CHROMOSOME BEHAVIOUR IN SPECIES HYBRIDS WITH *TRITICUM TIMOPHEEVI*

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INTRODUCTION

THE 28 chromosome wheat species *Triticum timopheevi* has attracted interest on account of its reported cytological behaviour and its application to the genome concept. Lilienfeld and Kihara (1934) had examined the F_1 hybrids between tetraploid wheat species. They had found that the hybrids involving *timopheevi* differed from the rest, were normally sterile, and had poor chromosome pairing. On the basis of chromosome pairing in hybrids they designate the chromosome sets of *timopheevi* by the formula AG in contrast to the AB formula given to the chromosome sets of the other tetraploid species. In their classification of the genus *Triticum*, the species *timopheevi* is also placed in a section of its own thus suggesting a different origin. This suggestion is followed by Sears (1948). Kostoff (1937) obtained similar results to those of Lilienfeld and Kihara, but he interprets them as showing "partial homology" (as measured by metaphase chromosome pairing in hybrids) between the chromosome sets of *timopheevi* and of the other tetraploid species. Kostoff therefore suggests for *timopheevi* the formula A β .

In view of this reported behaviour of *timopheevi*, it was decided to investigate hybrids with this species using both F_1 's and a range of colchicine derived amphiploids. The results obtained do not support either the genome concept or the suggested mode of origin of *timopheevi*.

MATERIAL AND TECHNIQUES

The following parental species and varieties have been used in this investigation :—

$2^n = 14$ chromosomes

T. monococcum L. var. *vulgare* Körn.

$2^n = 28$ chromosomes

T. dicoccoides (a) Körn. var. *nudiglumis* Nabalek

T. dicoccoides (b) Körn. var. *kotschyannum* Perc.

T. dicoccum Schübl. var. *farrum* Körn.

T. polonicum L. var. *levissimum* Körn.

T. turgidum L. var. *iodurum* Körn.

T. turanicum Jacobz. (= *T. orientale* Perc.)
var. *notabile* Perc.

T. carthlicum Nevski. (= *T. persicum* Vav.)

T. timopheevi Zhuk var. *typicum* Zhuk.

T. dicoccoides var. *nudiglumis* will be referred to as *dicoccoides* (a). Specimens of this variety were obtained from Mr J. B. Gillett (now at the Kew Herbarium, England) who had found the plants growing in Iraq, and following the botanical description of Nabalek (1929) they have been assigned to the variety *nudiglumis*. *T. dicoccoides* var. *kotschyianum* will be referred to as *dicoccoides* (b). Seeds of some of the F_1 hybrids and of the amphiploids were placed at my disposal by Dr G. D. H. Bell.

After a preliminary examination of meiosis on temporary acetocarmine smears, all cytological observations were made on Feulgen squashes. Anthers were fixed in 1:3 acetic alcohol and stained according to the Feulgen technique. Permanent preparations mounted in "Euparal" were made after the schedule outlined in Darlington and La Cour (1947, p. 128). For a study of chromosome morphology in root tips, best results were obtained after pre-treatment for approximately three hours in a saturated solution of mono-bromo-naphthalene (O'Mara, 1948). This gave clearer chromosome figures than pre-treatment with either low temperatures, paradichlorobenzene, chloral hydrate, or colchicine. Permanent preparations of root tips were also made by means of Feulgen squashes.

Unless otherwise stated, the figures on chromosome pairing are in each case based upon an analysis of 50 complete nuclei at the first metaphase of meiosis.

CHROMOSOME BEHAVIOUR IN F_1 SPECIES HYBRIDS

Chromosome pairing in six 28 chromosome F_1 hybrids between *timopheevi* and other $4x$ species of the genus *Triticum* is shown in table 1. The first five of these hybrids show a reduction from the possible 14 bivalents per cell and from the 29.94 chiasmata per nucleus found in the species *timopheevi*. In addition:—

carthlicum $\times$ *timopheevi* ($4x$) showed an average of 6.16 I, 9.44 II, 0.96 III and 0.02 IV.

timopheevi $\times$ *polonicum* ($4x$) showed an average of 7.76 I, 8.66 II, 0.92 III and 0.04 IV.

timopheevi $\times$ *monococcum* ($3x$) showed an average of 7.80 I, 6.09 II and 0.34 III.

The anthers did not dehisce in any of these F_1 hybrids and no seed was set. All these F_1 hybrids were therefore completely sterile.

Although previous workers have presented no adequate data for chiasma frequencies, these results broadly agree with those obtained by Lilienfeld and Kihara (1934) and Kostoff (1937). The $3x$ hybrid shows that the chromosome pairing in a hybrid between *timopheevi* and a diploid species of *Triticum* is not very different from some other $4x \times 2x$ species hybrids in *Triticum*. The $4x$ hybrids show that there is a decreased chromosome pairing in hybrids between *timopheevi* and

other 4x species of *Triticum*, but there is no hybrid which even approaches an average of 14 univalents per cell. There is therefore always some chromosome pairing between the two chromosome sets of *timopheevi* and those of the other species of *Triticum*.

Chromosome pairing in the 4x F₁ hybrid *dicoccoides* (a) × *timopheevi* (table 1) is, however, different from the chromosome pairing found in all the other 4x F₁ hybrids involving *timopheevi*. This hybrid shows 13.90 bivalents per cell and 28.54 chiasmata per nucleus. No chromosome bridges were found at anaphase and the tetrads appeared to be normal. Despite this apparently normal meiosis the anthers did not dehisce and under the glasshouse conditions of 1949 the hybrid plants were completely sterile.

TABLE 1

*Chromosome pairing in F₁ hybrids of T. timopheevi
with other 4x species*

Hybrid	Mean chromosome pairing per cell					
	I	II	III	IV	Xta per nucleus	Term coeff.
<i>timopheevi</i> × <i>durum</i> * . . .	3.90	10.55	1.00	0	20.85	0.59
<i>dicoccum</i> × <i>timopheevi</i> . . .	4.98	10.30	0.78	0.02	19.30	0.51
<i>timopheevi</i> × <i>turanicum</i> . . .	5.78	9.44	1.06	0.04	17.88	0.57
<i>timopheevi</i> × <i>turgidum</i> . . .	6.32	9.04	1.12	0.06	18.04	0.57
<i>dicoccoides</i> (b) × <i>timopheevi</i> . .	5.62	10.00	0.74	0.04	18.46	0.56
<i>dicoccoides</i> (a) × <i>timopheevi</i> . .	0.20	13.90	0	0	28.54	0.60

* = 20 cells; in all other hybrids 50 cells were analysed.

Xta = chiasmata. Term. coeff. = terminalisation coefficient.

In view of this result, hybrids were again made in 1949 using *dicoccoides* (a) on this occasion as both male and female parent. These hybrid plants were grown in two different lots in two open fields surrounded by many other fertile plants in order to ensure an ample opportunity for their pollination by foreign pollen.

Twenty-six F₁ plants were grown in 1950 and independently of whether *dicoccoides* (a) had been used as male or female parent the meiotic investigations confirmed the results which had been obtained in the previous year. Meiosis in the anthers was apparently normal in all cases, but none of the anthers dehisced. Degeneration of the gametes must therefore have occurred after the tetrad stage. From artificially opened mature anthers, a count of 500 pollen grains stained in aceto-carmin gave an estimate of 5 per cent. good pollen. Under the conditions of open pollination prevailing in the field in 1950 there was however some seed set. This was probably due to the greater viability of female gametes.

CHROMOSOME BEHAVIOUR IN AMPHIPLOIDS

Further evidence on the chromosome behaviour in hybrids of *timopheevi* can be obtained by a study of colchicine-derived amphiploids from the $4x$ F_1 hybrids. The chromosome pairing of six amphiploids (derived from the six F_1 hybrids described in table 1) is given in table 2.

Meiosis was studied in the first generation after colchicine treatment of the F_1 hybrid plants. Of particular interest is the 56 chromosome amphiploid *dicoccoides* (a) $\times$ *timopheevi* which had shown 13.90 bivalents in its 28 chromosome sterile F_1 hybrid. In contrast to its $4x$ F_1 hybrid,

TABLE 2
Chromosome pairing in $8x$ amphiploids of *T. timopheevi*

Amphiploid	Mean chromosome pairing per cell						
	I	II	III	IV	V/VI	Xta per nucleus	Term coeff.
<i>timopheevi</i> $\times$ <i>durum</i>	1.70	23.18	0.38	1.70	0	54.70	0.57
<i>dicoccum</i> $\times$ <i>timopheevi</i>	1.04	23.94	0.24	1.56	0.02	50.74	0.60
<i>timopheevi</i> $\times$ <i>turanicum</i>	0.86	23.50	0.26	1.84	0	54.22	0.56
<i>timopheevi</i> $\times$ <i>turgidum</i>	0.92	24.06	0.18	1.58	0.02	55.76	0.59
<i>dicoccoides</i> (b) $\times$ <i>timopheevi</i>	1.48	23.28	0.36	1.72	0	51.44	0.64
<i>dicoccoides</i> (a) $\times$ <i>timopheevi</i> *	1.47	21.10	0.47	2.73	0	51.44	0.64

* = 30 cells : in all other amphiploids 50 cells were analysed.

this $8x$ amphiploid *did* show dehiscence of the anthers. Two plants were examined for male and female fertility in 1950 :—

- (i) A count of 1000 pollen grains stained in aceto-carmin gave an average of 75 per cent. good pollen.
- (ii) Primary florets, open pollinated, of 125 spikelets showed a range of seed set per spike from 29 to 72 per cent. giving an average of 55 per cent. seed set.

The $8x$ amphiploid was therefore (like all the others) both male and female fertile.

The chiasma frequency per nucleus in the amphiploid *dicoccoides* (a) $\times$ *timopheevi* with 2.73 IV (54.8 per cent. of which formed rings) and 0.47 III, is the same as the chiasma frequency per nucleus in the amphiploid *dicoccoides* (b) $\times$ *timopheevi* with 1.72 IV (54.7 per cent. of which formed rings) and 0.36 III. Multivalent formation, therefore, did not influence the chiasma frequency per nucleus in these two amphiploids. In common with the other hybrids, multivalent formation in the amphiploid *dicoccoides* (a) $\times$ *timopheevi* is lower than bivalent formation in the F_1 hybrid. This is probably due to differential affinity (*cf.* Darlington, 1937).

CHROMOSOMAL STERILITY IN SPECIES HYBRIDS

Dobzhansky (1941) distinguishes between genic and chromosomal sterility in species hybrids. He points out that the principal source of evidence for the existence of chromosomal sterility in an F_1 hybrid is the behaviour of its allopolyploid. The production of a fertile amphiploid from the sterile F_1 *dicoccoides* (a) $\times$ *timopheevi* would thus indicate that the F_1 sterility is chromosomal, and the same applies to the other five amphiploids described in the previous section. The F_1 sterility of these other five amphiploids is, however, at least partly due to the formation of univalents and the subsequent abnormalities in meiosis, whereas the F_1 hybrid *dicoccoides* (a) $\times$ *timopheevi* was sterile despite an apparently normal meiosis.

TABLE 3
Chiasma frequency of parents, F_1 hybrid, and amphiploid
T. dicoccoides (a) $\times$ *T. timopheevi*

	Ploidy	Xta per nucleus
<i>dicoccoides</i> (a)	4x	29.06
<i>timopheevi</i>	"	29.94
F_1 hybrid	"	28.54
Theoretical amphiploid (sum of the parents)	8x	59.00
Experimentally produced amphiploid	"	51.44

50 cells analysed in each species and hybrid.

Table 3 shows the chiasma frequency of the parent species, F_1 hybrid, and amphiploid *dicoccoides* (a) $\times$ *timopheevi*. This shows that the chiasma frequency of the F_1 hybrid was almost as high as that of the parent *dicoccoides* (a) and only slightly less than the chiasma frequency of the parent *timopheevi*. The observed amphiploid chiasma frequency was lower than the chiasma frequency derived from the sum of the two parent species. The ratio of observed to calculated chiasma frequency is 0.87 for chiasmata per nucleus. This ratio is comparable to that found in the other *Triticum* amphiploids, and in *Primula kewensis* (Upcott, 1939). The multivalent frequency in *Primula kewensis* is lower however than that found in the amphiploid *dicoccoides* (a) $\times$ *timopheevi*.

The behaviour of *Primula kewensis* has been explained by Darlington (1937) followed by Dobzhansky (1941) and Stebbins (1950). It is assumed that the chromosomes of the two parent species are sufficiently alike to ensure chromosome pairing in the F_1 hybrid, but that non-homologous segments are involved in this apparently normal chromosome pairing. The gametes produced by the F_1 hybrid will then be inviable because recombination between the chromosomes of the two parent species has produced inviable combinations of genic

material. Pairing and segregation in the amphiploid produced by somatic doubling would, however, tend to produce gametes containing one complete set of chromosomes derived from one parent and one complete set of chromosomes derived from the other parent. These gametes would then be viable.

The type of chromosomal sterility in F_1 hybrids, which is brought about by chromosomal differences which do not materially affect metaphase chromosome pairing at meiosis, has been called cryptic structural hybridity by Stebbins (1945, 1950). The high degree of sterility in the F_1 hybrids, such as *timopheevi* $\times$ *durum* with a mean of 3.90 I per cell and in F_1 hybrids between *timopheevi* and hexaploid species of *Triticum*, may also be partly due to cryptic structural hybridity.

TABLE 4
Chromosome pairing in $4\times F_1$ hybrids of *T. timopheevi*,
T. dicoccoides (a) and *T. dicoccoides* (b)

Hybrid	Mean chromosome pairing per cell					
	I	II	III	IV	Xta per nucleus	Term coeff.
<i>dicoccoides</i> (a) $\times$ <i>timopheevi</i> . . .	0.20	13.90	0	0	28.54	0.60
<i>dicoccoides</i> (b) $\times$ <i>timopheevi</i> . . .	5.62	10.00	0.74	0.04	18.46	0.56
<i>dicoccoides</i> (a) $\times$ <i>dicoccoides</i> (b) . .	10.16	8.02	0.60	0	13.36	0.52

50 cells analysed in each hybrid.

Further evidence on these questions can be obtained indirectly. If chromosome pairing in the F_1 hybrid *dicoccoides* (a) $\times$ *timopheevi* involves non-homologous segments (as is indicated by the evidence presented above) these two parent forms may show a difference in chromosome pairing in other hybrid combinations. The amount of structural similarity sufficient to ensure good chromosome pairing between the two parent forms in the hybrid *dicoccoides* (a) $\times$ *timopheevi* may not be sufficient to ensure *equal* chromosome pairings when each of these parents is involved in other hybrid combinations. That this is actually the case is seen from the data in table 4.

With *dicoccoides* (b) as one of the parents, only 5.62 chromosomes remain unpaired in hybrids with *timopheevi* whereas 10.16 chromosomes remain unpaired in hybrids with *dicoccoides* (a). The possibility of genotypic (as opposed to structural) control of chromosome pairing producing the differences found in these two hybrids cannot be entirely ruled out. But these data on chromosome pairing can also be explained if some of the chromosomes of *dicoccoides* (a) and *timopheevi* are sufficiently unlike to give differences of pairing in their hybrids

with *dicoccoides* (b). These differences in pairing and the sterility of the F_1 hybrid *dicoccoides* (a) $\times$ *timopheevi* can thus both be explained by the existence of structural differences between the chromosomes of all three stocks.

THE GENOME CONCEPT AND THE ORIGIN OF TETRAPLOID *TRITICUM* SPECIES

Largely as a result of Kihara and his co-workers (Kihara, 1937, 1949) the concept of genome formulæ has become prominent within the sub-tribe *Triticinæ*. Metaphase chromosome pairing in hybrids is taken as an indication of chromosome homology and each chromosome set (called a genome) is given a specific formula. Some of the data from chromosome pairing can be used for the interpretation of phylogenetic relationships in conjunction with external plant morphology. Thus Kihara (1944) suggested that 14 chromosomes belonging to the chromosome sets of the 6x species of *Triticum* have been derived from the 14 chromosome species *Aegilops squarrosa*. This suggestion was experimentally confirmed by the actual synthesis of plants resembling 6x species of *Triticum* (MacFadden and Sears, 1946; Kihara and Lilienfeld, 1949).

Darlington (1937) has, however, stressed the undesirability of basing phylogenetic conclusions on chromosome pairing in hybrids. Dobzhansky (1941) has also pointed out that what is actually being studied is the chromosome pairing which is mainly determined by the gross structural arrangement of the chromosomes. The term genome implies that chromosome sets with the same genome formula contain the same gene complexes. There is, however, no evidence to suggest that the amount of genic differentiation is always proportional to the amount of structural differentiation which is able to influence chromosome pairing at the first metaphase of meiosis. Kihara (1937) has himself pointed out that there is no distinct dividing line between what is called a homologous and what is called a non-homologous genome, the one gradually merges into the other.

In most cases, metaphase chromosome pairing and chiasma formation in hybrids is assumed as being determined by the gross structural arrangements of the chromosomes. Phylogenetic speculations based only on the criterion of metaphase chromosome pairing can, however, lead to erroneous conclusions. The formulæ given to the chromosome sets of the 4x species of *Triticum* are a case in point.

The AG formula suggested by Lilienfeld and Kihara (1934) for *timopheevi* is also applied by Sears (1948) to the chromosome sets of *armeniicum*, and it is further suggested that the G chromosome set of both *armeniicum* and *timopheevi* is probably phylogenetically derived from a different species than the B chromosome set of the other tetraploids. The evidence for suggesting the formula G for one of the chromosome sets of *timopheevi* is based on the reduction of chromosome

pairing in $4x$ species hybrids involving *timopheevi*. The evidence for assigning the formula G to one of the chromosome sets of *armeniicum* is based on the data of Svetozarova (1939) that there is good chromosome pairing and apparently normal tetrads in the hybrid *timopheevi* $\times$ *armeniicum*. The data of Svetozarova (1939) however, also shows that despite an apparently almost normal meiosis the hybrid was sterile. The sterility in F_1 *timopheevi* $\times$ *armeniicum* may also be due to cryptic structural hybridity.

The chromosome behaviour of F_1 *timopheevi* $\times$ *armeniicum* is thus similar to that in F_1 *timopheevi* $\times$ *dicoccoides* (a) and in both cases meiosis would involve the pairing of chromosomes with non-homologous segments.

If one now follows the principles which are accepted in the giving of formulæ on the basis of metaphase chromosome pairing in hybrids, *dicoccoides* (a) would have to be given the formula AG in common with *timopheevi* and *armeniicum*. One would then be in a position either of having to elevate *dicoccoides* (a) into a new species (for which there is no justification) or of designating the variety *dicoccoides* (a) as AG and the variety *dicoccoides* (b) as AB. If the two varieties are designated as AB and AG one would then have to postulate that the tetraploid chromosome sets of these two varieties of *dicoccoides* are phylogenetically derived from two different species, which is highly improbable. This, therefore, shows the misleading conclusions that can be obtained when basing phylogenetic relationships only upon the amount of metaphase chromosome pairing at meiosis.

Considerable divergence in chromosome structure, as analysed by pairing at meiosis, has been found within the species *dicoccoides*. There is thus no reason to suppose that *timopheevi* and *armeniicum* may not also have diverged in the same way from an original $4x$ prototype. An examination of the chromosome morphology of *timopheevi* shows that, in common with the other $4x$ species of *Triticum*, it has at mitosis chromosomes with median or sub-median centromeres and four chromosomes with large satellites. It is not possible to identify with certainty all the individual chromosomes and chromosome measurements can differ appreciably in various varieties of the same species of *Triticum* (cf. Camara, 1947). The basic idiogram regarding the presence of median or submedian centromeres and the number of chromosomes with satellites is, however, the same in *timopheevi* as in the other $4x$ species. This evidence also conflicts with the suggestion that the tetraploid chromosome set of *timopheevi* has been phylogenetically derived from another species than the tetraploid chromosome set of e.g. *dicoccoides*.

The specimens designated as *dicoccoides* (a) are not morphologically identical with *armeniicum*. *Armeniicum*, among other characteristics, does not occur together with *Hordeum spontaneum*; it has no varieties with pubescent spikes; and it was found in Armenia and at Nakhichevan in Transcaucasia (Jukubziner, 1932; Tumanjan, 1934;

Makushina, 1938). Mr J. B. Gillett has informed me that there was considerable morphological variation in the specimens of *dicoccoides* which he found in Iraq. The plants were growing on the northern slopes of Handren Dagħ above Jundiyan village a few miles east of Rowanduz. There were pubescent and glabrous forms of various colours and noticeable differences in the size of spike and general vigour. In contrast to *armeniicum* in Transcaucasia, the *dicoccoides* in Iraq was found growing together with *Hordeum spontaneum*. The considerable morphological range of *dicoccoides* in Iraq may on further cytological examination also show a range of chromosome differentiation from the *Syrio-palestinicum* types such as *dicoccoides* (b) to the cytologically differentiated types such as *dicoccoides* (a) and *timopheevi*. There is thus nothing improbable in the suggestion that all the 28 chromosome species of *Triticum* have originated from a common 28 chromosome prototype. The various stages of cytological differentiation may, in fact, still be in existence in Iraq.

SUMMARY

1. Two types of *T. dicoccoides* (a) and (b), have been found to differ in their chromosome structure. These types show that all the cytological differentiation among the 4x species of *Triticum* can be found within the species *dicoccoides*.

2. All the cytologically different 4x species of *Triticum* could thus have been derived from an original 28 chromosome prototype.

3. Tetraploid species hybrids with *T. timopheevi* show sterility presumably owing to recombination between chromosomes containing non-homologous segments.

4. Metaphase chromosome pairing in hybrids is not sufficient to assign distinct genome formulæ for the properties of different chromosome sets in various species.

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REFERENCES

- CAMARA, A. 1947. Cromosomas somaticos de *Triticum turgidum*. *Agron. Lusitana*, 9, 171-180.
- DARLINGTON, C. D. 1937. *Recent Advances in Cytology*. 2nd Ed. London: Churchill.
- DARLINGTON, C. D., AND LA COUR, L. F. 1947. *The Handling of Chromosomes*. 2nd Ed. London: Allen & Unwin.
- DOBZHANSKY, T. 1941. *Genetics and the Origin of Species*. 2nd Ed. New York: Columbia University Press.
- JAKUBZINER, M. 1932. Contribution to the knowledge of wild wheats in Transcaucasia. *Bul. Appl. Bot. Gen. & Pl. Br.*, Series 5, No. 1, 147-198.
- KIHARA, H. 1937. Genomanalyse bei *Triticum* und *Aegilops* VII Kurze Übersicht über die Ergebnisse der Jahre 1934-36. *Kyoto Univ. Col. Agr. Mem.*, No. 41, 1-61.
- KIHARA, H. 1944. Discovery of the DD analyser, one of the ancestors of Vulgare wheats. *Agr. & Hort.*, 19, 889-890.

- KIHARA, H. 1949. Genomanalyse bei *Triticum* und *Aegilops* IX Systematischer Aufbau der Gattung *Aegilops* auf Genomanalytischer Grundlage. *Cytologia*, 14, 135-144.
- KIHARA, H., AND LILIENFELD, F. 1949. A new synthesised 6x wheat. *Proc. 8th Int. Genet. Congr. (Stockholm)*, pp. 307-319.
- KOSTOFF, D. 1937. Chromosome behaviour in *Triticum* hybrids and allied genera I interspecific hybrids with *Triticum timopheevi*. *Proc. Indian Acad. Sci.*, 5, 231-236.
- LILIENFELD, F., AND KIHARA, H. 1934. Genomanalyse bei *Triticum* und *Aegilops* V *Triticum timopheevi* Zhuk. *Cytologia*, 6, 87-122.
- MACFADDEN, E. S., AND SEARS, E. R. 1946. The origin of *Triticum spelta* and its free threshing hexaploid relatives. *J. Hered.*, 37, 81-89, 107-116.
- MAKUSHINA, E. N. 1938. A new species of wheat *Triticum armeniacum* (Jakubz.) sp. n. *C.R. Acad. Sci. U.S.S.R.*, 21, 345-348.
- NABALEK, F. 1929. Inter turco-persicum pars. V. *Publ. Fac. Sci. Masaryk Univ. Brno.*, 111, 27-28.
- O'MARA, J. G. 1948. Acetic acid methods for chromosome studies at prophase and metaphase in meristems. *Stain Tech.*, 23, 201-204.
- SEARS, E. R. 1948. The cytology and genetics of the wheats and their relatives. *Adv. Genet.*, 2, 239-270.
- STEBBINS, G. L. JR. 1945. The cytological analysis of species hybrids II. *Bot. Rev.*, 11, 463-486.
- STEBBINS, G. L. JR. 1950. *Variation and Evolution in Plants*. New York : Columbia University Press. London : Oxford University Press.
- SVETOZAROVA, V. V. 1939. Second genome of *Triticum timopheevi* Zhuk. *C.R. Acad. Sci. U.S.S.R.*, 23, 473-477.
- TUMANYAN, M. 1934. The botanical diversity of the wild wheats in Armenia. *Bul. Appl. Bot. Gen. & Pl. Br.*, Series 5, No. 2, 241-268.
- UPCOTT, M. 1939. The nature of tetraploidy in *Primula kewensis*. *J. Genet.*, 39, 79-100.

Plate

Microphotographs of pollen mother cells at Metaphase I.
Feuglen stained. $\times 1600$.

FIG. 1.—4x *timopheevi* $\times$ *turgidum* 5 I, 10 II, 1 III.

FIG. 2.—4x *dicoccoides* (a) $\times$ *timopheevi* 14 II.

FIG. 3.—8x *dicoccum* $\times$ *timopheevi* 3 I, 19 II, 1 III, 3 IV.

7 46 11 21 22 23 24

0 1 2 3 4 5 6 7 8 9

10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99