# EVIDENCE FOR *AEGILOPS SHARONENSIS* EIG AS THE DONOR OF THE *B* GENOME OF WHEAT

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ABSTRACT

A number of lines of evidence are advanced for the candidacy of *Aegilops sharonensis* Eig as the donor of the *B* genome of wheat. The cytoplasm of *Ae. sharonensis* is compatible with tetraploid wheat *Triticum turgidum dicoccoides*, as evidenced by the high level of chromosome pairing and fertility of the amphiploid *Ae. sharonensis* × *T. turgidum dicoccoides*. *Ae. sharonensis* chromosomes exhibit high levels of pairing with those of the B genome of wheat in hybrids with *Ph*-deficient hexaploid wheat and low levels of homoeologous pairing with *T. monococcum* chromosomes.——The amphidiploid between *Ae. sharonensis* and *T. monococcum* is very similar to *T. turgidum dicoccoides* in spike, spikelet and grain morphology. The karyotype of *Ae. sharonensis* resembles more closely that of extrapolated *B* genome karyotypes of wheat than do the karyotypes of other proposed *B*-genome donor species of Aegilops. Because of distinctiveness in cytological affinity and karyotype morphology between *Ae. sharonensis* and *Ae. longissima*, a separate genome symbol $S^{sh}$ is proposed for the former species.

SARKAR and STEBBINS (1956), using morphological analysis, proposed that the *B* genome of wheat was derived from a species of the Sitopsis Section Zhuk. of the genus Aegilops. EIG (1929) maintained that the Sitopsis Section (= Platystachys Eig) represented a link between Aegilops and Triticum in having species with Triticum-like morphological characters, *e.g.*, a slight keel on the empty glume and two-rowed spikes.

*Ae. speltoides* was the first species of this Section to be considered as a putative *B*-genome donor. SARKAR and STEBBINS (1956), using morphological evidence, proposed it as the *B*-genome donor. RILEY, UNRAU and CHAPMAN (1958), using karyotype studies, chromosome pairing and geographical evidence, also proposed it as the *B*-genome donor. However, KIMBER and ATHWAL (1972), using chromosome pairing data, and GILL and KIMBER (1974), using Giesma C-banding, showed that the chromosomes of *Ae. speltoides* were not homologous with those of the *B*-genome. MAAN and LUCKEN (1971) showed that *Ae. speltoides* does not possess the appropriate cytoplasm to be the *B*-genome donor.

The potential donors of the *B* genome would therefore appear to be the species of the second subsection of Sitopsis: Eumarginata Eig. *i.e.*, *Ae. bicornis*, *Ae. longissima*, *Ae. searsii* and *Ae. sharonensis*. *Ae. bicornis* was proposed as a possi-

ble *B*-genome donor by Sears (1956), mainly on the basis of the morphological resemblance between the amphiploid of *T. monococcum* × *Ae. bicornis* and *T. dicoccum*. This resemblance was closer than that between the amphiploid *T. monococcum* × *Ae. speltoides* and *T. dicoccum*. However, each amphiploid, when hybridized with *T. dicoccum*, gave completely sterile hybrids.

*Ae. longissima* was proposed as the *B-genome* donor (TANAKA 1956) on the basis of similarities in some morphological characters between the amphiploid *Ae. longissima* × *T. monococcum* and emmer wheat. However, because of the low pairing (mean of 7 bivalents per cell) and the sterility of the hybrid between this amphiploid and *T. durum*, TANAKA (1956) concluded that the genome of *Ae. longissima* was not homologous with the *B* genome of tetraploid wheat. FELDMAN (1978), using a line of *Ae. longissima* that was found by MELLO-SAMPAYO (1971) to promote homoeologous pairing, also suggested *Ae. logissima*'s candidacy as the *B*-genome donor. While he obtained increased amounts of pairing in the hybrid between the amphidiploid *T. monococcum* × *Ae. longissima* and *T. turgidum* var. *dicoccoides* as compared with that found by TANAKA (1956), the hybrid was completely sterile. Using telocentric analysis, he showed that the pairing affinity of the *B*-genome chromosomes of wheat with this line of *Ae. longissima* was only approximately twice that found with *A*- or *D*-genome chromosomes.

FELDMAN (1978) proposed *Ae. searsii* as a new species in the Sitopsis Section that was the likely *B*-genome donor. This was based on geographical evidence and the possession by *Ae. searsii* of a second large satellited chromosome pair, as is present in the *B* genome of wheat. Evidence by VARDI (1974) that *Ae. searsii* is possibly an introgression derivative between *T. turgidum dicoccoides* and *Ae. longissima* renders the *B*-genome ancestry of *Ae. searsii* somewhat questionable.

While a number of studies have been made of *Ae. sharonensis*'s candidacy as the *B*-genome donor (SARKAR and STEBBINS 1956; RILEY, UNRAU and CHAPMAN 1958; JOHNSON and DHALIWAL 1978), none involved an exhaustive study of this species.

*Taxonomic status of* Ae. sharonensis: The absence of a thorough investigation of *Ae. sharonensis* as the possible donor of the *B* genome stems mainly from the genome analyses of KIHARA (1954) and TANAKA (1955), who used cytological evidence to rank *Ae. sharonensis* as a variety of *Ae. longissima* with the same genome symbol $S^l$. However, from their data, it could equally well have been regarded as a variety of *Ae. bicornis* (WAINES and JOHNSON 1972). This identification has led to general confusion between the two taxa, with many workers regarding them as almost identical. *Ae. sharonensis*, though closely related to *Ae. longissima*, is clearly different from it in morphological, phenological and ecological characteristics (ANKORI and ZOHARY 1962). Over their sympatric natural distributions, they generally produce hybrid swarms only in sites disturbed by man, *e.g.*, roadsides and edges of cultivation (ANKORI and ZOHARY 1962). Morphological and cytological studies of these natural hybrids further support their independent taxonomic status. Seed collections of *Ae. sharonensis* made near roadsides often contain hybridization derivatives with *Ae. longissima*

so that, in many laboratories, seed stocks regarded as *Ae. sharonensis* could contain such derivatives (ANKORI and ZOHARY 1962).

EIG (1929) established a systematic status for *Ae. sharonensis* separate from that of *Ae. bicornis* and *Ae. longissima* and more closely related to *Ae. bicornis* in spite of closer ecological affinity with *Ae. longissima*. WAINES and JOHNSON (1972), using electrophoresis of seed proteins, demonstrated consistent genetic differences between the three taxa and a closer relationship between *Ae. sharonensis* and *Ae. bicornis* than between *Ae. sharonensis* and *Ae. longissima*. ROY (1959) also found genetic differentiation between the genomes of *Ae. sharonensis* and *Ae. longissima*.

Ae. sharonensis–*wheat relationships*: As yet there is little information on the evolutionary affinity of *Ae. sharonensis* with tetraploid and hexaploid wheat compared with that of *Ae. longissima* and *Ae. bicornis*. PARODA (1977) found *Ae. sharonensis* to have smaller divergence in DNA-base sequences from tetraploid and hexaploid wheat than *Ae. longissima* and *Ae. speltoides*. A more recent indication for the possible involvement of *Ae. sharonensis* in the evolution of wheat comes from evidence that chromosome *4A* of wheat is morphologically very similar in C-banding pattern and possibly derived from chromosome *4* $S^{sh}$ (= *4* $S^{l}$) of *Ae. sharonensis* (MILLER, personal communication).

The aim of the present study was to investigate the possibility of *Ae. sharonensis* being the *B*-genome donor of wheat.

## MATERIALS AND METHODS

The *Ae. sharonensis* line chosen for this study was collected by the senior author from the coastal plain of Israel from an undisturbed habitat having no contact with *Ae. longissima* populations. The *Triticum turgidum dicoccoides* line was collected from Upper Galilee in Israel and the *T. monococcum* line was collected in Turkey. The $ph_{1b}$ mutant of *T. aestivum* cv. Chinese Spring was obtained from E. R. SEARS, University of Missouri, Columbia, Missouri, U.S.A.

The following hybridizations were carried out:

*Ae. sharonensis* × *T. monococcum*

*Ae sharonensis* × *T. turgidum dicoccoides*

*T. turgidum dicocoides* × (*Ae. sharonensis* × *T. monococcum* amphidiploid)

*T. aestivum* — $ph_{1b}$ cv. Chinese Spring × *Ae. sharonensis.*

The hybrids were grown during the winter period in a glasshouse which was heated and cooled to maintain reasonably high temperatures for growth. Amphiploids of the *Ae. sharonensis* × *T. monococcum* hybrids were produced with the application of 0.05% colchicine solution to the apices of seedlings at the 5-leaf stage for 4 hr. For meiotic studies, spikes were collected and fixed in Carnoy's solution for 48 hr. These were stored in 70% alcohol and stained in 1% aceto-carmine. Somatic chromosome counts were made on root-tips of germinating seeds that had been placed in colchicine ($10^{-3}$) for 24 hr and stained in 1% acetocarmine for 48 hr.

Karyotype analyses were made of *Ae. sharonensis* and *T. turgidum dicoccoides* following the methods of GIORGI and BOZZINI (1969a). These were based on the position of the centromere and the presence or absence of satellited chromosomes. It gave four groups of chromosomes as follows: SAT = satellited chromosomes; M = median chromosomes (arm ratio between 1.00 and 1.25); SM = sub-median chromosomes (arm ratio between 1.26 and 1.75); ST = subterminal chromosomes (arm ratio 1.76 or above).

Pollen fertility was determined by dissecting mature anthers soaked in 2 % acetocarmine and scoring 500 pollen grains for the percentage of normal grains. Grains were considered normal when they were rounded and deeply stained.

Floret fertility in the hybrids was measured as the percentage of florets in 50 spikelets (2 outer florets) that contained well-developed kernels.

## RESULTS AND DISCUSSION

*Compatibility of* Ae. sharonensis *cytoplasm with tetraploid wheat*: SEARS (1977) suggested that the possession of a cytoplasm compatible with that of tetraploid wheat should be one criterion for identifying the *B*-genome donor. To examine the interaction of *Ae. sharonensis* cytoplasm with tetraploid wheat chromosomes, it was hybridized as the female parent with *T. turgidum dicoccoides*, and the chromosome number of the hybrid was doubled with colchicine to avoid sterility. The amphiploid of *Ae. sharonensis* × *T. dicoccoides* grew vigorously and was found to be fertile, with 73% normal pollen and 43.4% seed fertility. A typical spike of the amphiploid is shown in Figure 1. At first metaphase of meiosis (Table 1), there was regular bivalent formation, with occasional multivalents.

The comparison of these results with those of the reciprocal cross between *Ae.*

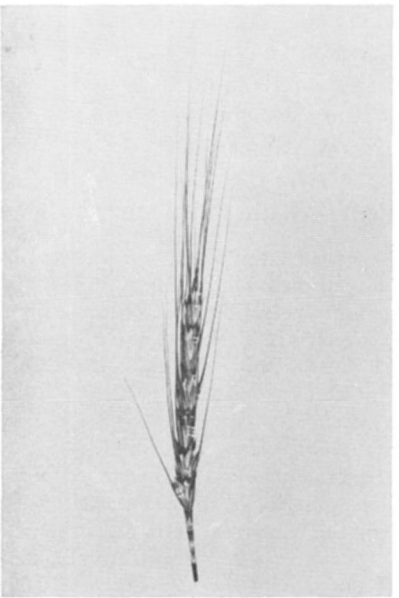

FIGURE 1.—Fertile spike of the amphiploid *Ae. sharonensis* × *T. turgidum dicoccoides* ($S^{sh}S^{sh}A^aA^aB^aB^a$).

TABLE 1

*Chromosome pairing at first metaphase of meiosis in the amphiploid* Ae. sharonensis × T. turgidum dicoccoides

| No. of cells examined | Univalents | Bivalents | | | Trivalents | Quadrivalents |
|---|---|---|---|---|---|---|
| | | Ring | Rod | Total | | |
| 40 | 1.83 ± 0.32 (0–8) | 15.70 ± 0.45 (10–21) | 4.00 ± 0.34 (0–10) | 19.70 ± 0.22 (16–21) | 0.13 (0–1) | 0.08 (0–1) |

*sharonensis* and *T. turgidum* obtained by Roy (1959) shows that, while meiotic pairing was similar, there was a drop of about 20% in the pollen fertility and 45% in seed fertility in the amphiploid possessing *Ae. sharonensis* cytoplasm compared with that containing *T. turgidum* cytoplasm. Despite some disparity, the compatibility in both cases was high enough for the production of reasonably high frequencies of functional gametes. This finding reflects a close relationship between the cytoplasm of *Ae. sharonensis* and that of tetraploid wheat. This is in line with the studies of nucleo- cytoplasmic interactions in wheat and Aegilops (Maan and Lucken 1971; Suemoto 1973), which did not preclude the Eumarginata species as possible donors of the cytoplasm of polyploid wheat.

*Morphology of the* Ae. sharonensis × T. monococcum *amphidiploid*: Hybridization of *Ae. sharonensis* as female parent with *T. monococcum* and chromosome doubling of the hybrid with colchicine resulted in an amphidiploid that closely resembled *T. turgidum dicoccoides* (Figures 2, 3; Table 2). The form of *dicoccoides* used for the comparison was a profusely tillered, small-headed type, presumably more primitive than the less-tillered, large-headed cereal form. The amphidiploid was very similar to *dicoccoides* in spike and spikelet morphology, seed size and morphology, and seed-size differentiation within the spikelet (*i.e.*, the kernel of the first-flowering floret was smaller than that of the second floret). Like *dicoccoides*, it also possessed the two-awned spikelet, giving the arrow-like dispersal unit after wedge disarticulation of the ripened head.

*Meiotic pairing in the* Ae. sharonensis × T. monococcum *amphidiploid*: The meiotic pairing of the amphidiploid was quite regular, with a mean of 13.85 bi-

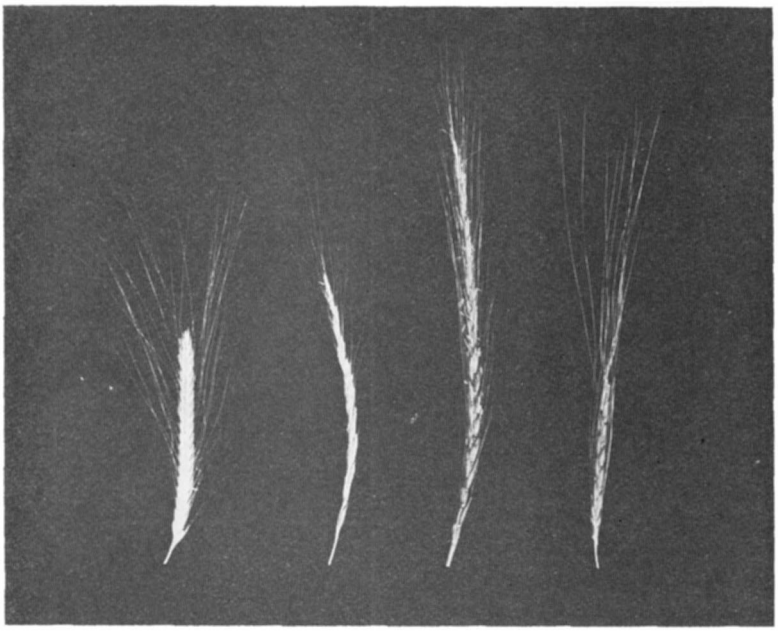

Figure 2.—Spike morphology (from left to right) of *T. monococcum*. *Ae. sharonensis*, the amphidiploid *Ae. sharonensis* × *T. monococcum* ($S^{sh}S^{sh}A^mA^m$) and *T. turgidum dicoccoides*.

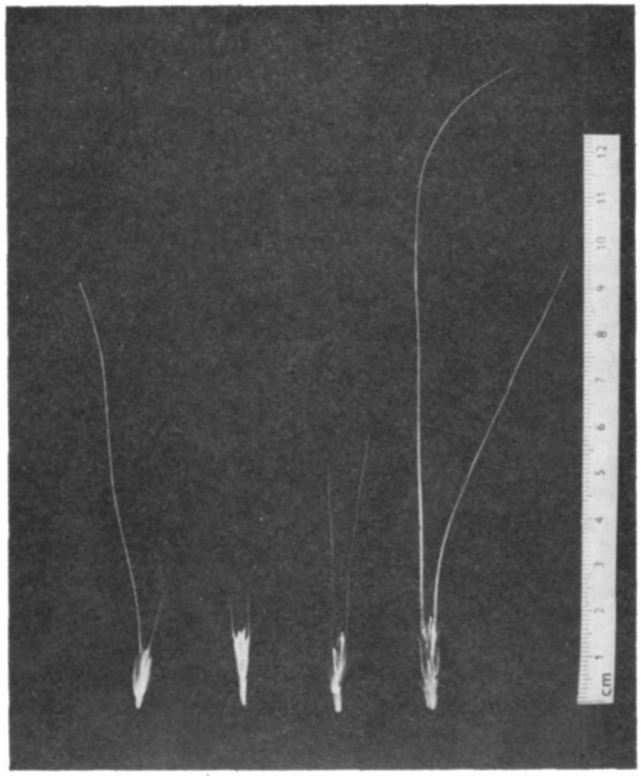

FIGURE 3.—Spikelet morphology (from left to right) of *T. monococcum*, *Ae. sharonensis*, the amphidiploid *Ae. sharonensis* × *T. monococcum* ($S^{sh}S^{sh}A^mA^m$) and *T. turgidum dicoccoides*.

valents per cell (Figure 4; Table 3). Pollen fertility was high, 81%, seed set averaged 50%, with a range of 30–70%. The high meiotic stability of the amphidiploid, coupled with its high fertility, indicates that it had the potential to become established, either in competition with its putative diploid parental species or in environments beyond their ranges.

*Meiotic pairing in the* Ae. sharonensis × T. monococcum *hybrid*: To further elucidate the affinity between *Ae. sharonensis* and *B*-genome chromosomes of wheat, chromosome pairing was examined in the *Ae. sharonensis* × *T. monococcum* hybrid (Table 4). At first metaphase of meiosis, there were 0.3 rod bivalents per cell. This value falls between the mean value of 0.9 bivalents per cell found in haploids of *T. aestivum* (KIMBER 1961) and the mean of 0.18 bivalents per cell found in haploids of *T. turgidum* (KIMBER, SALLEE and BATES 1978). This indicates that the chromosome affinity between *Ae. sharonensis* and *T. monococcum* ($S^{sh}$–$A^m$) is low and comparable to values obtained for the *A* and *B* genomes of wheat.

*Meiotic pairing in the* Ae. sharonensis × T. turgidum dicoccoides *hybrid*: In the hybrid obtained by crossing *Ae. sharonensis* as female with *T. turgidum dicoccoides*, there were only 2.23 bivalents per cell at first metaphase of meiosis

TABLE 2

*Comparative morphology of the amphidiploid* Ae. sharonensis × T. monococcum *and* T. turgidum dicoccoides

| Comparisons between *Ae. sharonensis* × *T. monococcum* amphidiploid and *T. turgidum dicoccoides* | Morphology |
|---|---|
| *Similarities*: | Purple coleoptile. Leaves 7–8 mm wide, 20–23 cm long, with well-defined longitudinal pubescent ridges on upper surface. Auricles and blade margins pubescent. Shoot prostrate in early growth. Sheath glabrous with fringes of hairs on outer edge only. Ears bearded and laterally compressed. Lateral spikelets usually with three florets. Seed set mainly in the two outer florets, but occasionally in third floret. Lateral empty glumes yellow-black, 10–11 mm long and 5-nerved, narrow with scabrid keel covered with silky hairs. Apical tooth straight, acute, 3–7 mm long, the strongest nerve ending in a secondary tooth 2–3 mm long. Awns present on outer flowering glumes of spikelet and of equal length. Palea as long as flowering glume, smooth and membranous, divided at tip, 2-nerved and bicarinate, the two ciliate keels slightly scabrid near the tip. Kernels reddish, long and narrow, pointed at both ends and compressed laterally, the dorsal side forming a ridge. Apex of kernel with tufted "brush" of whitish hairs 0.5 to 1.0 mm long. When two kernels are present in a spikelet, that in the lower floret is the smaller. Kernels 8–10 mm long, 2.0 mm wide and 2.0–2.5 mm high. Rachis of ripe ear disarticulates commencing near apex; internodes forming beaks 4–5.0 mm long at base of detached spikelets. Beaks convex-concave and derived at free end so that the plane of disarticulation scar is almost parallel to the flat side of rachis. |

| | Character | *Ae. sharonensis* × *T. monococcum* amphidiploid | *T. turgidum dicoccoides* |
|---|---|---|---|
| *Differences*: | Top spikelet | Undeveloped and sterile | Developed and fertile |
| | Awn length | 3–5 cm | 10–18 cm |
| | Rachis hairiness | Sparse hairs 0.2 cm long at edge and glabrous at base of spikelet | Densely fringed with hairs 1–5 mm long at edge and 5 mm long at base of spikelet |
| | Head length | 12–14 cm (20–30 spikelets) | 8–10 cm (12–22 spikelets) |

(Table 5). This is quite similar to the mean value of 2.22 bivalents per cell obtained in the reciprocal of this cross by RILEY, UNRAU and CHAPMAN (1958) and the mean of 2.5 bivalents per cell obtained by ROY (1959). These values, while generally low, appear to be still higher than those obtained for other Eumarginata species, *e.g.*, 1.78 bivalents for *Ae. bicornis* and 1.60 for *Ae. longissima* (RILEY, UNRAU and CHAPMAN 1958).

TABLE 3

*Chromosome pairing at first metaphase of meiosis in the amphidiploid* Ae. sharonensis × T. monococcum

| No. of cells examined | Univalents | Bivalents | | | Trivalents | Quadrivalents |
|---|---|---|---|---|---|---|
| | | Ring | Rod | Total | | |
| 125 | 0.29 ± 0.06 (0–2) | 11.64 ± 0.12 (8–14) | 2.21 ± 0.11 (0–6) | 13.85 ± 0.03 (12–14) | — | 0.01 (0–1) |

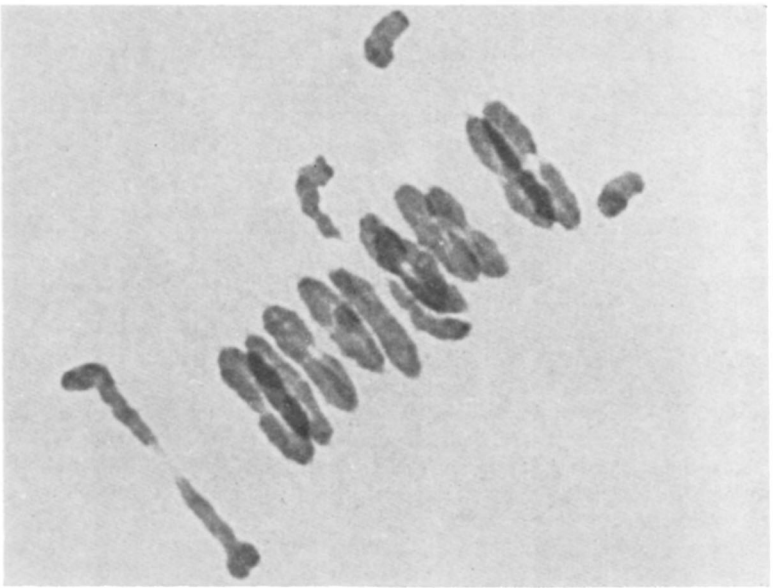

FIGURE 4.—First meiotic metaphase of the amphidiploid *Ae. sharonensis* × *T. monococcum* ($S^{sh}S^{sh}A^mA^m$) showing 13 bivalents (2 rod + 11 ring) and 2 univalents (× 1750).

TABLE 4

*Chromosome pairing at first metaphase of meiosis in the $F_1$ hybrid of* Ae. sharonensis *and* T. monococcum

| No. of cells examined | Univalents | Bivalents | Trivalents |
|---|---|---|---|
| 200 | 13.35 ± 0.07 (10–14) | 0.30 ± 0.03 (0.2) | 0.01 (0–1) |

*Meiotic pairing in the* T. turgidum dicoccoides × (Ae. sharonensis × T. monococcum) *hybrid*: In the hybrid obtained by crossing *T. turgidum dicoccoides* with the amphiploid (*Ae. sharonensis* × *T. monococcum*), there was a mean of 8.11 bivalents per cell at first metaphase of meiosis, with a maximum of 12 per cell (Table 6). This value is similar to that obtained with *Ae. bicornis* (8.05 bivalents per cell) by SEARS (1956) and higher than that obtained with *Ae. longissima* (7 bivalents per cell) by TANAKA (1956). The above hybrid was sterile as also were the reported hybrids with *Ae. bicornis* and *Ae. longissima*. This partial pairing and sterility could possibly be due to the spatial nature of the action of the *Ph* gene. It is possible that the *Ph* gene (on chromosome 5*BL*) exerts a specific and pronounced effect on chromosomes of closest ancestry, *i.e.*, those in the *B* genome. This control might be weaker for pairing occurring in the other genomes (*i.e.*, *A* and *D*). FELDMAN (1978) suggested that this effect is derived from the interaction of *Ph* (on chromosome 5*BL*) and *Ph*-like genes in normal-pairing *Ae. longissima*. While FELDMAN (1978) proposed the existence of a *Ph*-like gene in *Ae. longissima*, there is certain evidence against this: the lack of any

TABLE 5

*Chromosome pairing at first metaphase of meiosis in the $F_1$ hybrid of* Ae. sharonensis *with tetraploid and hexaploid wheats*

| Hybrid | No. of cells examined | Univalents | Bivalents | | | Trivalents | Chiasmata | Reference |
|---|---|---|---|---|---|---|---|---|
| | | | Rod | Ring | Total | | | |
| *Ae. sharonensis* × *T. turgidum dicoccoides* | 100 | 16.62 ± 0.22 (13–21) | 2.20 ± 0.10 (0–4) | 0.03 ± 0.01 (0–1) | 2.23 ± 0.11 (0–6) | | 2.26 | KUSHNIR and HALLORAN (unpublished) |
| *T. turgidum* × *Ae. sharonensis* | 62 | 16.06 ± 0.33 (11–21) | 2.50 (0–5) | — | 2.50 ± 0.165 (0–5) | | 2.5 | ROY (1959) |
| *T. turgidum dicoccoides* × *Ae. sharonensis* | | 16.48 | | | 2.23 | 0.22 | 1.78 | RILEY and CHAPMAN (1958) |

TABLE 6

*Chromosome pairing at first metaphase of meiosis in the $F_1$ hybrid between* T. turgidum dicoccoides *and the amphidiploid* (Ae. sharonensis × T. monococcum)

| No. of cells examined | Univalents | Bivalents | | | Trivalents | Quadrivalents |
|---|---|---|---|---|---|---|
| | | Ring | Rod | Total | | |
| 150 | 11.34 ± 0.22 (6–18) | 3.50 ± 0.11 (0–7) | 4.60 ± 0.14 (1–11) | 8.11 ± 0.10 (5–12) | 0.12 ± 0.02 (0–2) | 0.006 (0–1) |

compensating ability for the deficiency of *5B* within this species in crosses with hexaploid wheat nullisomic for chromosome *5B* (RILEY and LAW 1965). Likewise, the regular chromosome behavior in the amphiploid *T. turgidum* × *Ae. longissima* (ROY 1959), which would contain four *Ph* factors if *Ae. longissima* possessed *Ph*, is further support for the absence of such a gene in this species. The results of ROY (1959) and those of the present study indicate the absence of a *Ph* gene in *Ae. sharonensis*. There is evidence for the existence of *Ph*-like genes in diploid wheat species (OKAMOTO and INOMATA 1974; WAINES 1976). It seems, therefore, that in the case of *Ae. sharonensis* in the hybrid *T. turgidum dicoccoides* × $A^m A^m S^{sh} S^{sh}$ ($A^a A^m B^a S^{sh}$), as well as in the amphiploid *A. sharonensis* × *T. turgidum dicoccoides* ($A^a A^a B^a B^a S^{sh} S^{sh}$), *Ph* (*5B*) influences the chromosomes of the possible *B*-genome donor to behave as pseudo-homoeologues in relation to those of the *B* genome of wheat.

*Meiotic pairing in the* T. aestivum ($ph_{1b}$ *mutant*) × Ae. sharonensis *hybrid*: In order to distinguish between homoeologous and pseudo-homoeologous chromosome relationships, *Ae. sharonensis* was hybridized with the *T. aestivum* Chinese Spring $ph_{1b}$ mutant, which is deficient for the *Ph* locus on *5BL*. Data for homoeologous pairing with such a deficiency (RILEY and LAW 1965) were compared with those in the present study (Table 7). At first metaphase of meiosis, there were 9.66 bivalents per cell, which is 25 times higher than that of homoeologous bivalents with the deficiency of *Ph*. Furthermore, subtracting the 3.82 homoeo-

TABLE 7

*Chromosome pairing at first metaphase of meiosis in hybrids between Aegilops species of the Sitopsis Section and* Ph-*deficient* T. aestivum

| Hybrid | No. of cells examined | Univalents | Bivalents | Trivalents | Quadrivalents |
|---|---|---|---|---|---|
| *T. aestivum* ($ph_{1b}$ mutant) × *Ae. sharonensis* | 101 | 5.2 ± 0.25 (2–12) | 9.66 ± 0.14 (7–12) | 0.52 ± 0.06 (0–3) | 0.29 ± 0.05 (0–2) |
| *5B*-deficient *T. aestivum* × *Ae. longissima** | — | 7.50 | 7.58 | 0.70 | 0.56 |
| *5B-deficient T. aestivum* × *Ae. speltoides** | — | 6.13 | 5.23 | 1.76 | 1.23 |

* Data for *Ae. longissima* and *Ae. speltoides* taken from RILEY and LAW (1965).

logous bivalents present in *5BS* haploids given by RILEY and LAW (1965) results in 5.84 bivalents. Since in the hybrid of *Ae. sharonensis* × *T. monococcum* (again in the absence of *Ph*) there were 0.3 bivalents per cell (Table 4), one can assume, based on relative genetic affinity between the chromosomes of the *A* and *B* genomes (SEARS and OKAMOTO 1958; DVORAK 1976), that a similar level of pairing should occur between *Ae. sharonensis* and *D*-genome chromosomes. Further subtraction of possible $S^{sh}$–*A* and $S^{sh}$–*D* associations would leave a pairing affinity $S^{sh}$–*B* of 5.24 bivalents per cell. This value of about 5 bivalents per cell was the level considered as evidence for the identification of *T. monococcum* as the *A*-genome donor (KIHARA 1924; RILEY, UNRAU and CHAPMAN 1958). In the nulli-*5B* hybrid between *T. aestivum* and *Ae. longissima*, RILEY and LAW (1965) found a mean of 7.58 bivalents per cell. After the above consideration and deductions, only 3.16 bivalents per cell are left as homologous bivalents between *Ae. longissima* and the *B* genome. This pairing affinity is significantly lower than that of *Ae. sharonensis*. It provides further support for the distinctiveness of the two species and supports the validity of the different genome symbols $S^l$ and $S^{sh}$.

*Karyotypes*: The karotype for *Ae. sharonensis* in the present study is similar to that described for *Ae. sharonensis* by CHENNAVEERAIAH (1960), except that the small satellites are smaller in the latter (Figure 5). *Ae. bicornis* in CHENNAVEERAIAH (1960) has a karyotype similar to that of *Ae. sharonensis* in the present study, except that the small satellites are smaller in the former. GIORGI and BOZZINI (1969b) found *Ae. bicornis* to be different, having two satellited, four submedian and one median chromosome pair. The same chromosome types appear in the idiogram for *Ae. longissima* in CHENNAVEERAIAH (1960). The

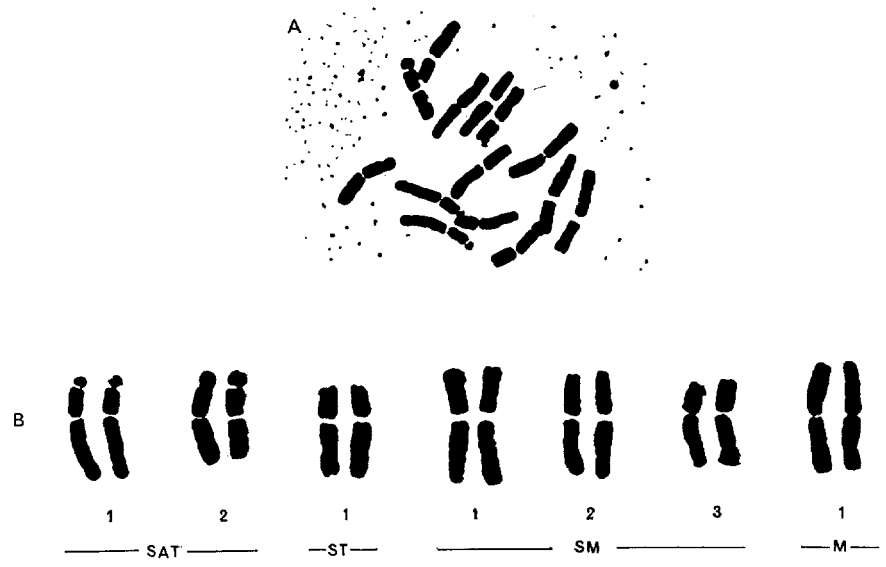


FIGURE 5.—Metaphase plate of root-tip mitosis (A) and idiogram of chromosomes (B) of *Ae. sharonensis* (A × 2200; B × 3200).

karyotype of *Ae. speltoides* of both CHENNAVEERAIAH (1960) and GIORGI and BOZZINI (1969b) (Figure 6) appears to contain two pairs of satellited, one pair of subterminal, two pairs of submedian and two pairs of median chromosomes. The karyotype of *Ae. searsii* (FELDMAN 1978) appears to have two satellited, three submedian and two median chromosome pairs. The karyotype of *T. turgidum dicoccoides* (Figure 7) shows two satellited, two subterminal, three median and seven pairs of submedian chromosomes. This result is in full agreement with that obtained by GIORGI and BOZZI (1969a). The karyotype of the *A*-genome donor, *T. monococcum*, according to GIORGI and BOZZINI (1969b), comprises two pairs of very small satellited, three pairs of submedian and two pairs of median chromosomes. Since the satellites of *T. monococcum* are not visible in tetraploid

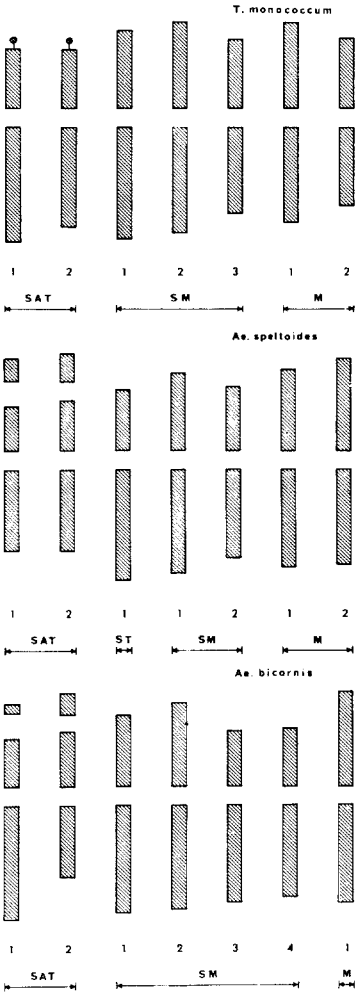


FIGURE 6.—Idiograms of *T. monococcum*, *Ae. speltoides* and *Ae. bicornis*, after GIORGI and BOZZINI (1969b).

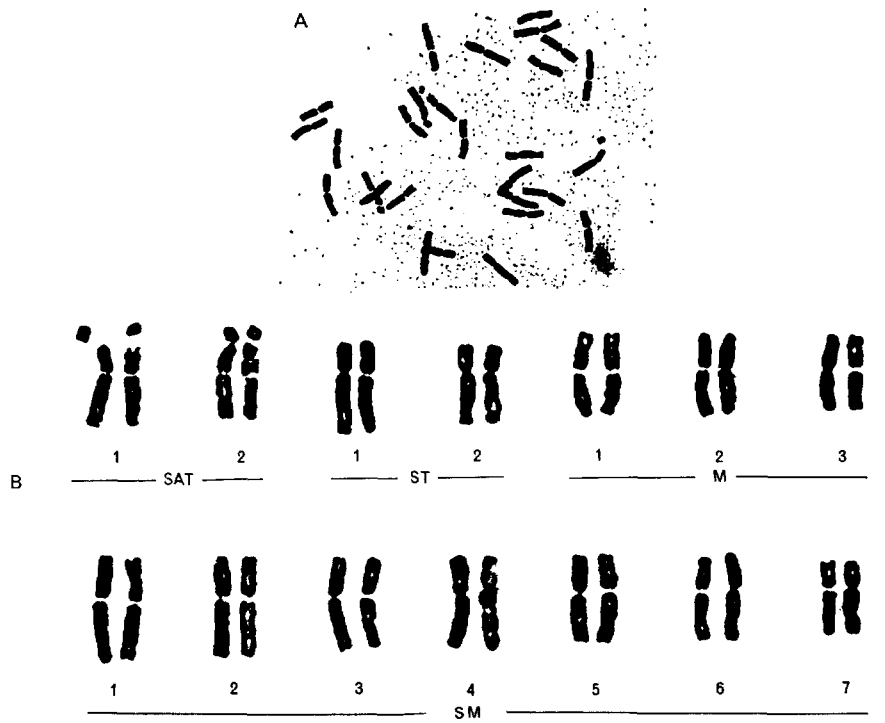


FIGURE 7.—Metaphase plate of root-tip mitosis (A) and idiogram of chromosomes (B) of *T. turgidum dicoccoides* (A × 1300; B × 3200).

wheat (RILEY, UNRAU and CHAPMAN 1958; GIORGI and BOZZINI 1969c), one of the two satellited chromosome pairs with an arm ratio of 1.95 (GIORGI and BOZZINI 1969c) must be one of the subterminal chromosome pairs of tetraploid wheat. Such an assumption is supported by the fact that chromosome *1A* in hexaploid wheat, with an arm ratio of 1.91, is subterminal (SEARS 1954). This chromosome was found by CROSBY (1959) to have nucleolar activity in micronuclei when in the monosomic condition in common wheat. The second satellited chromosome pair of *T. monococcum* with an arm ratio of 1.73 (GIORGI and BOZZINI 1969c) probably became one of the submedian pairs of the tetraploid wheat. By subtracting the rest of *T. monococcum* chromosomes from the chromosome set of *T. turgidum dicoccoides*, a karyotype of the possible *B*-genome donor emerges.

Such a putative donor should contain two pairs of satellited chromosomes with considerably large satellites, one pair of subterminal, three pairs of submedian and one pair of median chromosomes. Such a karyotype is provided by *Ae. sharonensis* and, less closely, by *Ae. bicornis*. *Ae. longissima* does not possess the required karyotype, and *Ae. speltoides* and *Ae. searsii* possess superfluous chromosomes of the median type. The two subterminal chromosome pairs in *T. turgidum dicoccoides* were found to have arm ratios of 1.97 and 2.08 in the present study and of 1.98 and 2.09 by GIORGI and BOZZINI (1969a). Since chromosome *5B* in the

N-banded karyotype of *T. turgidum dicoccoides* (GERLACH 1977) appears to have an arm ratio of 1.9, the subterminal chromosome of *Ae. sharonensis*, with an arm ratio of 1.8, could possibly be the prototype of chromosome *5B*. Hence, this chromosome must have become more asymmetric in its transfer from the diploid to the tetraploid level. A further change in symmetry is likely to have occurred in this chromosome from the tetraploid to the hexaploid level since SEARS (1954) found chromosome *5B* in hexaploid wheat to have an arm ratio of 2.65. Hence, it appears that, in the course wheat evolution, there was increased subterminalization of the centromere position of chromosome 5B.

Previous karyotype studies of the origin of the *B* genome concentrated on the satellited chromosomes. Based on the close similarity of two pairs of large-satellited chromosomes with those of the *B* genome, RILEY, UNRAU and CHAPMAN (1958) advanced *Ae. speltoides* as the putative *B*-genome donor; similarly FELDMAN (1978) suggested *Ae. searsii* as the donor. This evidence in rejecting other related forms not possessing the second large-satellited chromosome pair was criticized by KIMBER and ATHWAL (1972) because it is based only on the presence or absence of a very small piece of chromatin in the distal region of the satellite in one pair of chromosomes. The satellite size of the smaller satellited chromosomes in *Ae. sharonensis* of the present study is larger than that obtained for *Ae. sharonensis*, *Ae. longissima* and *Ae. bicornis* by CHENNAVEERAIAH (1960) and for *Ae. bicornis* by GIORGI and BOZZINI (1969b) and slightly larger in size than that of *Ae. searsii* (FELDMAN 1978). It appears that the significance of the evidence was overestimated because satellite size is a character that exhibits high structural polymorphism in the Triticeae, as shown in *Elymus rechingeri* by HENEEN and RUNEMARK (1962), and in *T. monococcum* by WAINES and KIMBER (1973). Therefore, karyotypic data are better considered as supporting evidence in evolutionary studies. Comparison of the complete idiograms of the putative *B*-genome donors with the extrapolated *B*-genome karyotype from *T. turgidum dicoccoides* in this study reveals that *Ae. sharonensis* fits it more closely than does *Ae. bicornis*, and much more closely than do *Ae. longissima*, *Ae. speltoides* and *Ae. searsii*.

Further verification of the karyotype of *Ae. sharonensis* as fitting the extrapolate *B*-genome of wheat could come from C- or N-banding. GILL and KIMBER (1974), using Giemsa C-banding, demonstrated the relationships of *T. monococcum* and *T. tauschii* with the *A* and *D* genomes, respectively. A distinctive N-banding pattern of the *B* genome has also been demonstrated (GERLACH 1977). The use of these techniques could provide further evidence on the *B*-genome candidacy of *Ae. sharonensis* and will be the subject of a further report.

Ae. sharonensis-bicornis *comparisons*: *Ae. bicornis* is very similar in head morphology to *Ae. sharonensis*; they both have two-rowed heads with awned lateral spikelets and wedge-type disarticulation. Only minor morphological differences favor *Ae. sharonensis* as being more putative than *Ae. bicornis*; *Ae. sharonensis* is larger and has 2–3 kernels per spikelet, compared with only 1–2 in *Ae. bicornis*. The small satellites of *Ae. sharonensis* found in the present study are much larger than those of *Ae. bicornis*; hence, they are closer in size to those of the *B* genome in wheat. One of the main points rendering *Ae. bicornis* ques-

tionable as the *B*-genome donor is its phytogeographic distribution. Being a different phytogeographical element (Saharao-Arabian) from *T. monococcum*, it is very distant from the most southern edge of the distribution of the *A*-genome donor, *T. monococcum*. Since it is known that the present phytogeographical territories of the Middle East were already established in extent and composition in the Pleiostocene (ZOHARY 1973), contact between *Ae. bicornis* and *T. monococcum* would be unlikely.

*Geographical distribution*: The present distribution of *Ae. sharonensis* is on the sandy soils of the Israeli Mediterranean coastal plain. In the uppermost northern part of its distribution, it is separated by 100–150 km from contact with *T. monococcum*, as it occurs in the southern part of Lebanon and Syria. A relatively small geographic separation of *T. monococcum* and *Ae. sharonensis* in the same phytogeographical region should not limit *Ae. sharonensis's* candidacy as a possible *B*- genome donor. Two lines of evidence indicate that the present-day distribution of the ancestral species of wheat in these areas may not reflect ancient distribution. First, the present extent and composition of the floras and phytogeographical territories of the Middle East were already established in the Pleistocene (ZOHARY 1973). However, from pollen analysis of Pleistocene sediments, ROSSIGNOL (1962) found that vegetation distribution on the Israeli coastal belt has been subject to alteration by cycles of marine transgression and regression. The distribution of three plant groups, one of them the Gramineae-Cyperaceae, were significantly affected by these changes. The present-day distribution of a littoral species such as *Ae. sharonensis* is likely to have been affected by these cycles.

Second, in more recent times—the Segetal Period (ZOHARY 1973)—man has interfered to a large extent with the flora of the Middle East. His impact was so severe that botanists doubt whether even "a small portion of natural vegetation has been left in its primary state" (ZOHARY 1973). Furthermore, species most vulnerable to these influences were those preferred by man or livestock; these include the wild wheat ancestors and their hybridization products. It seems likely therefore that the present distributions of *Ae. sharonensis* and *T. monococcum* in the Middle East do not closely reflect their past distributions and that they could have occurred sympatrically in this area. The recent indication that one of the *A*-genome chromosomes of wheat is similar to, and possibly derived from, chromosome *4* $S^{sh}$ of *Ae. sharonensis* (MILLER, personal communication) strengthens the assumption of possible past contact between *Ae. sharonensis*, *T. monococcum* and *T. turgidum dicoccoides* during the early stages of wheat evolution. Such chromosome substitution could have occurred through introgression between tetraploid wheat and *Ae. sharonensis*, resulting in a selectively retained *sharonensis* chromosome within the *A* genome. This type of chromosome substitution has been shown to be possible by artificial chromosome transfers from several Aegilops species into common wheat (MAAN 1975; ENDO and TSUNEWAKI 1975; ENDO and KATAYAMA 1978; ENDO 1979).

Another possibility is that chromosome *4A* became, in part, *sharonensis*-like through nonhomologous translocation with a member of the *B* genome, assuming that the *B* genome was donated by *Ae. sharonensis*. Support for such an event comes from the nullisomic-tetrasomic analysis of wheat by SEARS (1965), who

suggested that chromosome *4A* of wheat was possibly involved in a nonhomologous translocation with chromosome *6B*.

## CONCLUSIONS

A number of lines of direct and indirect evidence give support to *Ae. sharonensis* as the possible *B* genome donor of wheat. These are as follows: (1) it possesses a cytoplasm homologous with that of tetraploid wheat, *i.e.*, compatible with the Triticum genome chromosomes, (2) it possesses a karyotype that closely fits the karyotype extrapolated from tetraploid wheat for the *B* genome donor, (3) it exhibits high levels of homologous pairing with the *B*-genome chromosomes when the *Ph* gene is absent, (4) it exhibits levels of homoeologous pairing with *T. monococcum* that are comparable with the known levels between *A* and *B* genomes in the haploid condition in wheat, (5) it can be hybridized with *T. monococcum* to produce an amphidiploid that exhibits very close morphological resemblance to wild emmer, *T. turgidum dicoccoides*, (6) the *Ae. sharonensis* × *T. monococcum* amphidiploid is vigorous, fertile and stable, (7) *Ae. sharonensis* exhibits a small divergence in DNA base sequences in DNA-DNA hybridization with tetraploid and hexaploid wheat, a divergence that is smaller than exhibited by *Ae. longissima* and *Ae. speltoides*, and (8) the possible presence of a chromosome pair of *Ae. sharonensis*, *4* $S^{sh}$, in the *A* genome indicates possible contact and gene flow between *Ae. sharonensis*, *T. monococcum* and the initial tetraploid wheats during the early stages of wheat evolution.

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