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Diploidization and Chromosomal Pairing Affinities in the Tetraploid Wheats and Their Putative Amphiploid Progenitor

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Summary. The genomes of the diploid wheats *Triticum boeoticum* and *T. urartu* are closely related, giving 7II in the F_1 hybrid (T^bT^u) and 8.4 (0–14) II + 2.5 (0–7) IV in the derived amphiploid ($T^bT^bT^uT^u$). The genomes of the tetraploid wheats are also closely related, giving up to 7II at the polyhaploid level (AB) in the absence of the gene *Ph* but 14II at the tetraploid level (AABB) in the normal presence of *Ph*. If the amphiploid is the progenitor of the tetraploids, one or the other homoeologue (T^b or T^u) in each of the 7 homoeologous groups (the 7 potential IV) must have differentiated with respect to pairing affinity in order to account for 14II in the tetraploid. Consequently, in tetraploid × amphiploid hybrids (T^bT^uAB) carrying the *Ph* gene from the tetraploid, the seven differentiated chromosomes (B) would be expected to give 7I while, on the basis of their observed chiasma frequency, T^b, T^u and the less differentiated A would be expected to give 4.17I + 3.57II + 3.23III), assuming homoeologous pairing. The expected chromosomal configuration freqencies at MI (11.17I + 3.57II + 3.23III) closely fit the observed values (11.22I + 3.45II + 3.19III + 0.07IIV) for such hybrids ($X^2 = 0.0046$; $P > 0.99$). Thus diploidization of the *boeoticum-urartu* amphiploid clearly could account for the origin of the tetraploid wheats. Furthermore, *T. aestivum* × amphiploid hybrids (T^bT^uABD) with and without *Ph* indicated that B as well as A chomosomes tended to pair with their presumed T^bT^u homologues in the absence of *Ph*. Other tests showed that the tetraploid wheats could not plausibly have originated from any postulated *Triticum-Sitopsis* (TTSS) parental combinations with or without such chromosomal differentiation.

Key words: *Triticum urartu* – *Sitopsis* – Tetraploids – Differentiation – Diploidization

Introduction

Identification of the diploid donor of a given polyploid genome on the basis of chromosomal pairing affinities at MI (first meiotic metaphase) in diploid × polyploid hybrids theoretically is feasible in the case of strict allopolyploids whose genomes, already effectively differentiated with respect to pairing affinity in the diploid parents, continue to retain their separate identities unmodified at the polyploid level. However, by far the most common type of polyploid is that derived from parents whose chromosomes (homoeologues) are still homologous enough to pair in the F_1 hybrid (Jackson 1976). Raw amphiploids from such hybrids tend to produce multivalents owing to the persistent association of homoeologues at the polyploid level; and differentiation of these homeologues with respect to pairing affinity ostensibly is required if a diploidized, fertile polyploid species is to evolve.

The hexaploid bread wheat *Triticum aestivum* L. em. Thell. (AABBDD, 2n = 42) evidently originated under cultivation in the early foredawn of historical times as a typical allopolyploid resulting from chromosome doubling in a hybrid between the cultivated tetraploid emmer wheat (AABB; 2n = 28) and the wild diploid Goat Grass, *Aegilops squarrosa* L. (DD, 2n = 14) (McFadden and Sears 1946; Kuckuck 1959, 1964). Chromosome pairing in emmer × *aestivum* hybrids (AABBD) results in essentially 7I + 14II at MI, while *squarrosa* × *aestivum* hybrids (ABDD) give essentially 14I + 7II, indicating that the A, B and D genomes have undergone no detectable modification with respect to chromosomal pairing affinity since the relatively recent origin of the hexaploids.

In contrast, the origin of the tetraploid wheats clearly involved the evolutionary time scale; and it has not been possible to identify unequivocally either A or B with a specific diploid parent on the basis of

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chromosome pairing. The emmer wheats that fed emerging Near Eastern civilizations were domesticated from the wild *T. dicoccoides* (Korn.) Schweinf. occupying the western arc of the Fertile Crescent, while the rare *timopheevii* types were domesticated from the wild *T. araraticum* Jakubz. found in the eastern arc of the Crescent and adjacent areas of Transcaucasia.

Triticum boeoticum Boiss. (T^bT^b, 2n = 14), until recently the only wild diploid wheat recognized by western wheat geneticists, has been assumed to be the donor of the A chromosomes to both tetraploid species. Tetraploid × *boeoticum* hybrids (T^bAB) give 5.6II on an average and by means of telocentric markers, the T^b chromosomes were shown to pair with A (Okamoto 1962; Chapman and Riley 1966). Similar attempts to identify the B chromosomes with those of species belonging to the Section *Sitopsis* of *Aegilops,* including *Ae. speltoides* Tausch. (Riley et al. 1958). *Ae. bicornis* Jaub. et Spach. (Sears 1956) and *Ae. searsii* Feld. (Feldman 1979), seemingly were based on the tacit assumption that the tetraploid wheats, like the hexaploids, are essentially typical allopolyploid. The implication of *Ae. searsii* was based on chromosome pairing in the closely related *Ae. longissima* Schweinf. et Musch.

However, during more than four decades of research no species has been found whose chromosomes pair appreciably with those of the normal B genome. This led to speculation that (1) the B parent was an unknown species or that (2) the B chromosomes had become modified after the origin of the tetraploids so that they no longer pair with those of their donor (Sarkar and Stebbins 1956).

More recently, comparisons of seed protein electrophoretic patterns in *Triticum* and *Aegilops* (Johnson 1972) indicated that the missing parent was not a species of *Aegilops* but, more probably, an unrecognized diploid wheat. Studies based on extensive seed collections yielded evidence that a second wild diploid species of wheat, *T. urartu* Tum. (T^uT^u) previously known only as an Armenian endemic was, in fact, sympatric with *T. boeoticum* throughout the range of the wild tetraploids (Johnson 1975). The tetraploids and diploids all gave very similar electrophoretic patterns from proteins decomplexed with SDS (sodium dodecyl sulfate) (Dhaliwal and Johnson 1976a). Hybrids (T^bT^u) between *T. boeoticum* and *T. urartu* gave 7II but were invariably completely sterile (Johnson and Dhaliwal 1976). Fertile synthetic amphiploids ($T^bT^bT^uT^u$) derived from the hybrids were virtually indistinguishable from the tetraploid wheats on the basis of diagnostic morphological characters, whereas synthetic amphiploids (TTSS) involving either *T. boeoticum* or *T. urartu* with four species of *Sitopsis* (SS) differed markedly from the tetraploid wheats (Dhaliwal and Johnson 1976b; Johnson and Dhaliwal 1978). On the basis of this evidence *T. urartu* was inferred to be the B-genome donor.

Meanwhile, Chapman et al. (1976) and Dvořák (1976), using telocentric chromosomes as markers, showed that the *urartu* like the *boeoticum* chromosomes paired with A. Presumably discounting the fact that the *boeoticum* × *urartu* hybrid was completely sterile, they concluded that *T. urartu* like *T. boeoticum* carried an A genome and could not be the donor of B. However, precisely such anomalous chromosome pairing, where one tetraploid genome (A) pairs with both putative parental genomes and the other tetraploid genome (B) pairs with neither parental genome, is to be expected due to chromosomal differentiation in the case of tetraploids derived from diploids whose genomes show high pairing affinity for one another.

Clear evidence suggests that B and, to a less extent, A have differentiated from their respective prototypes. Differentiation of B at the tetraploid level is indicated by its very failure to pair with the genome of any plausible donor; and such evidence is widely accepted in the literature both tacitly and overtly. Differentiation of A from its averred prototype (T^b) is shown by the fact that the synthetic *boeoticum*-emmer amphiploid (T^bT^bAABB) shows preferential diploid pairing (1.48I + 18.90II + 0.24III + 0.52IV) (Sachs 1952) giving 18.90II per PMC where, instead, up to 7IV (T^bT^bAA) per PMC could be expected if A were homologous with T^b. Evidently B comprises the seven more effectively differentiated homoeologues of the tetraploid wheats, and A the seven less differentiated ones, irrespective of the parental origin of a given homoeologue.

With reference to any tetraploid derived from diploids of high chromosomal pairing affinity, Johnson and Dhaliwal (1978) pointed out that "if one of two homoeologues became sufficiently differentiated so that it no longer paired with the other, then it presumably would not pair with the corresponding chromosome of either parent. The other homoeologue that differentiated little or not at all presumably would still pair, arm for arm, with the corresponding chromosome of either parent in most instances, depending on the degree of differentiation." Thus, the probability is small that all of the A or B chromosomes of the tetraploid wheats could have been derived from only one of the parental genomes. Consequently, unequivocal identification of either A or B with one or the other specific parental genome on the basis of chromosome pairing presumably would not be possible.

Nevertheless, that inference does not preclude the possibility of identifying the tetraploid AB complement as a whole with a specific combination of parental genomes by means of chromosome pairing. The cited evidence that A and B are modified genomes together with new evidence presented here shows that dip-

loidization of the *boeoticum-urartu* amphiploid specifically can account for the anomalous pairing behavior of the tetraploid AB complement, whereas none of four tested *Triticum-Sitopsis* amphiploids can account for the pairing behavior of AB either as typical allopolyploids or as a result of any plausible mode of diploidization.

Materials and Methods

Chromosome pairing data were obtained from hybrids between species in the Riverside wild species collection of *Triticum* and *Aegilops* and from amphiploids produced by colchicine treatment of such hybrids. Crown divisions of vegetative young hybrids were treated for 3 h with a 0.2% solution of colchicine when new tillers began to appear. Chromosome pairing data were obtained also from hybrids between the synthesized amphiploids and tetraploid wheats of the emmer and *timopheevii* groups. The former group comprises the wild *T. dicoccoides,* and cultivars derived from it while the latter group consists of the wild *T. araraticum* and its cultivated derivative *T. timopheevii* Zhuk. Comparable data from other authors with reference to hybrids and amphiploids involving *Ae. bicornis, Ae. longissima* and *Ae. speltoides* are included in the tables.

Chromosome pairing between the T^bT^u genomes on the one hand and the AB genomes of the polyploid wheats on the other in the presence vs. the absence of *Ph* was assessed by means of hybrids between the *boeoticum-urartu* amphiploid and the hexaploid *T. aestivum* cv. 'Chinese Spring' monosomic for chromosome 5B. Seed of the monosomic line was provided through the courtesy of Dr. E. R. Sears.

Microsporocyte material was fixed in Carnoy's fluid (6:3:1) for 12 h, and squashes were made with 1% propionoorcein. Chromosome association was studied at MI.

Amphiploids involving *T. boeoticum, T. monococcum* L. or *T. urartu* with species of Section *Sitopsis* of *Aegilops* are referred to as *Triticum-Sitopsis. Triticum monococcum* is a cultivated derivative of *T. boeoticum.* Neither the wild nor the cultivated form functions well as the female parent in crosses with *Ae. speltoides.*

The genome symbology T^b and T^u adopted for the diploid wheats follows that in use for the genus *Aegilops.* Continuing the use of A for *T. boeoticum* would be inconsistent with published evidence that either *T. boeoticum* or *T. urartu* could be the A donor, and with further evidence treated here which suggests that both A and B are quasi genomes each possibly consisting of some chromosomes from each of the parental diploids.

Results and Discussion

The T. boeoticum-T. urartu Combination

Triticum boeoticum × *T. urartu* hybrids (T^bT^u) (Table 1) showed virtually complete chromosomal pairing, 6.97II of which 6.07 were ring II; yet the hybrids were completely self sterile, presumably due to cryptic differences between the pairing homoeologues.

Such differences between T^b and T^u evidently also account for preferential diploid pairing in the derived *boeoticum-urartu* amphiploids ($T^bT^bT^uT^u$) (Table 1). The amphiploids gave 13.75 equivalent II and were highly but not completely fertile. On an average, 5II associated to give 2.52IV; but more significantly, all 14 potential bivalents were capable of associating to give the full range of 0–7IV.

Clearly, the derivation of fully diploidized tetraploid species from *boeoticum-urartu* amphiploids would require effective differentiation with respect to pairing affinity of either the T^b or T^u homoeologue of each of the seven potential quadrivalents, as postulated by Johnson and Dhaliwal (1978). As a result, the derived tetraploids would carry seven modified homoeologues (B) that would not be expected to pair with its seven unmodified (or less modified) homoeologues (A) nor with either T^b or T^u.

The evident occurrence of such differentiation is indicated by the fact that the 2.52 (0–7)IV in the amphiploid ($T^bT^bT^uT^u$) (Table 1) are reduced to 3.19 (0–7)III in hybrids (T^bT^uAB) (Table 2) between the tetraploid wheats and the amphiploid. Moreover, considering the expected pairing configuration frequencies of the T^bT^uAB hybrid in greater detail, if A and B in fact evolved by differentiation of T^bT^u homoeologues, the seven more modified ones (B) would be expected to give 7I. Assuming homoeologous pairing among the closely related genomes T^bT^uA, they would be expected to account for 4.17I + 3.57II + 3.23III on the basis of their observed chiasma frequency (Table 2), using the method of estimation provided by Driscoll et al. (1979). Alternatively, assuming homologous pairing among T^bT^uA, they would be expected to account for 3.82I + 3.42II + 3.45III, using the method of estimation described by Jackson and Casey (in press). In the first case, the expected meitotic configuration frequencies of the hybrid would be 11.17I + 3.57II + 3.23III, and in the second case, they would be 10.82I + 3.42II + 3.45III. In both instances, they closely fit the observed values 11.22I + 3.45II + 3.19III + 0.07IV (Table 2) ($X^2 = 0.0046$, $P > 0.99$ vs. $X^2 = 0.0347$, $P > 0.98$ respectively).

The tetraploid × amphiploid hybrids were completely self-sterile, which is consistent with the evidence that the tetraploids differ from their presumed amphiploid progenitor with respect to seven effectively modified chromosomes.

The inference that the AB complement differentiated from the T^bT^u homoeologues also is consistent with evidence that in the absence of *Ph,* which inhibits synapsis of the B chromosomes, A and B pair homoeologously in genomic combination such as ABD (Riley 1960) and ABS^1S^1 (Mello-Sampayo, see Johnson and Dhaliwal 1978) where the option of A and B to pair with homologues is not available. The ABS^1S^1 hybrid gave up to 14 bivalents per cell of which seven clearly must have been AB bivalents.

Table 1. Chromosome associations at MI in F_1 hybrids and amphiploids of *Triticum* × *Triticum* and *Triticum* × *Sitopsis*

Cross	No. of crosses	Mean no. PMC's/ plant	Chromosome associations					Other	Chiasmata per PMC	Equiv. II
			I	II		III	IV			
				Ring	Rod					
F_1 hybrids										
Triticum × *Triticum* (T^bT^u)										
T. boeoticum × *T. urartu*[a]	16	75	0.06	6.07	0.90	–	–	–	13.04	6.97
Triticum × *Sitopsis* (TS)										
T. boeoticum × *Ae. bicornis*[b]	–	150	8.62	0.23	2.28	0.11	0.01	–	–	2.69
T. boeoticum × *Ae. longissima*[c]	–	40	10.77	0.02	1.47	0.07	–	–	–	1.59
Ae. speltoides II × *T. monococcum*[d]	–	150	8.42	0.44	2.34	0.15	–	–	–	2.99
Ae. speltoides I × *T. monococcum*[d]	–	50	0.82	2.44	3.84	0.18	0.02	–	–	6.59
Averages (*Triticum* × *Sitopsis*)			7.76	2.99		0.19	0.01	–	–	3.19
Amphiploids										
Triticum-Triticum ($T^bT^bT^uT^u$)										
T. boeoticum – *T. urartu*[a]	6	58	0.37 (0–4)	6.59 (0–12)	1.82 (0–8)	0.20 (0–3)	2.52 (–7)	–	24.72 (17–28)	13.75
Triticum-Sitopsis (TTSS)										
T. boeoticum – *Ae. bicornis*	2	42	0.13 (0–3)	12.56 (8–14)	1.36 (0–6)	0.01 (0–1)	–	–	26.52 (22–28)	13.94
T. boeoticum – *Ae. longissima*	2	32	0.03 (0–1)	12.19 (9–14)	1.79 (0–5)	–	–	–	26.18 (23–28)	13.98
Ae. speltoides II – *T. monococcum*[d]	1	20	1.60 (0–8)	10.84 (7–14)		0.20 (0–1)	0.96 (0–3)	0.04 VII	–	13.06
Ae. speltoides – *T. monococcum*	1	50	4.88 (0–11)	3.16 (0–7)	6.30 (3–14)	0.96 (0–3)	0.32 (0–1)	–	15.44 (11–21)	11.54
Ae. speltoides – *T. urartu*	3	37	4.34 (0–21)	5.08 (0–11)	6.27 (0–13)	0.17 (0–2)	0.13 (0–01)	–	17.22 (6–25)	11.86
Averages (*Triticum* – *Sitopsis*)			2.34	12.20		0.21	0.16	–	–	12.73

[a] Data from Johnson and Dhaliwal (1978)
[b] Data from Sears (1941). *T. monococcum* is a cultivated derivative of *T. boeoticum*
[c] Data from Feldmann (1979)
[d] Data from Sears (1956)

Tests for Homologous Pairing of Genome B

Finally, if the AB complement was derived from T^bT^u, some residual homologous pairing of A and B chromosomes with their respective prototypes could be expected in the absence of *Ph.* The persistence of such pairing was tested by crossing *boeticum-urartu* amphiploids with the hexaploid *T. aestivum* cultivar Chinese Spring monosomic for chromosome 5B. In each cross (T^bT^uABD) a normal 35-chromosome plant was compared with its 34-chromosome sibling nullisomic for 5B (Table 3). Chromosome pairing among the four genomes in question (T^bT^uAB) is better visualized by subtracting the 7I attributable to D, which results in the following frequencies:

5B present: 11.06I + 3.74II + 3.13III (See also Table 2)

5B absent: 2.09I + 6.08II + 3.07III + 0.82IV + 0.09V.

The frequencies of the various meiotic configurations show that virtually all of the B chromosomes pair in the absence of *Ph.* Removal of 5B results in a decrease in I from 11.06 to 2.09 and an increase in

Table 2. Chromosome associations at MI in F_1 hybrids between the tetraploid wheats and *T. boeoticum-T. urartu* and *Tritium-Sitopsis* amphiploids

Cross	No. of crosses	Mean no. PMC's/ plant	Chromosome associations					Other	Chiasmata per PMC	Equiv. II
			I	II Ring	II Rod	III	IV			
Tetraploids × *T. boeoticum-T. urartu* amphiploids (T^bT^uAB)										
emmer × (*boeoticum-urartu*)	12	35	11.52 (4–22)	1.74 (0–5)	1.72 (0–6)	3.11 (0–7)	0.05 (0–2)	–	12.00 (3–18)	8.22
timopheevii × (*boeoticum-urartu*)	4	28	10.09 (5–16)	1.43 (0–4)	2.02 (0–5)	3.50 (1–7)	0.13 (0–2)	–	12.20 (7–17)	8.96
Averages			11.22 (4–22)	1.67 (0–6)	1.78 (0–6)	3.19 (0–7)	0.07 (0–2)	–	12.04 (3–18)	8.38
Tetraploids × *Triticum-Sitopsis* amphiploids (TSAB)										
emmer × (*boeoticum-bicornis*)	2	42	9.93 (2–20)	3.19 (0–7)	4.86 (1–9)	0.59 (0–3)	0.05 (0–1)	–	12.40 (6–19)	9.04
timopheevii × (*boeoticum-bicornis*)	2	28	8.93 (0–17)	2.11 (0–5)	5.18 (1–9)	1.04 (0–5)	0.37 (0–2)	–	12.41 (8–19)	9.59
Tetraploids × *Triticum-Sitopsis* amphiploids (TSAB)										
emmer × (*boeoticum-longissima*)	2	22	15.03 (10–20)	2.27 (0–5)	3.68 (0–7)	0.16 (0–2)	0.14 (0–1)	–	8.98 (5–14)	6.47
timopheevii × (*boeoticum-sharonensis*)	1	35	9.12 (3–18)	2.53 (0–6)	6.29 (3–10)	0.37 (0–2)	0.06 (0–1)	–	12.26 (6–18)	9.50
emmer × (*speltoides-monococcum*)[a]	1	20	6.50	3.10	4.05	1.10	0.70	0.15 V, 0.05 VII	–	10.75
emmer × (*speltoides-urartu*)	2	32	9.03 (4–15)	4.01 (0–7)	4.00 (1–8)	0.78 (0–3)	0.14 (0–1)	–	14.04 (8–18)	9.46
Averages			9.97 (0–20)	2.95 (0–7)	4.68 (0–10)	0.66 (0–5)	0.19 (0–2)	trace	12.22 (6–19)	9.02

[a] Data from Sears (1956)

Table 3. Chromosome associations in F_1 hybrids (T^bT^uABD) between hexaploid wheat with and without chromosome 5 B and *T. boeoticum-T. urartu* amphiploids

Mono-5 B × (amphiploid):	Chromosome 5 B	No. PMC's/ plant	Chromosome association						Chiasmata per PMC	Equiv. II
			I	II Ring	II Rod	III	IV	V		
(1,076 × 1,546)	Present	25	17.58 (15–21)	2.27 (0–4)	1.54 (0–4)	3.27 (2–6)	–	–	12.69 (10–14)	8.72
	Absent	20	11.71 (6–15)	2.38 (1–6)	2.14 (0–6)	3.71 (2–6)	0.43 (0–2)	0.05 (0–1)	15.81 (14–19)	11.07
(1,004 × 1,754)	Present	27	15.30 (12–21)	1.93 (0–4)	1.19 (0–4)	4.52 (2–6)	–	–	14.37 (11–17)	9.90
	Absent	23	8.17 (3–11)	2.91 (1–6)	2.70 (1–4)	3.39 (1–6)	0.91 (0–4)	0.17 (0–1)	18.74 (6–21)	12.94
1,004 × 1,545	Present	50	18.63 (13–23)	1.94 (0–5)	1.64 (0–4)	3.00 (1–5)	–	–	12.00 (8–18)	8.08
	Absent	20	7.78 (3–12)	5.14 (2–9)	3.05 (1–6)	1.86 (0–4)	1.14 (0–3)	–	20.95 (17–24)	13.26
1,004 × 1,734	Present	30	20.74 (16–26)	1.42 (0–5)	3.06 (0–6)	1.74 (0–5)	–	–	9.45 (6–14)	7.09
	Absent	20	8.70 (1–14)	3.00 (1–5)	3.00 (0–6)	3.35 (0–7)	0.65 (0–2)	0.15 (0–1)	18.90 (15–25)	12.70
Average	Present (mono-5 B)		18.06	1.89	1.85	3.13	0.00	0.00	12.12	8.43
Average	Absent (nulli-5 B)		9.09	3.36	2.72	3.07	0.82	0.09	18.60	12.55

equivalent II from 8.43 to 12.55 (Table 3) where the maximum possible pairing among the 27 chromosomes is 13 equivalent bivalents.

Moreover, both B and A chromosomes can be inferred to pair with their authentic T^b or T^u homologues in the absence of *Ph* since the increase in chromosomal association in the absence of chromosome 5B consists primarily of II and IV while the frequency of III each carrying a homoeologue as well as a homologue of A remains unchanged. Also in the absence of 5B there is an increase in the chiasma frequency involving an increase in ring over rod bivalents.

While asynapsis of the B chromosomes is regulated by *Ph*, that gene obviously would be unable to distinguish between B chromosomes and their prototypes unless B had acquired differences with respect to pairing affinity at the tetraploid level. The nature of such differentiation is speculative, but recent evidence reviewed by Johnson and Dhaliwal (1978) tends to implicate constitutive heterochromatin specifically in the case of the B genome.

Triticum-Sitopsis Combinations

The *Triticum* × *Sitopsis* hybrids (TS) (Table 1) also were completely sterile, but unlike the T^bT^u hybrids they showed low residual pairing affinity between genomes (1.59–2.99 equivalent II) except in the case of *Ae. speltoides* I × *T. monococcum* where high pairing (6.59II) presumably was due specifically to the *speltoides* I genotype. Genotypes that promote homoeologoues pairing have been found in various species of *Aegilops* (Sears 1976).

The *boeoticum-bicornis* and *boeoticum-longissima* amphiploids (Table 1), like strict allopolyploids, were highly diploidized (13.96II per PMC) and fertile. The somewhat less fertile *speltoides-monococcum* and *speltoides-urartu* amphiploids showed 0.30–1.28 multivalents per PMC, probably due to the persisting effect of different *speltoides* genotypes on homoeologous pairing at the tetraploid level. The highest IV frequency was 0.96 in *Ae. speltoides* II-*T. monococcum*. None of the TTSS amphiploids gave enough IV to account for the origin of the seven asynaptic B chromosomes of the tetraploid wheats by differentiation of TS homoeologues.

Alternatively, the origin of the tetraploid wheats from a *Triticum-Sitopsis* amphiploids as strict allopolyploids without chromosomal differentiation is equally improbable. In that case the tetraploid × amphiploid hybrid (TSAB), like the amphiploid (TTSS) itself (Table 1) would be expected to show preferential diploid pairing approaching 14II, and high fertility. To the contrary, all of the TSAB hybrids (Table 2) gave high I and low II frequencies (average 9.97I + 7.63II) and all were completely sterile. The high I frequency obviously is attributable to the asynaptic B chromosomes of the tetraploid parent in this case as well as in the case of the T^bT^uAB hybrids, but the evidence presented shows that the B chromosomes could not have originated by differentiation of TS. Feldman's (1979) inference that *Ae. searsii* is the B donor was based on the chromosomal pairing behavior of the closely related *Ae. longissima* which on the basis of 15.03I + 6.21II + 0.30 multivalents in the TSAB hybrid (Table 2) would appear to be a highly improbable B donor.

The small amount of pairing that does occur between S and B chromosomes in TSAB hybrids presumably is attributable (1) to S genotypes that suppress the expression of *Ph* or (2) to persisting primitive homoeologies between S and B.

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