HAPLOIDS AND POLYHAPLOIDS IN *ÆGILOPS* AND *TRITICUM*

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1. INTRODUCTION

THE examination of chromosome behaviour in haploids and polyhaploids is of importance for two reasons. First, the amount of bivalent formation at meiosis is a measure of the level of chromosome structural duplication in the species from which the haploid was derived. Many investigators have drawn conclusions about the phylogenetic relationships of species from the meiotic pairing in hybrids between them. In such work, however, it is necessary to be aware, as has been shown by Stebbins and Pun (1953), how much of the pairing is autosyndetic. The most useful measure of the amount of autosyndesis is provided by records of structural duplication within species obtained from studies of their haploids. Further, knowledge of the extent of structural duplication in species at different chromosome levels may be a valuable aid in understanding the processes of evolution by allopolyploidy, especially in relation to the theory of increasing differentiation between initially semi-homologous chromosome sets proposed by Darlington (1937). Secondly, meiosis in haploids, particularly of wheat, may show how general are the relationships between bivalents and the two types of univalent associations recently described by Person (1955) in a polyhaploid *Triticum vulgare*. In this plant it was shown that the parallel, side-by-side, association of univalents at metaphase, widely described elsewhere, was a function of their homology, but that end-to-end association of univalents was not due to homology.

2. ORIGINS OF THE HAPLOIDS

A haploid plant of *Ægilops longissima*, a polyhaploid of *Triticum timopheevi*, and two polyhaploids of *Triticum vulgare* have been studied. Their origins are described below.

(i) Ægilops longissima

Amongst the progeny of the cross *Ægilops longissima* Schwein. et Musch. ($2n = 14$) × *Triticum durum* Desf. var. *cærulescens* Körn. ($2n = 28$) there was one plant which was morphologically like the seed parent and was at first thought to be a self. When it was noted that its anthers were non-dehiscent and that the glumes gaped open at flowering the plant was examined cytologically and it was found to have only seven chromosomes. It was, therefore, a haploid *A. longissima* which had arisen parthenogenetically. It set no seed.

(ii) Triticum timopheevi

One seed with twin embryos was produced in the cross *Triticum timopheevi* Zhuk. var. *typicum* Zhuk. ($2n = 28$) × *Triticum monococcum* L. gr. *flavescens* Körn. ($2n = 14$). Both embryos developed, one formed a plant, with 21 chromosomes, which was morphologically similar to other hybrids of the same parentage. The other embryo formed a plant which was morphologically identical with *T. timopheevi* though somewhat less vigorous, and with only 14 chromosomes. This plant, which was therefore polyhaploid *T. timopheevi*, was colchicined and produced some grains which gave rise to 28-chromosome progeny. There were, however, also some undoubled tillers available for cytological examination.

(iii) Triticum vulgare

Two types of polyhaploid *Triticum vulgare* Vill. var. Holdfast ($2n = 42$), = *Triticum æstivum* L., were available. One was found in the progeny of a 45-chromosome plant which had the full complement of *T. vulgare* plus three *Secale cereale* chromosomes. At meiosis in the parent there were always 21 bivalents and 3 univalents. and in its progeny, apart from the polyhaploid, there were no plants with less than 42 chromosomes and none which at meiosis formed fewer than 21 bivalents. It is, therefore, most unlikely that the 21-chromosome plant which occurred in the progeny was any other than normal polyhaploid *T. vulgare*. This was confirmed by the phenotype of the plant which was identical with that of a normal Holdfast plant, except for the effects of complete sterility on the spikes, and for reduced vigour.

In the progeny of a 44-chromosome (rye chromosome II disomic addition) plant of *T. vulgare* variety Holdfast (Chapman and Riley, 1955) there was a plant with 22 chromosomes. This plant presumably arose parthenogenetically following a normal reduction in disomic addition II, and would then possess the polyhaploid complement of *T. vulgare* plus one rye chromosome II. The status of this plant may be represented by the formula $3x\mathrm{T}+1\mathrm{S}$. The presence of the rye chromosome follows from the cytological results and from the phenotype of the plant which was characteristic of Holdfast plus rye chromosome II : with short flag leaves, considerable mildew resistance, tapering ears and lengthened lemma points at the apex of the ear. A few grains were obtained from crossing this plant with normal Holdfast plants. These grains were red skinned as are those of disomic addition rye II, although the grain of Holdfast is white.

(iv) Ægilops longissima × Triticum timopheevi

One hybrid, derived from two of the forms of which haploids were available, was examined. This was the F_1 of the cross *Ægilops longissima* Schwein. et Musch. ($2n = 14$) × *Triticum timopheevi* Zhuk. var. *typicum* Zhuk. ($2n = 28$).

3. NOTE ON TERMINOLOGY

In the present material, as in that of earlier workers on haploids and polyhaploids in the Triticinae (Gaines and Aase, 1926 ; Krishnaswamy, 1939, McGinnis and Unrau, 1952, and Person, 1955), it was difficult to distinguish first metaphase of meiosis from first anaphase. This was due to the absence of a clear metaphase plate in cells with univalents only, the arrangement of univalents at the poles and the non-synchronous separation of bivalents when a limited number were present. It is therefore proposed to use the term *metaphase* to apply to the period of division which commenced when the body repulsions of the chromosomes were overcome and the bivalents were orientated on the plate and the univalents at the poles. In the present sense *metaphase* will be considered to have ended by the time that the chromosomes at the poles had opened-out, except at the centromeres, into double strand X shapes. From this time until interphase will be termed *telophase*.

The segmental similarity of non-partner chromosomes of a species which results in the formation of bivalents in its haploids or polyhaploids will be referred to as *structural duplication.*

The 22-chromosome plant ($3x$T+1S) will be termed *aneupolyhaploid T. vulgare.*

4. METHODS

Chromosome counts were made on squashes of root-tips pre-treated with α-bromonaphthalene, fixed in glacial acetic acid, and stained by the Feulgen technique. Meiosis was examined on permanent Feulgen squashes of pollen mother cells of anthers fixed in acetic-alcohol.

5. OBSERVATIONS

(i) *Chromosome associations*

By the commencement of metaphase in all the plants under consideration in addition to associations dependent upon chiasmata—bivalents and trivalents—there were two main types of univalent associations. These may be called, following the terminology of Person (1955), side-by-side (s-s) and end-to-end (e-e) associations.

In s-s associations two univalents lay alongside and parallel to each other (plate, fig. 5) and sometimes appeared to be connected. Occasionally the members of s-s associations diverged from each other at one end, and often they were similarly flexed, the convex side of one lying within the concave side of the other (plate, fig. 2). The s-s pairs were usually in the polar groups of univalents where they orientated at random, but occasionally they occurred at the equator always at right angles to the polar axis (plate, fig. 5). Univalents which appeared to have taken part in s-s pairing were sometimes seen at equivalent positions on either side of the equator (plate, fig. 3) as though the chromosome halves of the association had just separated.

The members of e-e associations lay in tandem, and sometimes the ends were clearly connected by a single chromatin thread (plate, fig. 5). These associations were generally at the poles (plate, fig. 2) where they were orientated at random. Those at the equator usually lay along (plate, fig. 5), and rarely at right angles (plate, figs. 1 and 4) to, the plane of division. There were occasional multi-e-e associations in the two *T. vulgare* polyhaploids and in the *A. longissima* × *T. timopheevi* hybrid, but usually only two univalents were paired. The maximum number of univalents involved in multiple e-e's was five.

A few end-to-side pairs were observed in which the end of one univalent was connected by a staining thread to the centre of another (plate, fig. 3). Very rarely mixed multiple associations occurred combining various arrangements of s-s, e-e and end-to-side associations (plate, figs. 4 and 6).

The mean frequencies of bivalents, trivalents, and s-s and e-e associations, and the frequency distributions of bivalents are recorded

in table 1. Usually there was one terminalised chiasma per bivalent, although in the aneupolyhaploid *T. vulgare* and in the *A. longissima* × *T. timopheevi* hybrid there were a few bivalents with two chiasmata. The trivalents were V-shaped chains with adjacent chromosomes joined by one chiasma. Trivalents were found only where inter- and intra-genome homologies were possible in the polyhaploids and never in the haploid of the diploid *A. longissima*. There were never more than three bivalents in cells with a trivalent in the *T. vulgare* polyhaploids and the hybrid, and no bivalents in cells with a trivalent in polyhaploid *T. timopheevi*.

In order to determine the relationships between the three types of association, chiasmata, s-s, and e-e, the correlation coefficients between the numbers of chromosomes involved in each have been estimated (table 2). The estimates were based on the numbers of chromosomes rather than on the numbers of associations in order to accommodate associations in which more than two chromosomes were sometimes involved : trivalents and multiple e-e's.

The key to this set of data is the pattern of correlations found in polyhaploid *T. vulgare*. In this plant there were significant negative correlations between the numbers of chromosomes in s-s and chiasmata associations and between the numbers in s-s and e-e associations. Although the pattern of correlations is less marked in the other plants there is none which reverse the relationships in polyhaploid *T. vulgare*. Indeed in the *A. longissima* × *T. timopheevi* hybrid the correlations were all in the same direction as in that plant, although only the coefficient between s-s and e-e was significant. These data may be interpreted to mean that chromosomes which frequently participate in chiasmata associations may also, on different occasions, be found in s-s associations. On the other hand chromosomes which are frequently found in e-e associations may sometimes participate in s-s but rarely in chiasmata associations.

It has not been shown, despite the detailed investigation of the problem by Levan (1942) that chiasma formation can take place between non-homologous regions of chromosomes. Therefore the presence of chiasmata associations in this material may be accepted as evidence of some segmental correspondence. Thus the significant correlation between s-s and chiasmata associations must imply that the formation of s-s associations was also due to the segmental homology of the partners. However, the non-significant correlation between chiasmata and e-e associations provides no evidence of the homologous or non-homologous status of this type of pairing.

Further evidence regarding the significance of the univalent associations may be obtained from a comparison of the 21-chromosome polyhaploid and the 22-chromosome aneupolyhaploid *T. vulgare* plants. In the aneupolyhaploid there was a significantly higher mean number of univalents per cell (table 1) than in the polyhaploid ($t_{=(142)} = 3{\cdot}52$, $P = <0{\cdot}001$), whereas the means of bivalents per

TABLE 1

Bivalent frequency and mean pairing at metaphase

Plant	No. cells	Bivalent frequency (cells)						Mean pairing				
		0	1	2	3	4	5	univ.	biv.	triv.	s-s	e-e
polyhaploid *T. vulgare* ($3x = 21$)	104	0·15	0·45	0·28	0·10	0·02	...	18·05±*0·19*	1·38±*0·09*	0·07	1·32±*0·12*	0·75±*0·07*
aneupolyhaploid *T. vulgare* ($3x+1 = 22$)	40	0·17	0·47	0·27	0·09	...	...	19·28±*0·29*	1·25±*0·13*	0·08	1·73±*0·17*	1·15±*0·14*
polyhaploid *T. timopheevi* ($2x = 14$)	60	0·77	0·21	0·02	...	...	...	13·45±*0·13*	0·25±*0·06*	0·02	0·45±*0·08*	0·32±*0·07*
haploid *A. longissima* ($1x = 7$)	100	0·89	0·09	0·02	...	...	...	6·74±*0·25*	0·13±*0·12*	0·00	0·21±*0·13*	0·15±*0·11*
A. longissima × *T. timopheevi* ($3x = 21$)	75	0·21	0·37	0·26	0·08	0·01	0·01	17·99±*0·28*	1·43±*0·13*	0·05	0·53±*0·07*	0·51±*0·06*

TABLE 2

Correlation coefficients between the numbers of chromosomes in different types of associations

Plant	d.f.	Xta.-s-s			Xta.-e-e			s-s-e-e		
		n	*t*	P	*n*	*t*	P	*n*	*t*	P
polyhaploid *T. vulgare* ($3x = 21$)	102	−0·2810	2·63	0·02-0·01	0·1184	1·21	0·2-0·1	−0·2202	2·01	0·05-0·02
aneupolyhaploid *T. vulgare* ($3x+1 = 22$)	38	−0·0293	0·18	0·9-0·8	−0·1384	0·86	0·4-0·3	−0·5332	3·89	<0·001
polyhaploid *T. timopheevi* ($2x = 14$)	58	−0·1451	1·12	0·3-0·2	−0·0851	0·65	0·6-0·5	−0·0279	0·21	0·9-0·8
haploid *A. longissima* ($1x = 7$)	98	−0·0474	0·47	0·7-0·6	−0·0703	0·70	0·5-0·4	−0·1478	1·48	0·2-0·1
A. longissima × *T. timopheevi* ($3x = 21$)	73	−0·1707	1·48	0·2-0·1	0·2019	1·76	0·1-0·05	−0·2241	1·91	0·05

cell were not significantly different ($t_{(142)} = 0{\cdot}78$, P = 0·5-0·4). Indeed frequencies of cells with from 0-3 bivalents, and with trivalents, were strikingly similar in these plants. The extra chromosome in the aneupolyhaploid was thus behaving as a univalent and not affecting the numbers of associations with chiasmata. It was, therefore, not homologous with any of the chromosomes of the wheat complement. This confirms the impression, formed by the phenotype of the plant, that the extra chromosome was rye chromosome II. In the aneupolyhaploid the mean number of s-s associations (table 1) was not significantly higher than that in the polyhaploid *T. vulgare* ($t_{(142)} = 1{\cdot}89$, P = 0·1-0·05) whereas there was a significant increase in the number of e-e associations ($t_{(142)} = 2{\cdot}57$, P = 0·02-0·01). Since the number of e-e associations may be increased by the presence of an additional non-homologous chromosome this type of pairing cannot be dependent on structural similarity.

Thus participation in s-s associations is between segmentally homologous partners. In contrast e-e associations are formed between non-homologous chromosomes.

(ii) *Univalent distributions*

In the majority of cells in the three *Triticum* polyhaploids and in haploid *A. longissima* most univalents had moved to the poles by metaphase (plate, figs. 1, 3 and 6). However, in the polyhaploid *T. vulgare* plants there were from 0-5, and in the polyhaploid *T. timopheevi* from 0-4, univalents left at the equator (plate, figs. 2, 3, 5 and 6). These univalents were generally orientated parallel to the equator but occasionally lay along the polar axis. However, those at the poles were dispersed at random to the plane of division and to each other, except where they were involved in s-s or e-e associations.

The segregation of univalents to the poles has been compared with the calculated random distribution in polyhaploid *T. vulgare*, polyhaploid *T. timopheevi* and haploid *A. longissima*. A varying number of chromosomes were excluded from the polar groups because of their participation in bivalents or trivalents, or because they remained at the equator as univalents. The number segregating was thus not always the full complement, but ranged for example in polyhaploid *T. vulgare* from 10 to 21. In order to overcome this difficulty in calculation, the ratio at the poles for each cell was so adjusted that its sum was the haploid number concerned. This was achieved, for example, in polyhaploid *T. vulgare* by multiplying each side of the ratio by the proportion by which 21 exceeded the actual number segregating. Thus in a cell in which 6 chromosomes remained at the plate and the others segregated to the poles in the ratio 10 : 5 the adjusted ratio became 14 : 7. The ratio 6 : 8 became 9 : 12 and so on. Where the adjusted ratio did not involve whole numbers it was taken to the nearest whole number. An advantage of this method

is that no assumptions were made concerning the behaviour of the chromosomes at the equator.

The segregation of univalents to the poles at metaphase was not significantly different from random in polyhaploid *T. vulgare* ($\Sigma\chi_{(4)} = 5{\cdot}27$, $P = 0{\cdot}3\text{-}0{\cdot}2$) and in haploid *A. longissima* ($\Sigma\chi_{(2)} = 2{\cdot}11$, $P = 0{\cdot}5\text{-}0{\cdot}3$). In polyhaploid *T. timopheevi*, however, there was a significant divergence from random (table 3) largely due to an excess in the 6-8 class and a deficiency in the 5-9 class. Random segregation of univalents in Triticinæ haploids have been reported in *T. monococcum* (Chizaki, 1934), *T. durum* (Kihara, 1936), *T. vulgare* (Yamamoto,

TABLE 3

Segregation of univalents to the poles at metaphase in polyhaploid T. timopheevi

Class	Cells observed	Random	Deviation	χ^2
7-7	11	9·84	1·16	*0·14*
6-8	26	17·23	8·77	*4·46*
5-9	6	11·48	5·48	*2·56*
4-10	4	5·74	1·74	
3-11	0	2·09	2·09	
2-12	0	0·53 } 8·44	0·53 } 4·44	*2·34*
1-13	0	0·08	0·08	
0-14	0	0·00	0·00	
Total .	47	47·00	...	9·50

$\Sigma\chi^2_{(3)} = 9{\cdot}50$ $P = 0{\cdot}05-0{\cdot}02$.
The bracketed data were summed to bring the expected to more than 5·0.

1936) and *A. ovata* (Matsumura, 1940) and excessive regularity in *T. monococcum* (Katayama, 1935) and *T. vulgare* (McGinnis and Unrau, 1952 and Person, 1955). Excessive regularity may be due to the disjunctional separation of s-s associations at early metaphase proposed by Person and observed to occur in the present material (plate, fig. 3). Differences in the behaviour of different haploids, even in the same species, might then be conditioned by genetically or environmentally determined variations in the numbers of s-s associations.

In the 40 cells which it was possible to analyse at telophase in polyhaploid *T. vulgare* the mean number of univalent laggards was $4{\cdot}75\pm0{\cdot}19$. This is significantly greater than the mean number of univalents ($1{\cdot}22\pm0{\cdot}19$) at the equator at metaphase ($t_{(98)} = 12{\cdot}74$, $P = <0{\cdot}001$). There is therefore confirmation for observations of Person that some univalents move from the poles to the equator at the end of metaphase in *T. vulgare* polyhaploids.

The ratios of complete chromosomes at the poles at telophase in this plant were adjusted to bring their sums to 21, as with metaphase ratios. The frequency distribution of telophase segregations did not

differ from random ($\Sigma\chi_{(3)} = 3{\cdot}27$, P = 0·5-0·3) or from segregations at metaphase ($\Sigma\chi_{(3)} = 6{\cdot}06$, P = 0·1-0·05). The increased number of univalents at the equator had therefore resulted from movements from either pole at random.

6. DISCUSSION

(i) *Chromosome behaviour*

The end-to-end pairing of univalents has previously been reported in *Triticum* haploids (Chizaki, 1934, fig. 10; Katayama, 1935; Krishnaswamy, 1939; McGinnis and Unrau, 1952, and Person, 1955). The present results confirm those of Person that these associations do not depend upon homology. Person inclined to Ribbands' (1937) view that they arose from accidents in positioning. This seems unlikely since the ends of the paired univalents are often connected by a staining thread (plate, fig. 5). However, these connections closely resemble those demonstrated by Thomas and Revell (1946) to join secondarily paired bivalents at metaphase in *Cicer*. In this material it was shown that the secondary pairings of bivalents was due to the fusion, during pachytene, of regions of heterochromatin of chromosomes already homologously paired. The similarity in the appearance of the connections suggests that the end-to-end association of univalents in *Triticum* may also be due to the fusion of heterochromatin, as was originally proposed by Kostoff (1938). It can be demonstrated, by cold treatment, that there are some chromosomes with terminal and some with intercalary regions of heterochromatin in *T. vulgare*.

End-to-side pairing was much less frequent than end-to-end. If, therefore, both types were due to connections of heterochromatin then the fusion of terminal with terminal segments was much more frequent than the fusion of terminal with intercalary segments.

The general conclusion from the previous work (Richardson, 1935; Ribbands, 1937; Östergren and Vigfusson, 1953; Person, 1955) has been, as at present, that the side-to-side pairing of univalents was a function of their homology. The observations of Richardson, Ribbands, and Östergren and Vigfusson showed that the metaphase association was preceeded by zygotene pairing, but that chiasma-formation failed. Most authors have believed that the continued pairing was due to secondary association, made possible by the proximity of the partners as a result of coiling or positional correlation. Östergren and Vigfusson considered the continuance of pairing to metaphase in asynaptic rye to be due to stickiness. Since, however, the secondary association of bivalents is due to the fusion of heterochromatic regions it seems possible that secondary association between s-s partners has a similar cause. If homologous pairing, without chiasma-formation, at prophase were followed by the fusion of more than one, or of one long, region of heterochromatin of the partners then the parallel alignment would be maintained.

Therefore, on the basis of the hypothesis of heterochromatin fusion, side-by-side, end-to-end and the rare end-to-side associations would all have the same origin. The distinction between them would arise because the fusions in end-to-end and end-to-side pairs had occurred between segments of chromosomes which lay adjacent by chance. Whereas the fusions in side-by-side pairs had occurred between regions of chromosomes already homologously paired. Mixed multiple associations must then have resulted from various combinations of fusions of terminal with terminal, intercalary with intercalary and intercalary with terminal segments.

(ii) *Structural duplication in polyploids*

The bivalent-univalent frequency in haploid *A. longissima* was of much the same order as that reported in haploid *T. monococcum* (Kihara

TABLE 4

Mean proportion of complement as univalents, bivalents and trivalents in a haploid and two polyhaploids

Species	univalents	bivalents	trivalents
A. longissima ($1x = 7$) .	0·96	0·04	0·00
T. timopheevi ($2x = 14$) .	0·96	0·04	0·00
T. vulgare ($3x = 21$) . .	0·86	0·13	0·01

and Katayama, 1933 ; Chizaki, 1934 ; Smith, 1946). Further, the bivalent frequency in haploid *A. longissima* was in the same relationship to that reported for the polyhaploid of a tetraploid *Ægilops* species, *A. ovata* (Matsumura, 1940), as was that in *T. monococcum* to the frequency in the polyhaploid of *T. durum* (Kihara, 1936). The frequency in the polyhaploids of the tetraploids *T. timopheevi*, *T. durum*, and *A. ovata* was essentially similar. Finally, the pairing in the present polyhaploid of *T. vulgare* falls within the range previously described in polyhaploids of hexaploid wheats (Gaines and Aase, 1926 ; Yamamoto, 1936 ; Raw, 1937 ; Krishnaswamy, 1939 ; Person, 1955).

The three examples which are at present available may therefore be accepted as typical of the behaviour of haploids of species at the diploid, tetraploid and hexaploid levels in the closely related genera *Triticum* and *Ægilops*. The amount of pairing in haploids may be used as a measure of the level of structural duplication in the species concerned. When the amount of pairing is considered as a proportion of the chromosome number (table 4) it is found that there is relatively no more structural duplication in the tetraploid *T. timopheevi* than in the diploid *A. longissima*. However, *T. vulgare* has more than three times as much duplication as the diploid and the tetraploid.

The two species contributing to the tetraploid may have possessed karyotypes within which there was about the same amount of duplication as in *A. longissima* or *T. monococcum* but between which there were no similarities. Whereas the third genome added in the origin of the hexaploids may have had some homology with either, or both, genomes of the tetraploid. That is, the differences may be residual from the original structural condition at the establishment of the polyploid species.

Alternatively, however, Darlington (1937) has suggested that there may be selection for those structural alterations which increase the differentiation of the chromosome sets of polyploids, since the multivalents which resulted from duplications would lead to reduced fertility and genetic instability. If selection favoured cytological " diploidisation " in allopolyploids, through a reduction in the level of structural duplication, it might be expected that more duplication would remain in the younger polyploids. Therefore the present results may mean that there has been more divergence between the two chromosome sets of the tetraploid species than between the third and the original two sets of the younger, hexaploid, species.

The accounts of polyhaploids in hexaploid wheats indicate pairing in excess of that in the synthetic polyhaploids produced as hybrids between the putative parents (McFadden and Sears, 1946 ; Kihara and Lilienfeld, 1949). It is unlikely, therefore, that there has been any decrease in the structural duplication at this level. The synthetic polyhaploid of a tetraploid wheat has not been produced so that a similar comparison is not possible at this level. However, polyhaploid *A. ovata* (Matsumura, 1940) has considerably less pairing than the hybrids between its putative parents (Kihara, 1937 ; Lilienfeld, 1951). The development of cytological " diploidisation " in *A. ovata* must strengthen the probability that a similar process is responsible for the very different amounts of structural duplication in species of different levels of polyploidy in *Triticum*.

(iii) *Pairing in haploids and hybrids*

One of the difficulties in the interpretation of synaptic pairing in hybrids is the possibility that some pairing may be autosyndetic. This has been shown by Stebbins and Pun (1953) to have been responsible for some mistaken diagnoses with regard to the genome relationships between *Triticum* and *Agropyron*. It is therefore desirable to know the amount of structural duplication in the parents of hybrids, and the most useful information on this is obtained from the meiotic pairing in haploids.

The hybrid *A. longissima* × *T. timopheevi* combined the haploid complements of its parent species. The mean bivalent frequency in this hybrid was markedly higher than that expected from a simple summation of the frequencies of the haploids of its parents (table 5). There were also more trivalents. Further, the maximum pairing

possible from combining the haploids would be 4 bivalents whereas the maximum observed in the hybrid was 5 bivalents.

It is clear, therefore, that there was allosyndetic pairing in this hybrid. Without knowledge of the level of structural duplication in the parents, however, all the pairing might have been thought to be autosyndetic. This stresses the importance of utilising information obtained from haploids in the interpretation of the behaviour of interspecific hybrids.

TABLE 5

Mean pairing at metaphase in A. longissima × T. timopheevi F_1 *and the sum of the means of the haploids of the parents*

	univ.	biv.	triv.	s-s	e-e
A. longissima × *T. timopheevi* . .	17·99	1·43	0·05	*0·53*	*0·51*
Haploid *A. longissima* + polyhaploid *T. timopheevi*	20·19	0·38	0·02	*0·66*	*0·47*

7. SUMMARY

1. At first meta-anaphase of meiosis in haploid *Ægilops longissima* ($1x = 7$), polyhaploid *Triticum timopheevi* ($2x = 14$), polyhaploid *Triticum vulgare* ($3x = 21$) and aneupolyhaploid *Triticum vulgare* ($3x+1 = 22$) there were some bivalents, but the majority of chromosomes remained as univalents. In the polyhaploids there were occasional trivalents.

2. There were two main types of univalent associations : side-by-side (s-s) in which the chromosomes lay parallel to each other, and end-to-end (e-e) in which they lay in tandem. End-to-side associations occurred infrequently, and there were rare mixed multiple associations.

3. Members of s-s associations were segmentally homologous but members of e-e's were not. It is suggested that all types of univalent association were due to heterochromatin fusion. Such fusion would maintain the parallel alignment of chromosomes which had paired homologously at prophase, without chiasma-formation, and lead to s-s association. Chance fusions would result in e-e and other associations.

4. Univalents segregated to the poles at random at metaphase in all the plants except polyhaploid *T. timopheevi*. Univalents returned to the equator at random from either pole at late metaphase in polyhaploid *T. vulgare*.

5. Relative to their chromosome numbers *A. longissima* and *T. timopheevi* have about the same amount of structural equivalence within their haploid complements. Both have considerably less than *T. vulgare*. It is suggested that this is due to the development, in the course of evolution, of greater differentiation between the chromosome

sets of the older tetraploid species than between those of the younger hexaploid.

6. The hybrid *A. longissima* × *T. timopheevi* had more chromosome pairing than might have been expected from a simple summation of the pairing in the haploids of the parent species. This demonstrated chromosome homologies between the two species which might otherwise have been unsuspected. The importance is emphasised of using information from haploids in the interpretation of chromosome behaviour in hybrids.

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Plate

Photomicrographs of first metaphase of meiosis in Feulgen stained pollen mother cells of a haploid, two polyhaploids and a triploid hybrid, in the Triticinæ. × 1000.

FIG. 1.—*Ægilops longissima* ($1x = 7$), oII 7I, an e-e along the equator.

FIG. 2.—*Triticum timopheevi* ($2x = 14$), oII 14I, 1 e-e (left) and 1 s-s (right).

FIG. 3.—*Triticum vulgare* ($3x = 21$), 1II 19I, a separating s-s at the equator, an e-s and an s-s at the lower pole.

FIG. 4.—*Triticum vulgare* ($3x = 21$), 3II 15I, an e-e at the equator, a multiple association of 3 univalents combining s-s, e-e and e-s at the lower pole.

FIG. 5.—*A. longissima* × *T. timopheevi* ($3x = 21$), 3II 15I, 2 e-e's and 1 s-s.

FIG. 6.—*A. longissima* × *T. timopheevi* ($3x = 21$), 4II 13I, a multiple association of six, combining s-s, e-e and e-s at the upper pole.

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