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Interspecific variation in C-banded chromosomes of diploid *Aegilops* species

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Summary. Based on an improved C-banding technique, the C-banding patterns of all 11 diploid *Aegilops* species were described and compared. All diploid species exhibit characteristically different patterns which enable the chromosomes of any complement to be identified individually. These patterns confirm existing genome symbols and provide further evidence for the suggested changes in genome symbols of *Ae. umbellulata* and *Ae. sharonensis,* U and S^{sh} respectively. Furthermore, *Ae. uniaristata* should be given a separate symbol, probably N. *Aegilops speltoides* and *Ae. sharonensis* could be possible donors to the B genome of wheat. Interspecific divergence in these diploid species has been accompanied by either amplification or deletion as well as massive repatterning of heterochromatin from the centromere to the telomere.

Key words: C-banding – Improved technique – Diploid *Aegilops* – Genome symbols – Heterochromatin repatterning

Introduction

Within the family Graminae, the genus *Aegilops* bears a close and important evolutionary relationship with *Triticum.* A few attempts have been made in elucidating these relationships using a variety of banding techniques (see for example, Gill and Kimber 1974; Natarajan and Sarma 1974; Gerlach 1977). However progress has been admitted to be modest and most of these earlier reports were, in fact, only preliminary (Gill 1981) and did not allow for a detailed comparative analysis. One exception, however, is *Ae. speltoides,* where conflicting interpretations exist as to its relationship with the B genome of wheat (Gill and Kimber 1974; Natarajan and Sarma 1974; Hadlaczky and Belea 1975; Iordansky et al. 1978). As yet no attempt has been made to investigate the complete and basic C-banding pattern variation of all the diploid species available. We report here the characteristic C-banding patterns of 11 diploid species. To accomplish this, a modified technique of Seal and Bennett (1981) was developed which was more rapid and produces the maximum number of C-bands consistently.

Materials and methods

1 Stocks

The following plant stocks were used: *Aegilops umbellulata, Ae. caudata, Ae. comosa, Ae. uniaristata, Ae. bicornis, Ae mutica, Ae. speltoides, Ae. longissima, Ae. sharonensis, Ae. searsii* and *Ae. squarrosa.* All the diploid *Aegilops* species were from the collections of the Plant Breeding Institute, Cambridge. All are A accessions except for *Ae. speltoides,* which is H2.

2 C-banding technique

Actively growing root tips were pretreated with a saturated solution of 1-bromonaphthalene or 0.05% w/v colchicine for 4 h at room temperature. Excised root-tips were fixed in 3:1 ethanol-acetic acid. Cells were squashed gently as far as possible only from the meristematic region into 45% acetic acid. Squash preparations were made in the usual manner. Cover slips were removed after dipping in liquid nitrogen and the slides placed immediately in absolute alcohol for approximately 30 min. They were then air dried for 12–18 h followed by treatment with 0.2 N HCl at 30–35 °C for 35–60 min. Dehydration was carried out in 70% and absolute alcohol for 5 min each. Slides were air dried again for about an hour before treatment with 5% $Ba(OH)_2 \cdot 8\,H_2O$ w/v at 30–35 °C for 5–20 min. Incubation in 2XSSC was performed at 52 °C for 1–1½ h. The staining solution used was 20% v/v Leishman stain diluted with 1/15 M Na_2HPO_4 at pH 9.0.

Squash preparations must be flat with well spread chromosomes and the quality of preparations checked using phase contrast microscopy. For each species, well prepared slides were used two at a time to determine the optimum period of hydrolysis and barium hydroxide treatment. Overhydrolysis and prolonged barium hydroxide treatment led to gross chromosome morphology distortion, loss of bands and staining intensity, while incomplete hydrolysis resulted in incomplete expression of banding pattern as well as over stained chromosomes. The duration of staining usually does not exceed 20–30 min for maximum contrast between bands and the rest of the chromosomes. The whole procedure from hydrolysis to completion of staining lasts up to 5 h but could be shortened considerably if the slides are blow dried. If necessary, slides could be stored desiccated at 4 °C after the first air-drying step. However the length in which they are kept in this manner influences the duration of hydrolysis and has to be determined accordingly. D.P.X. should be used as mountant and not euparal.

3 Analysis of C-bands

The complete C-banding patterns of 5–10 metaphases were scored for each species and a composite of these was taken as representative of that particular species. The chromosomes were arranged according to size and arm ratios following the comprehensive karyotypic study of *Aegilops* by Chennaveeraiah (1960). The chromosomes are lettered A to G to avoid confusion with homoeologous groups. The karyotype of *A. searsii* follows that of Feldman (1978) with measurements performed on chromosomes of two metaphases.

Only minor variation between preparations from the same accession was observed and confined to staining intensity of minor bands (Seal 1982). These are represented by dots rather than bands in the karyograms. Wherever possible, all the chromosomes of a karyogram are taken from one metaphase plate. However variation does exist, especially between accessions of the same species and these will be dealt with separately in another paper. Only prominent and consistent bands are described.

Results

The C-banded metaphase chromosomes of all 11 diploid species are illustrated in Figs. 1 and 2. Each of the seven chromosomes comprising the haploid set of any one species displays its own characteristic banding pattern and could be identified individually and clearly.

Description of C-banded chromosomes

Section polyeides: *Aegilops umbellulata*

The composite banding pattern of this species is shown in Fig. 3.1. Chromosomes C, D and F are easily distinguishable. Nucleolar organiser regions (NORs) were unbanded and could be clearly seen as such in some cells scored. Telomeric bands occur on most of the long arms. Chromosomes B and C have very similar lengths and arm ratios but are clearly differentiated by their banding pattern.

A: The centromeric region of the long arm consists of two very close bands often fused into a single band. The subtelomeric band in the long arm and the interstitial band in the short arm are intensely stained.

B: Two proximal bands can be found adjacent to a small centromeric band on either arm and often appear as a single large band. Two interstitial bands are also present in the long arm.

C: The long arm has one centromeric and telomeric band with a series of possibly five evenly spaced interstitial bands. A proximal band is seen in the short arm.

D: The NOR arm has a band located centrally. Both proximal and telomeric bands occur in the long arm.

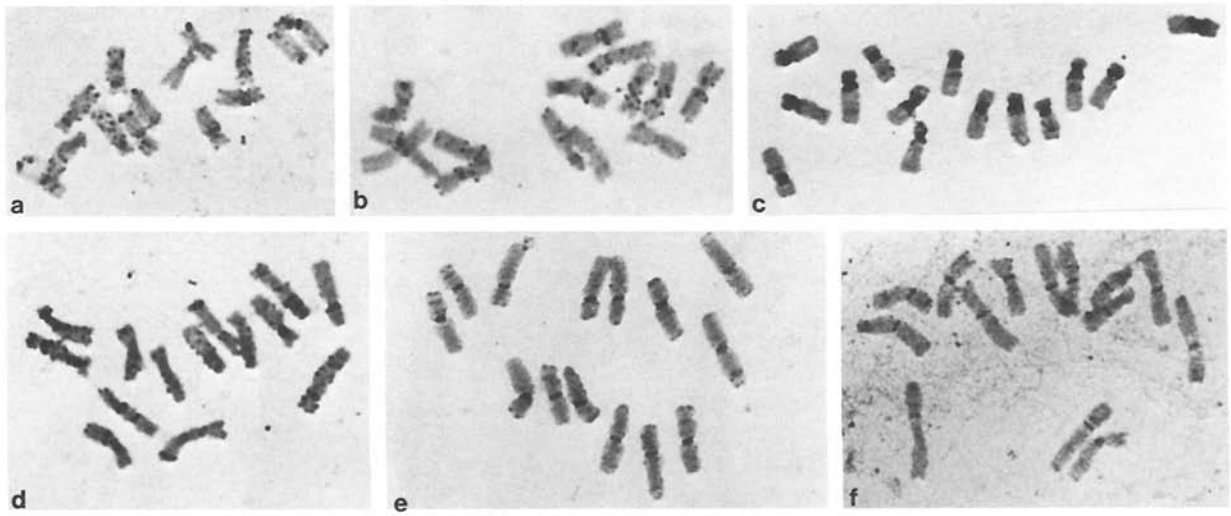

Fig. 1 a–f. C-banded mitotic chromosomes at metaphase of diploid *Aegilops* species (2n = 2x = 14), **a** *Ae. umbellulata*, **b** *Ae. comosa*, **c** *Ae. uniaristata*, **d** *Ae. caudata*, **e** *Ae. mutica*, **f** *Ae. squarrosa*

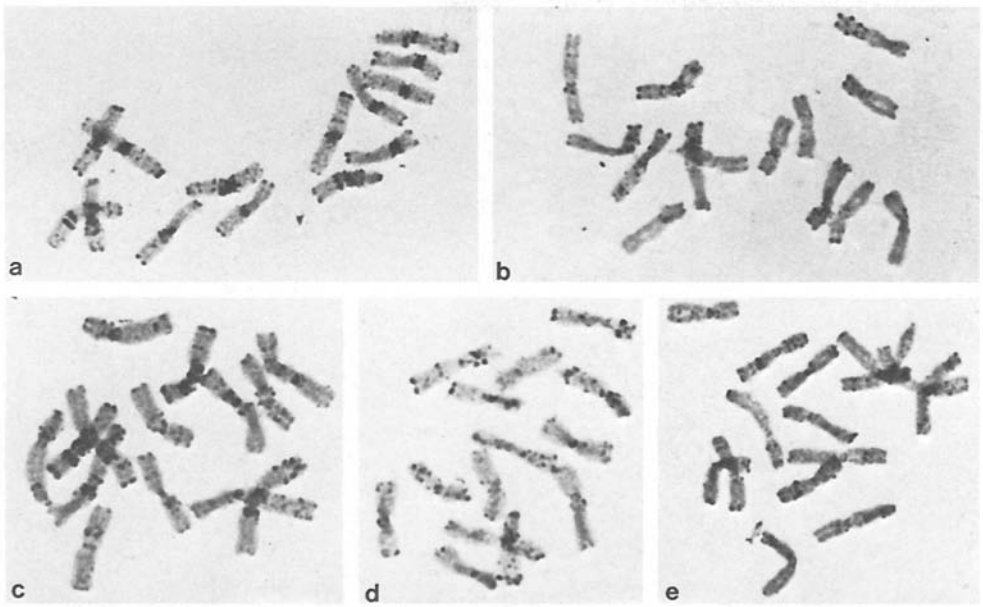

Fig. 2 a–e. C-banded mitotic chromosomes at metaphase of diploid *Aegilops* species (2n = 2x = 14) of the section Sitopsis. **a** *Ae. speltoides*, **b** *Ae. longissima*, **c** *Ae. sharonensis*, **d** *Ae. bicornis*, **e** *Ae. searsii*

E: This chromosome possesses an intensely stained centromeric region in its long arm as well as a proximal band in its short arm.

F: This chromosome is highly heterobrachial. Except for a small terminal portion, virtually all of its small arm is banded. The banded centromeric part of the long arm is not always as intensely stained as the short arm. There are also two terminal bands in the long arm.

G: As in D, there is an interstitial band in the short NOR arm. The long arm has a proximal band.

Section cylindropyrum: *Ae. caudata*

All chromosomes have at least one intensely stained centromeric band and most have variable numbers of interstitial bands (Fig. 3.2). This characteristic, also shared by chromosome C of *Ae. umbellulata,* can be especially seen in B and G. The NORs are often indistinct. There is also a lack of prominent telomeric bands.

A: Two very intensely stained bands, one centromeric and the other interstitial, occur in the long arm.

B: This chromosome is easily identifiable by its many interstitial bands on both arms. The long arm has up to seven interstitial bands but no observable telomeric band.

C: A proximal band can be seen in the short arm very close to the centromeric band. The long arm possesses a very intensely stained subtelomeric band.

D: The short arm has two very closely associated bands, very often seen as a single band. Faint interstitial bands occur in both arms.

E: A very prominent and large centromeric band can be found involving virtually the whole short arm except the small terminal portion. This actually consists of four very closely associated bands usually seen fused together and is probably the same band described by Gill (1981). The long arm is further characterised by one interstitial and two telomeric bands.

F: The terminal band in the short arm as well as the centromeric band is faintly stained in contrast to all four bands in the long arm, of which the most distal is subtelomeric.

G: The short arm possesses a very prominent large centromeric band whereas the long arm has six interstitial bands.

Section comopyrum: *Ae. comosa, Ae. uniaristata*

Even though these two species belong to the same section, they possess very different and contrasting patterns, as illustrated in Figs. 3.3 and 3.4. However one common feature shared by both species is the absence of prominent telomeric bands.

Ae. comosa. This species has very faint and small centromeric bands in all chromosomes. NORs can be seen clearly in many cells but are not banded. Chromosomes C, D and E are easily identified.

A: Bands on this chromosome are usually not as intensely stained as those on other chromosomes. The only easily identifiable band is the proximal one in the short arm.

B: The long arm has two proximal bands whereas the equivalent bands in the short arm are interstitial.

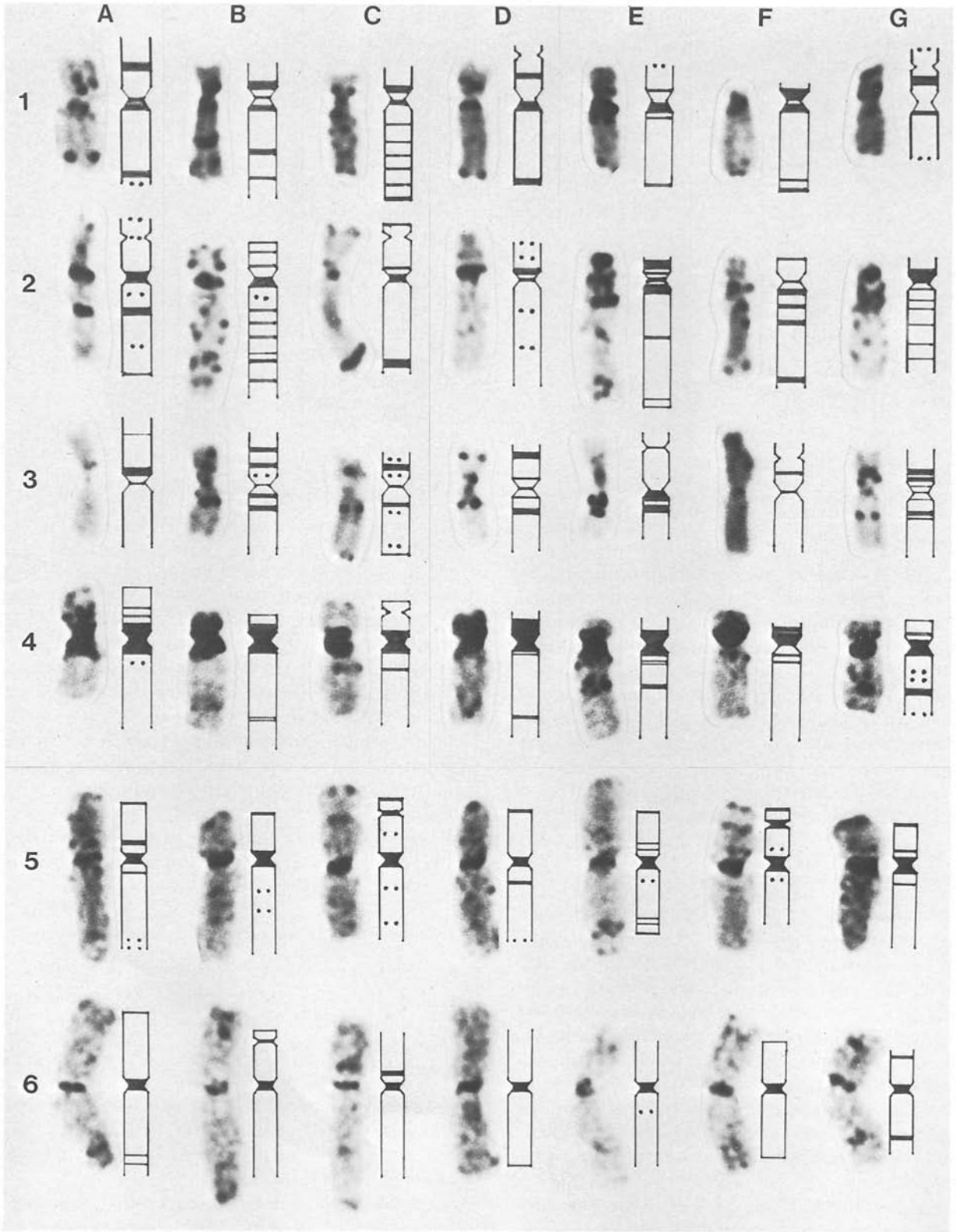

Fig. 3. C-banded karyograms of six diploid *Aegilops* species. *1 Ae. umbellulata, 2 Ae. caudata, 3 Ae. comosa, 4 Ae. uniaristata, 5 Ae. mutica, 6 Ae. squarrosa*

C: This chromosome possesses three distinct bands; one in the middle of the short arm and the other two, proximal and telomeric, in the long arm.

D: The short arm has a very distinct subtelomeric band as well as a proximal band. In the long arm, the smaller and more proximal of the two bands is usually fused with the centromeric band.

E: The arm with the NOR is longer than the other. The shorter arm has two closely associated but intensely stained bands proximal to the centromere.

F: This chromosome with the second NOR has only two bands; one is centromeric and the other is located interstitially on the short arm.

G: The most proximal bands on either arms are small and are often seen as a single centromeric band. The short arm has two adjacent interstitial bands of equal size, whereas those in the long arm are of unequal size and usually fused into a single band.

Ae. uniaristata. All the centromeric regions have large and intensely stained bands. In less contracted chromosomes, each of these regions can be seen to be made up of a series of closely associated bands. There are very few interstitial bands in both arms, which makes identification of chromosomes easier. Telomeric bands are virtually absent in the long arms.

A: The short arm possesses two interstitial bands close to each other and adjacent to the centromeric band.

B: Most of the short arm is banded except for a small terminal portion. Two distally located bands often appearing as one can be seen in the long arm.

C: The NOR is not banded. A small telomeric band is present in the short arm.

D: Almost the whole of the short arm is banded. The long arm is distinguished by a distal band.

E: The short arm is not as extensively banded as B or D. A prominent band is located in the middle of the long arm.

F: This is the only chromosome where only the short arm has a band close to the centromere. It consists, in fact, of two closely associated bands leaving only a small terminal portion unstained. Two proximal bands can also be seen in the long arm usually appearing as one.

G: The short arm has a terminal band and a proximal band. An intensely stained band can be found approximately in the middle of the long arm together with faintly stained interstitial and telomeric bands.

Section amblyopyrum: *Ae. mutica*

This species also has distinct centromeric bands which are however not as extensive or as large as those of *Ae. uniaristata* but are slightly larger than those of *Ae. squarrosa.* Both NORs in C and F are clearly banded and easily discernible as such in many cells. Telomeric bands are found in all short arms (Fig. 3.5). Clear proximal bands occur in both arms in A and G only. D has an interstitial band in its long arm. Chromosome E has telomeric bands on both arms. In addition, it has two pairs of closely associated bands, one pair is located proximally in the short arm and the other, distally in the long arm. Faintly stained bands occur in vitually all chromosomes. Some similarities exist between these chromosomes and those reported by Gill (1981) for this species.

Section vertebrata: *Ae. squarrosa*

Centromeric bands of almost equal staining intensity and size are present in all chromosomes (Fig. 3.6). Chromosome C is the only one with a proximal band in the short arm. D has subterminal bands in both arms. The two distal bands in the long arm of A usually appear as a single band. Terminal bands are usually faint and difficult to distinguish accurately. The banding pattern here is not comparable to those reported by Gill and Kimber (1974) but bears some resemblance to those of Iordansky et al. (1978).

Section sitopsis: *Ae. speltoides, Ae. sharonensis, Ae. longissima, Ae. bicornis* and *Ae. searsii*

This section only has diploid species. All have telomeric, interstitial as well as centromeric bands, varying in size and staining intensity (Fig. 4). *Ae. speltoides* and *Ae. sharonensis* have exceptionally distincitve and extensive centromeric bands. However centromeric heterochromatin appears to be more evenly distributed among the chromosome complement in the former than in the latter. Furthermore there is evidence for intragenomic heterozygosity in the banding pattern of *Ae. speltoides,* (Teoh, Miller and Reader, in preparation). Differences in the amount of heterochromatin between *Ae. longissima* and *Ae. sharonensis* are evidently related to the degree of heterochromatisation of the centromeric region. Both *Ae. searsii* and *Ae. bicornis* have relatively smaller centromeric bands. Some of the chromosomes of *Ae. speltoides* reported here have similar patterns to those presented by Iordansky et al. (1978) but are very different from those reported by Gill and Kimber (1974).

Ae. speltoides (Fig. 4.1). A: The short arm has a proximal and a telomeric band. On the long arm, a small subtelomeric band is found next to the telomeric band.

B: Telomeric bands are present in both arms but more intensely so in the long arm which has in addition 3 distal bands.

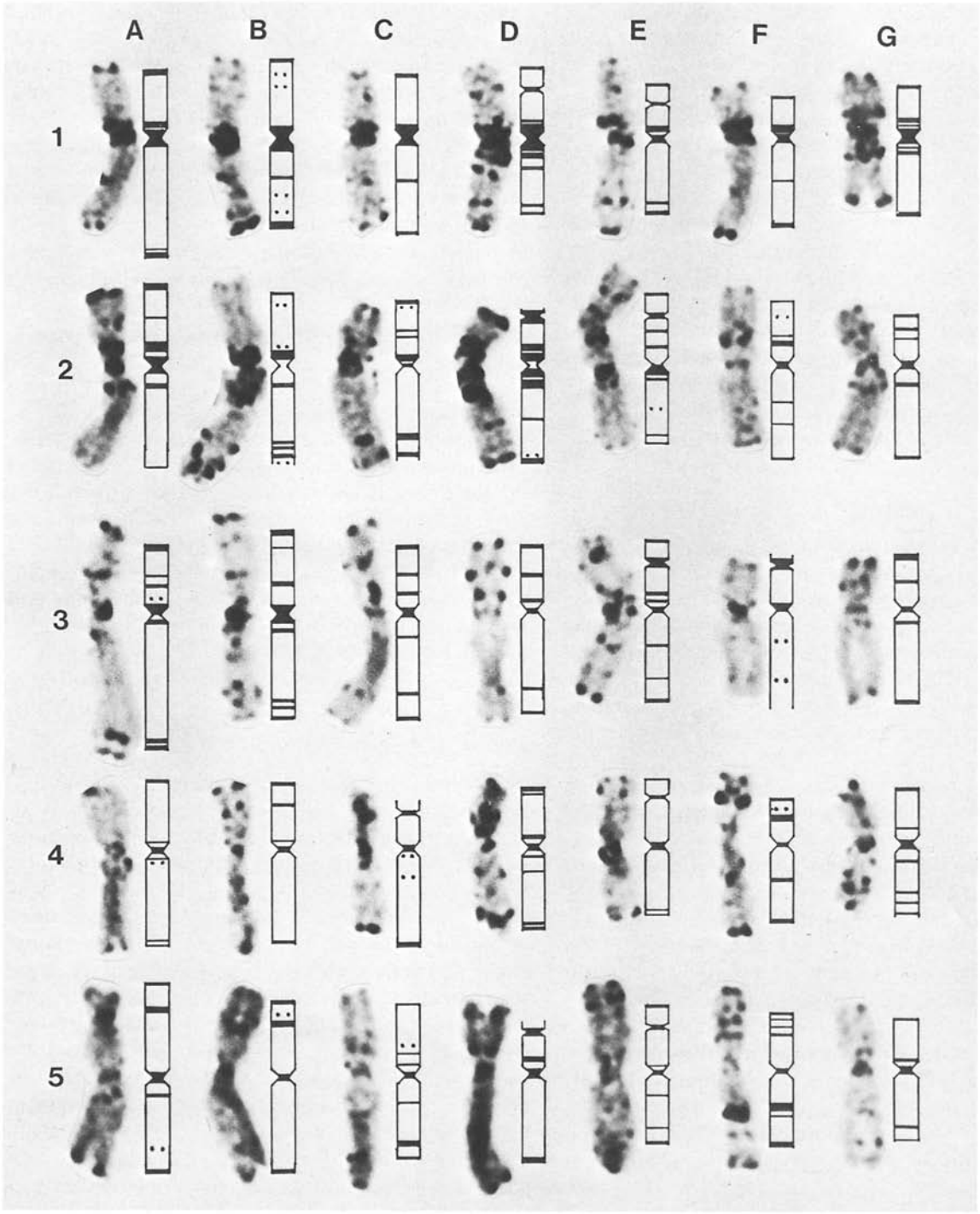

Fig. 4. C-banded karyograms of diploid *Aegilops* species belonging to the section Sitopsis. *1 Ae. speltoides, 2 Ae. sharonensis, 3 Ae. longissima, 4 Ae. bicornis, 5 Ae. searsii*

C: This chromosome has mainly centromeric bands and small telomeric bands. There is an interstitial band in the long arm.

D: The NOR is banded. One proximal band occurs in both arms adjacent to the centromeric band. The long arm has two interstitial bands and a telomeric band as well.

E: The short arm is banded at the NOR, telomere and proximally. The long arm has a subtelomeric and telomeric band.

F: This chromosome is the most heterobrachial where the short arm possesses a telomeric and proximal band. The long arm is distinguished by a clear, intensely stained, telomeric band and an interstitial band as well.

G: Banding patterns appear symmetrical in both arms with centromeric and telomeric bands. This chromosome appears to have the most heterochromatin content.

Ae. sharonensis (Fig. 4.2). A: The short arm has three distinctive bands; one large proximal, one telomeric and a smaller interstitial band. The long arm also has a proximal band, but the telomeric band is faint.

B: A proximal band occurs in the short arm. The long arm is characterised by three adjacent distal bands and a proximal band.

C: Prominent proximal and telomeric bands can be seen in the short arm. The long arm has two characteristic subtelomeric bands.

D: This chromosome contains the most heterochromatin, located mainly in four centromeric bands. The short arm NOR is intensely stained and involves most of the satellited portion. The long arm has prominent telomeric and interstitial bands.

E: The NOR is banded and can be clearly differentiated in some cells scored. There are two interstitial bands in the same arm. In the other arm there is a large centromeric band with a much smaller one next to it.

F: The centromeric band is relatively smaller than those of A to E. The short arm interstitial band is very intensely stained. Faint bands occur interstitially and telomerically in both arms.

G: The short arm has two interstitial bands situated midway between the telomeric and centromeric bands. One proximal and one telomeric band can be found in the long arm.

Ae. longissima (Fig. 4.3). A: The short arm has two interstitial bands and a telomeric band. Two characteristic terminal bands are clearly seen in the long arm.

B: Telomeric and proximal bands occur in both arms. There are also two subtelomeric bands in the long arm.

C: Both arms have two interstitial and one telomeric band.

D: The short arm is very distinctive with the one interstitial band located midway between the telomeric and proximal bands.

E: The NOR is banded. The short arm also has two proximal bands. The long arm possesses two well spaced interstitial bands and a telomeric band as well.

F: The NOR in this chromosome is also banded. The long arm has two faint intersititial bands.

G: The telomeric bands are very clear. The short arm also has a central band whereas a proximal band is found in the long arm. Similarities in banding pattern exist between chromosomes A, B and G of both *Ae. sharonensis* and *Ae. longissima.* Their NOR chromosomes are clearly very different.

Ae. bicornis (Fig. 4.4). A: The proximal and telomeric bands in both arms appear to be small and faint.

B: Both arms have telomeric bands. In addition, the short arm has an interstitial band.

C: This chromosome has three distinct bands; one in the NOR, the second is centromeric and the last, telomeric in the long arm.

D: The short arm has one proximal and two terminal bands. The long arm appears similar in banding pattern to the short one but has an additional interstitial band.

E: The NOR is banded. Faint telomeric bands occur in both arms.

F: A large and densely stained interstitial band in the short arm is the first to be recognised during staining. Telomeric bands are present in both arms.

G: The short arm has a proximal and a telomeric band. Three close distal bands as well as a proximal band occur in the long arm.

Ae. searsii (Fig. 4.5). A: Telomeric bands are present in both arms. In addition the short arm has a distal band whereas the long arm has a proximal band.

B: The short arm possesses clearly stained distal and telomeric bands. There is an absence of interstitial bands in the long arm.

C: A densely stained subtelomeric band is found in the long arm. There are small proximal bands in the short and long arms. Telomeric bands are seen in both arms.

D: The short arm is characteristically banded in the NOR and proximally. The long arm also has a telomeric band.

E: The NOR is banded as well as the telomeric end of the satellite. The long arm has two interstitial and one telomeric band.

F: This chromosome is highly characteristic. The large densely stained interstitial band in the long arm is the first to be recognised easily during staining. The short arm has a series of four distal bands one of which is telomeric.

G: A small proximal and a telomeric band are found in the short arm. The long arm has a subtelomeric and a telomeric band.

Interphase nuclei

The interphase nuclei of 4 species are shown in Fig. 5. Species which possess chromosomes with extensive centromeric heterochromatin such as those of *Ae. uniaristata-*

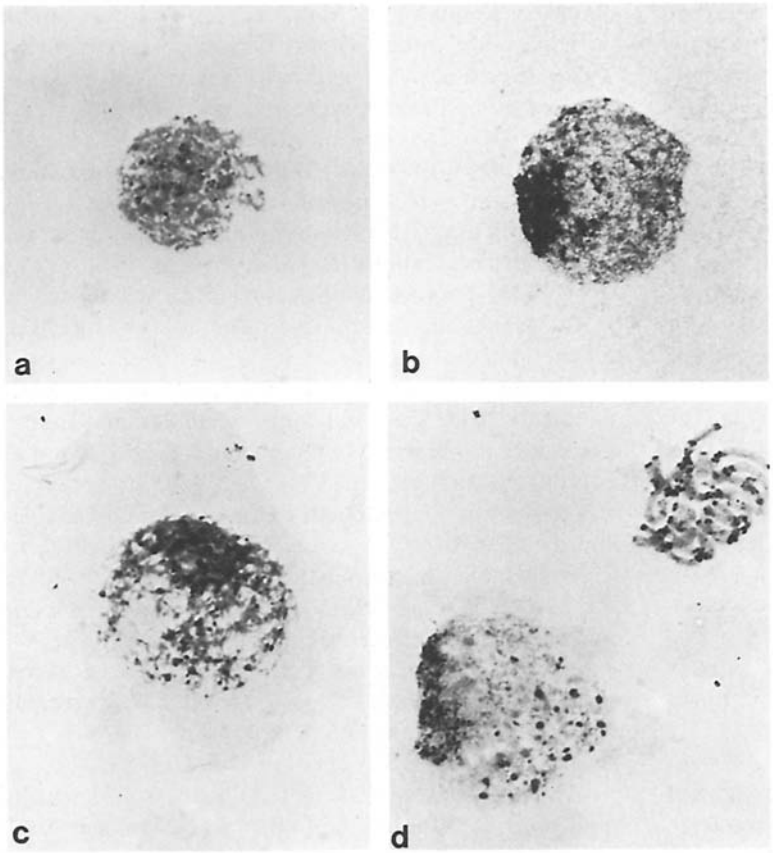

Fig. 5 a–d. Interphase nuclei of four *Aegilops* species after going through the C-banding procedure. **a** *Ae. comosa,* **b** *Ae. uniaristata,* **c** *Ae. sharonensis,* **d** *Ae. speltoides*

ta (Fig. 5 b) and *Ae. speltoides* (Fig. 5 d) tend to have polar aggregations of heterochromatin. However the difference between these two species is that the former has few interstitial and virtually no telomeric bands and this is reflected in a single polar aggregation of heterochromatin observed in its interphase nucleus. On the other hand, *Ae. speltoides* with all three types of bands appears to have compact heterochromatin at one pole and diffused heterochromatin at the opposite pole separating centromeric heterochromatin from the interstitial or telomeric types. Figure 5 d clearly illustrates this characteristic and also includes a late prophase nucleus where this characteristic is no longer evident. Species with relatively few bands, centromeric or otherwise, such as *Ae. comosa,* tend to have a scattered arrangement of heterochromatic dots (Fig. 5 a). The interphase nucleus of *Ae. squarrosa* has very little heterochromatin whereas the rest of the diploid species fall in between these interphase nuclei illustrated.

Discussion

It has been shown very clearly, for example in *Scilla* (Liliaceae) by Greilhuber et al. (1981), that modifications of existing C-banding techniques could lead to additional bands, especially the smaller and minor ones. Similarly the modified technique developed here with varying periods of hydrolysis and barium hydroxide treatment was absolutely essential to achieve a greater number of C-bands as well as maximum staining intensity. Thus many of the bands, large and small, shown here were not seen by Gill (1981).

Examination of all eleven *Aegilops* species showed extensive variation in C-banding pattern between species, with each species having its own distinctive pattern. Moreover, it is possible to identify each of the chromosomes of each haploid complement.

The differences in C-banding pattern between species provide an extra dimension for the allocation of genome symbols within the *Aegilops* genus. Major differences in the C-banding patterns of *Ae. caudata* and *Ae. umbellulata* provide additional evidence to the proposal that these two species should have two different genomic symbols i.e. C and U respectively (Kimber and Abu-Baker 1981). In the case of *Ae. uniaristata,* its genomic symbol, M^u, suggests that it is related to the M genome of *Ae. comosa* (Kihara 1954). However, Chennaveeraiah (1960) found major karyotypic differences between these two species. Maan and Sasakuma (1978)

observed high univalent frequencies in amphiploid combinations containing these two species, indicating non-homology of genomes. Their very contrasting and unique C-banded patterns shown here reinforces this conclusion. The genome symbol N suggested by Chennaveeraiah (1960) should perhaps therefore be adopted for *Ae. uniaristata.*

Members of the section Sitopsis share varying degrees of relationship with one another. All of their genomes are modifications of the S genome of *Ae. speltoides* (Kihara 1954). Based on chromosome pairing and frequency of univalent formation, Miller (1981) suggested that genome homology exists between *Ae. longissima* and *Ae. sharonensis* but not between those of *Ae. longissima* and *Ae. bicornis.* Their C-banding patterns tend to substantiate this conclusion. Even though *Ae. longissima* and *Ae. sharonensis* share some similarities their differences are sufficiently large to treat the latter as a subspecies and it should perhaps be given the genome symbol S^{sh} as proposed by Kushnir and Halloran (1981).

Based on their C-banding patterns, *Ae. longissima, Ae. bicornis* and *Ae. searsii* (Feldman 1978) are probably not directly related to the B genome. Also, *Ae. speltoides* was rejected as a possible donor of the B genome by Gill and Kimber (1974). However, its banding pattern shown here is in sharp contrast to that reported by them. A cursory comparison with the B genomes of some varieties of wheat published by Seal (1982) does show some similarities between chromosomes D, F and G of *Ae. speltoides* to 1 B, 5 B and 7 B of wheat respectively. Similarly chromosomes A and D of *Ae. sharonensis* bear remarkable resemblance to 3 B and 6 B. This would certainly be in line with the proposal that this species is involved as the B genome donor (Kushnir and Halloran 1981). However conclusive results must await detailed comparisons of these C-banded chromosomes with those of the B genome.

The observed extensive variation in C-banding pattern provides convincing evidence that interspecific divergence in the genus *Aegilops* has been accompanied by amplification or deletion as well as massive repatterning of heterochromatin from the centromere to the telomere. This is evident also amongst more closely related species in the section Sitopsis. The variation found within *Aegilops* is more extensive than that reported in the genera *Anacyclus* (Asterceae-Anthemideae) and *Scilla* (Lilaceae) by Schweizer and Ehrendorfer (1976) and Greilhuber et al. (1981) respectively. Because of this it is not possible to construct phylogenetic relationships of all the diploid *Aegilops* species.

A set of C-bands usually comprises several different types of constitutive heterochromatin (Jalal et al. 1974; Schweizer and Nagl 1976). The different durations of treatments given to effect maximum C-banding in different species is further evidence for this. Recently, these heterochromatic regions have been shown to contain different highly repeated sequences arranged in long tandem arrays (for a review, see Flavell 1980). It is uncertain whether the observed variation in the *Aegilops* species involves different types of repeated sequences, even though there is recent evidence to suggest that some highly repetitive sequences are localised in wheat (Gerlach and Peacock 1980; Hutchinson and Lonsdale 1982). The significance of these changes in evolutionary terms is unclear. It is certain however that having established the complete C-banded karyotypes of all the diploid species, it should now be possible to investigate genome evolution in the remaining polyploid *Aegilops* species and establish their precise relationships with the genomes of wheat.

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