic karyotype of the group of *Elymus* species carrying **SH** genomes is similar to the karyotype found in *E. glaucescens*. It may, however, be variously modified, e.g., by variation in the level of suppression of NOR activity and chromosomal rearrangements. The presence of chromosomal interchanges is supported by observations of multivalent formation in pollen mother cells at meiotic metaphase I in interspecific hybrids combining the genomes of, e.g., *E. magellanicus* (DESV.) LÖVE (probably = *E. glaucescens* or *E. angulatus*), *E. trachycaulus, E. sibiricus*, and *E. canadensis* (DEWEY 1968, 1974; JENSEN 1993). The observations in some species of more nucleoli than indicated by the number of SAT-chromosomes (DUBCOVSKY & al. 1992) are stressing the need for more studies on the karyotypes of the **SH** genome *Elymus* species.

Whereas the differential reaction to C- and N-banding and overall similarities in chromosome morphology clearly grouped the single chromosome of *E. dentatus* and *E. glaucescens* with the **S** and **H** genomes, respectively, the homologous relationships of all chromosomes could only be recognized reliably within species. Between species, the presence of C-banding pattern polymorphism prevented a safe identification of homologues/homoeologues besides that based an overall similarities in chromosome morphology, i.e., of the SAT-chromosomes and the shortest

metacentric of the **S** genomes and of the submetacentrics of the **H** genomes. Band heteromorphy was never observed in agreement with the inbreeding nature of both species.

It may be very difficult or almost impossible to identify the genome donors of polyploid species, and except in cases of wild polyploids of very recent origin or polyploid crop species, it is a highly dubious matter to consider one extant taxon as the ancestor of another extant taxon (KELLOGG & BIRCHLER 1993). The present discussion is based upon considerations of overall similarity of the chromosomes and genomes, with all the pitfalls implied by this. Hence a statement like *P. spicata* (PURSH) LÖVE is the donor of the **S** genome of *E. glaucescens* indicates that the karyotype of *P. spicata* is most similar to the **"S"** genome in *E. glaucescens*. However, by doing so, hypotheses that are testable are generated.

The donor of the **S** genome to *E. trachycaulus* was originally suggested to be the North American *P. spicata* (STEBBINS & SNYDER 1956). This may be extended to apply to the **S** genome of *E. glaucescens* as well, as no *Pseudoroegneria* species are found in South America. In agreement with its distribution area, a more likely donor of the **S** genome to *E. dentatus* may be one of the Central Asian *Pseudoroegneria* species, e.g., *P. cognata* (HACKEL) LÖVE. However, as all diploid *Pseudoroegneria* species studied have very similar karyotypes (DVOŘÁK & al. 1984, ENDO & GILL 1984, HSIAO & al. 1986, PARK & al. 1990), this needs verification using other approaches. The similarity of the *Pseudoroegneria* karyotypes allows identification of the **S** genome SAT-chromosomes of *E. dentatus* and *E. glaucescens* with their *Pseudoroegneria* homologues. The SAT-chromosomes with the small satellites are homologous with the *Pseudoroegneria* SAT-chromosome variously designated 5S, B, 2 (number in idiogram from the left), and 3, and those with the long satellites with the *Pseudoroegneria* SAT-chromosome 6S, A, 5 (number), and 1 (designations according to DVOŘÁK & al. 1984, ENDO & GILL 1984, HSIAO & al. 1986, PARK & al. 1990, respectively).

A recently produced gene tree (SEBERG & LINDE-LAURSEN, unpubl.) based on a phylogenetic analysis of the first 1181 bases of *rbc*L (the gene coding for the large subunit of ribulose-1,5-biphosphate carboxylase/oxygenase, *rubisco*), and including *E. glaucescens*, *E. trachycaulus*, and *P. spicata* adds support to the hypothesis that *Pseudoroegneria* is the donor of the **S** genome. In the consensus tree of the 10 equally parsimonious trees produced, *Pseudoroegneria* is included in an unresolved clade that otherwise includes tetra- and hexaploid *Elymus* species from the Americas.

MORRIS & GILL (1987) suggested that the donor of the **H** genome of *E. trachycaulus* might be the diploid *H. brachyantherum* NEVSKI subsp. *californicum* (COVAS & STEBBINS) BOTHMER, JACOBSEN & SEBERG. This taxon may also have been the donor of the **H** genome of *E. glaucescens* on the basis of the overall similarity of the C-banding patterns of the **H** genomes of the two taxa. However, our extensive studies on the C-banded karyotypes of diploid North and South American *Hordeum* species showed that most taxa had very similar karyotypes, including one or two SAT-chromosome pairs with little variation among C-banding patterns (see LINDE-LAURSEN & al. 1992), thus preventing a reliable identification of a probable donor based on karyotypic characters.

The karyotype of *E. dentatus* deviates from those of the other **SH** genome carrying *Elymus* species studied (SCHULZ-SCHAEFFER & JURASITS 1962, HUNZIKER 1966, RUNEMARK & HENEEN 1968, MORRIS & GILL 1987, DUBCOVSKY & al. 1989, PARK & al. 1990, AGAFONOV 1991, this study) by having a third SAT-chromosome pair (the metacentric pair with the satellites on the long arms). We have shown that this chromosome type most likely belongs to the **H** genome. Morphologically it resembles a similar SAT-chromosome found in the majority of the **H** genomes of the American *Hordeum* species (LINDE-LAURSEN & al. 1992) and in the diploid cytotype of the self-incompatible Asian *H. brevisubulatum* subsp. *brevisubulatum* (LINDE-LAURSEN & BOTHMER 1984 b) suggesting that it may be derived from any of these species. However, the lower number of conspicuous intercalary C-bands in the chromosomes of the latter taxon than in the diploid American species, corresponding with a similar tendency in the **H** genome of *E. dentatus* relative to those of *E. glaucescens* and *E. trachycaulus* (MORRIS & GILL 1987), may be judged in favour of a derivation from *H. brevisubulatum* subsp. *brevisubulatum*. We have previously proposed that this taxon may occupy a central position in the evolution of the East Asian and American *Hordeum* species (LINDE-LAURSEN & al. 1992). The difference in the number of conspicuous C-bands observed between *E. trachycaulus*/*E. glaucescens* and *E. dentatus* (MORRIS & GILL 1987, this study) was also observed between *E. sibiricus* and *E. canadensis* (PARK & al. 1990, AGAFONOV 1991). However, as the two latter species had not been subjected to N-banding, it could not be established whether this difference was primarily caused by a difference in the level of C-banding of the **H** genome as in the three former species.

The presence of a **H** genome chromosome pair with nucleolus forming activity in *E. dentatus* and its absence in *E. trachycaulus* and *E. glaucescens*, and probably in most **SH** genome species (SCHULZ-SCHAEFFER & JURASITS 1962, HUNZIKER 1966, RUNEMARK & HENEEN 1968, DUBCOVSKY & al. 1989, PARK & al. 1990, AGAFONOV 1991), demonstrates complete nucleolar dominance of the **S** genome NORs in *E. trachycaulus* and *E. glaucescens*. The contrasting levels of nucleolar dominance indicates that nucleolar organizers of the same basic genome, i.e., **H** or **S**, may have different "strengths" and supports that *E. dentatus* may have been derived from another *Pseudoroegneria* × *Hordeum* combination than the other **SH** genome *Elymus* species studied (cf. SOLTIS & SOLTIS 1993). It is not possible to establish whether the NORs of the **S** genome of *E. dentatus* have a "weaker" effect, or that of the **H** genome has a "stronger" effect than in the other **SH** genome species.

The significant difference in chromosome length between the genomes of *E. dentatus* and *E. glaucescens* must be referred to the influence of the pretreatment of the root-tips. This indicates that absolute chromosome length is a less dependable character (LINDE-LAURSEN & al. 1990) as also indicated by the much shorter chromosome lengths of the **SH** genome *Elymus* species studied by DUBCOVSKY & al. (1989).

LÖVE (1984) grouped *E. dentatus* in *Elymus* sect. *Goulardia* (HUSNOT) TZVELEV and *E. glaucescens* in sect. *Dasystachyae* LÖVE. Despite the presence of the same genomes, **S** and **H**, the overall similarity of the C-banded karyotypes, and the identical reaction of the chromosomes of the constituent genomes to N-banding, *E. dentatus* and *E. glaucescens* apparently have different histories. The consequence of this is that *Elymus*, as it has previously been stressed (KELLOGG 1989, SEBERG

& al. 1991), is polyphyletic. It even implies that the **SH** genome species constitute a polyphyletic group. Hence, if one choices to maintain *Elymus* as a taxon, it has no history of its own. It is only a man-made artifact.

The authors are grateful to Mrs ELLY IBSEN for her skilful technical assistance.

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Accepted May 18, 1994 by F. EHRENDORFER