

✓
Sanchez-Monge, E.
1948

E. Sánchez-Monge and J. Mac Key

ON THE ORIGIN OF SUBCOMPACTOIDS
IN TRITICUM VULGARE

ON THE ORIGIN OF SUBCOMPACTOIDS
IN TRITICUM VULGARE

ON THE ORIGIN OF SUBCOMPACTOIDS IN TRITICUM VULGARE ⁽¹⁾

By E. SANCHEZ-MONGE

Estación Experimental de Aula Dei, Zaragoza, Spain

and

J. MAC KEY

Swedish Seed Association, Svalöv, Sweden

IN 1904 NILSSON-EHLE found among the progeny of «squarehead» *Triticum vulgare* HOST. several plants resembling in their ear shape *Tr. spelta* L. He called them speltoids and showed conclusively (1917, 1920, 1921) that they arise through mutation. He also was the first to observe another aberrant form, resembling *Tr. compactum* HOST., the subcompactum or subcompactoid type. Since then, a great number of investigators (VESTERGAARD, AKERMAN, LATHOUWERS, LINDHARD, KAJANUS, WINGE, GOULDEN, HUSKINS WATKINS, PHILIPTSCHENKO, VASILIEV, HAKANSSON, MÜNTZING, OEHLER, DUMON, PHIPPS and GUERNEY, NISHIYAMA, ISHIKAWA, UCHIKAWA, CÂMARA, SMITH, MATSUMURA and LOVE; for complete bibliography cf. HUSKINS 1946) have studied the genetics and cytology of these off-types in order to ascertain their origin and relationship.

NILSSON-EHLE (1921) classified the speltoids in three types of series. According to the segregation ratio of the heterozygotes when self-fertilized, his series can be characterized thus:

Series	normals	het speltoids	hom speltoids
A	1	2	< 1
B	1	4-5	≤ 0.05
C	1	1	< 0.2

Series C rather often changes over to series B. Series A and B are more stable.

Subcompactoids arise generally as segregates of het B speltoids. Sometimes they appear in series C and even directly in normal *Tr. vulgare* Sub-

(1) This manuscript has been sent for publication to «HEREDITAS» on 10th of December of 1947. The investigations were carried out in the cytogenetic laboratory of the Swedish Seed Association.

compactoids are heterozygous but according to their different genetic origin the segregation is not uniform. HUSKINS (1946) distinguishes three main segregation types. One type gives only normal, subcompactoid and true-breeding compactoid progeny, another het speltoids and a third type het speltoids and subnormals in addition.

WINGE (1924), GOULDEN (1926) and HUSKINS (1927, 1928) discovered that several of these off-types showed irregularities in chromosome number and behaviour and were the first to establish the relationship between chromosome irregularities, origin and genetic behaviour of these mutants. Due to the work of the investigators mentioned and others, the origin of the three series of speltoid wheats seems definitively explained.

HUSKINS summarizes in a recent paper (1946) the investigations concerning the speltoid problem and concludes that:

Series A arises by a more or less complex gene mutation or by an undetectable deficiency in a C-chromosome.

Series B arises by a loss of a C-chromosome.

Series C arises by a visible deficiency in a C-chromosome.

The C-chromosome carries the inhibitors of the genes for bearded and speltoid, situated in the B-chromosome. The C-chromosome has a submedian centromere and following HUSKINS's nomenclature we use in this paper:

C for the normal chromosome.

Cd for the C-chromosome with an appreciable deficiency.

Cts for the telomitic short arm of the C-chromosome.

Ctl for the telomitic long arm of the C-chromosome.

Cil for the iso-chromosome composed of a duplicated longer arm of the C-chromosome.

As HUSKINS (l. c.) summarizes, the chromosome complements of the different types found in the speltoid series are the following:

Normal.....	(40 + 2 C).
B het speltoid	(40 + C) or (40 + Ctl).
B hom speltoid	(40).
C het speltoid	(40 + C + Cd) or (40 + C + Cts).
C hom speltoid	(40 + 2 Cd) or (40 + 2 Cts).
Subnormal	(40 + C + Ctl) or (40 + 2 Ctl) or (40 + Cil).
Subcompactoid	(40 + 3 C) or (40 + C + Cil) or (40 + Ctl + Cil) or (40 + 2 C + Cil).
Compactoid	(40 + 4 C) or (40 + 2 Cil) or (40 + C + 2 Cil) or (40 + 2 C + 2 Cil).

Thus less than two sets of genes suppressing the speltoid and the bearded characters will cause a speltoid phenotype, while more than two sets will give rise to compactoid types. As the inhibitors are situated in the longer arm of the C-chromosome, it may be observed that the Cts-chromosome does not influence the speltoid and compactoid characters.

In spite of the extensive work already carried out in order to explain the speltoid and compactoid mutations, these problems cannot, however, be said

definitely solved. In the present paper special interest is paid to the arising of subcompactoids. Earlier investigations hereof have mainly been concentrated upon the subcompactoid type itself. The writers now try to give an explanation of this problem by studying the behaviour of the C-univalent during meiosis in het speltoids of the B-series from which subcompactoids rather frequently are segregated. We devote special attention to the second meiotic division and the formation of micronuclei in the tetrads.

The material used in the present studies is three spring wheat series of B speltoids, kindly put to our disposal by professor A. AKERMAN. Series I originates from a het speltoid that he found in a purebred line of Börsum. Series II and III are B-types arisen through a second mutation in two C-series, in 1917 isolated from the crosses 0201 x 0715 and 0750 x Börsum, respectively. A genetic analysis of the three B-series will be given by AKERMAN and MAC KEY (1948) (1).

The anthers were fixed in CARNOY (6:3:1). Permanent smears of the anthers stained in FEULGEN were made according to HILLARY (1940).

The authors' sincere acknowledgements are due to DR. A. LEVAN for the facilities given and for much useful advice.

The authors' thanks are also due to MR. TJIO JOE HIN for his help in taking the microphotographs.

I. OBSERVATIONS IN PMC'S OF HET B SPELTIDS.

Metaphase I. — Four types of chromosome association were observed, namely.

20 bivalents + 1 univalent (Figs. 1, 7. Photos 1, 2)

19 bivalents + 3 univalents (Figs. 3, 8).

19 bivalents + 1 trivalent (Figs. 2, 9. Photo 3).

18 bivalents + 1 tetravalent + 1 univalent (Fig. 4).

The observed frequencies are given in table 1.

TABLE 1. *Chromosome association in metaphase I of B het speltoid.*

SERIES	Number of PMC's with:			
	20 _{II} + 1 _I	19 _{II} + 3 _I	19 _{II} + 1 _{III}	18 _{II} + 1 _{IV} + 1 _I
I	317	6	2	—
II	318	—	5	1
III	276	5	1	—
Total	911	11	8	1

The univalents generally lie outside the plates.

(1) Unpublished.

Anaphase I. — In all plates observed of the three series the bivalens separate normally, while the univalent remains as a laggard and splits longitudinally in late anaphase. (Fig. 11. Photo 5).

Telophase I. — Generally the two chromatids of the C-univalent are going one to each pole (Fig. 12) and are often included in the daughter nuclei (Photo 6).

In three cases out of 119 observations, the two univalent-halves are found, apparently without complete separation, going to the same pole (Figs. 14, 15) and in one case two quite separated halves were observed going together to the same pole (Fig. 16).

In two cases, one of the two separated halves of the univalent was broken at the centromere, evidently a misdivision has occurred.

Interkinesis. — Interkinesis with 0, 1 or 2 micronuclei (Fig. 17. Photo 7) were observed, according to the number of split halves of the univalent not included in the daughter nuclei. Corresponding with the anomalous cases found in first telophase, two micronuclei included in the same daughter cell were also observed in the interkinesis. This may be due to the arrival of the two halves of the univalent to the same pole, but fragmentation of one of the halves is also a possible explanation. No obvious difference could, however, be seen in the size of the two micronuclei (Fig. 18).

In one case 1 micronucleus was observed at one pole and 2 at the other, one of them was evidently smaller. This case must obviously be due to the fragmentation observed in telophase I.

The observed frequencies of micronuclei are given in table 2.

TABLE 2. *Formation and distribution of micronuclei in the interkinesis of B het speltoids.*

Series	Number of micronuclei in the interkinesis:				
	0 + 0	0 + 1	1 + 1	0 + 2	1 + 2
I	62	43	42	2	—
II	31	14	13	1	—
III	34	32	85	—	1
Total	127	89	140	3	1

Metaphase II. — The univalent appears frequently as a micronucleus in early metaphase (Fig. 19) and as the metaphase advances it takes the characteristic form of a chromosome with submedian constriction (Fig. 21).

In four cases out of 103 observations, the two halves of the original univalent appear in the same dyad cell. This case is the logical consequence of the type of first metaphase in which the two halves went to the same pole. Only

in one case, one of the univalent halves was fragmented (Fig. 20). This misdivision evidently has occurred in the first telophase.

Anaphase II. — The univalent has the same appearance as in late metaphase and remains as a laggard in late anaphase.

Telophase. II. — At this stage the univalent is observed either to be included in a daughter nucleus or to form a micronucleus (Figs. 21, 23. Photo 8). In late telophase inclusion of the two halves was observed in 21 cases, of one of the halves in 11 cases and of neither of the halves in 74 cases. Among the last distribution type misdivision of one of the halves was observed in 17 cases (Figs. 22, 24 — 27. Photo 9). This high frequency cannot be explained as a consequence of the misdivision found in first telophase. From table 3 it is clear that this phenomenon also must occur in second telophase.

TABLE 3. *The frequencies of misdivision observed in telophase I and II in B het speltoids.*

Number of PMC's with:	Telophase I	Telophase II
Normally divided C-chrom.	117	89
Misdivided C-chrom.	2	17
Total	119	106
Misdivision, %	1.7	16.0

Tetrads. — In the tetrads 0 to 4 micronuclei were observed (Figs. 29 - 34). When there were three micronuclei in the tetrads, one of them was always smaller than the others (Figs. 32, 33. Photos 10, 11) and when there were four micronuclei, two of them were smaller than the others (Fig. 34), all in accordance with observations in earlier stages.

The found frequencies and the distribution of micronuclei in tetrads are given in table 4.

TABLE 4. *Formation and distribution of micronuclei in tetrads of B het speltoids.*

Series	Number of micronuclei in the tetrads:						
	0+0+0+0	0+0+0+1	0+0+1+1	0+1+1+1	1+1+1+1	0+0+0+2	0+0+1+2
I	54	25	25	6	—	—	—
II	26	11	9	1	—	1	—
III	94	73	155	21	3	5	3
Total	174	109	189	28	3	6	3

II. OBSERVATIONS IN PMC'S OF SUBCOMPACTOIDS.

Cytological studies of subcompactoids have unveiled an univalent able to form a chiasma between its two arms (HAKANSSON's co-chromosome, HUSKINS's Cil-chromosome). In order to control this phenomenon also happening in our material, the meiosis of subcompactoids of the same pedigree as the examined het B speltoids was studied. The characteristic chiasma formation of the Cil-chromosome was frequently observed. (Fig. 5). The observation of chromosome association in first metaphase gave the following frequencies:

$20_{II} + C + \text{Cil} \dots\dots\dots$	60 cases
$20_{II} + \text{heteromorphic bivalent} \dots\dots\dots$	2 »
$19_{II} + 1_{III} + \text{Cil} \dots\dots\dots$	2 »

The examination thus shows that our subcompactoids are belonging to the same type as the «normaler Subcompactum», described by HAKANSSON (1932).

III. DISCUSSION.

Our observations concerning the different types of chromosome association at metaphase I, with $20_{II} + 1_I$ as the most common conjugation, are in complete agreement with the observations of other authors. The percentage of irregularities observed varies from 1.9 to 2.5 %. These figures are higher than those given by UCHIKAWA (1941) for his B-series, where he found 0.63 to 0.79 % of irregularities. Considering e. g., that HOLLINGSHEAD (1932) has found 2.9 to 9.7 % of metaphase plates with univalents in the first meiotic division of PMC's of varieties of *Tr. vulgare* and 5.2 to 39.1 % in 10 of their hybrids, we think that our material represents a quite normal behaviour.

As UCHIKAWA (1941) already has suggested, the origin of the trisomic subcompactoid type ($40 + 3 C$) can be explained by non-disjunction at first telophase. Thus the two C-univalent halves will be included in the same dyad cell and if during the second division they are distributed at random, as is stated by UCHIKAWA, germ-cells with $20 + 2 C$ chromosomes may be formed. This interpretation is quite in harmony with the observations made by the present writers. The low frequency of trisomic subcompactoids found as segregates from speltoid series may be explained by the rare cases of non-disjunction, the certainly low possibility of two daughter-univalents being included in the same tetrad nucleus and the necessary fertilization with a $20 + C$ gamete.

Attempts to explain the origin of the more common $40 + C + \text{Cil}$ subcompactoid type have also been made. HAKANSSON (1932) suggested that the Cil-chromosome (with his own nomenclature called the co-chromosome) may arise through crossing over between the two arms of the C univalent in B het speltoids. Thus the proximal part of the chromosome arms is thought to be unchanged, while the distal part of the arms must be identical. Postulating the speltoid-inhibiting genes situated in the distal part of the longer C-chromosome arm, the $40 + C + \text{Cil}$ plants will have three such gene

sets and, therefore, behave as subcompactoids. In order to explain the chiasma formation between the two arms of the C-chromosome a duplication is supposed to exist. The cytological observations of B het speltoids argue, however, hardly in favour of such a mechanism, at least not as the most common one. HÅKANSSON emphasizes that he never has observed any clear evidence of segmental duplication within the C-chromosome. HUSKINS and SMITH (unpublished; cf. HUSKINS, 1946) seem to be the only authors who have found that the single C-chromosome in B het speltoids is able to pair on itself. Nor the figuration of the heteromorphic C + Cil bivalent, observed in subcompactoids by several authors, seems in complete agreement with the duplication hypothesis as an universal explanation. After this hypothesis the Cil-chromosome must be able to homologous pairing with the C-univalent not only along the whole length of one arm but also along the proximal part of the other. This means the figuration $<X$ possible. As both HÅKANSSON (1932) and the present writers (Fig. 5) only have observed C + Cil bivalents with one chiasma, the hypothesis given in the following discussion seems more adapted to cytological data. The genetic consequence will, however, be the same for the two explanations.

The origin of the Cil-Chromosome is presumed primarily caused by misdivision of the C-univalent in B het speltoids. This phenomenon has not previously been observed in speltoid wheat but in the related fatuoid mutations in oats, NISHIYAMA (1931) has found fragmentation of the univalent at second telophase. Without knowing the occurrence of misdivision he stated that «the fragmentation appeared usually to occur at a point where the spindle fibres are attached» (l. c., p. 73). Other cases of transverse division of the centromere were observed by UPCOTT (1937), by KOLLER (1938) in *Pisum* and by DARLINGTON (1939) in *Fritillaria*. Misdivision has further been found by HÅKANSSON (1940) in a haploid plant of *Godetia Whitneyi* and in a mutant of the same species. New telocentric chromosomes produced by misdivision were observed by LEVAN (1942) in the second meiotic division of a haploid rye. MÜNTZING (1944) stated that certain extra fragment chromosomes in rye are produced by misdivision. The chromosomes with terminal centromere found in *Triticum* by HUSKINS and SPIER (1934), LOVE (1938) and HUSKINS and SMITH (l. c.) may also be explained as a product of misdivision.

The misdivision observed at first telophase of B het speltoids seems to be quite rare. It can, however, be traced from telophase I (1.7 %) over interkinesis (0.3 %) till metaphase II (1.0 %). As the phenomenon was observed in two of the three series (II and III) it cannot be said unique. The frequent occurrence of misdivision at telophase II cannot, however, as stated above be explained only as due to the fragmentation observed at telophase I. A frequency of 16.0 % misdivided C-univalents (or 8.0 % of splitted chromatid centromeres) observed at telophase II and an elimination of 6.2 % (or 3.6 %, respectively) of fragments in the tetrads must indicate that the second division is the most important source of telocentric fragments.

The occurrence of misdivision may explain the arise of B-series with a Ctl-chromosome instead of a whole C-chromosome (cf. HUSKINS, 1946) but also

C het speltoid, in a few cases observed in B-series (NILSSON-EHLE, 1921; LINDHARD, 1922, 1923, 1927), will thus have a simple explanation, if they are supposed to be of the $40 + C + Cts$ type. More importance may, however, be laid upon the possibility to explain the origin of the most common type of subcompactoids ($40 + C + Cil$). Here the present writers suggest *a misdivision of the C-univalent in a PCM followed by a non-disjunction of the two Ctl chromatids at the pollen mitosis* as the possible mechanism producing the isochromosome (Cil).

The first case of isochromosomes resulting from misdivision is the secondary trisomes observed in *Datura* by BELLING and BLAKESLEE (1924). Among the progeny of a maize having a telocentric fragment RHOADES (1938, 1940) found plants with an isochromosome. The explanation of the origin of isochromosomes by misdivision is given by DARLINGTON (1939, 1940), according to his observations in *Fritillaria*. DARLINGTON and THOMAS (1941) found an isochromosome among the B-chromosomes of *Sorghum*. Iso-fragments produced by misdivision have further been found by MÜNTZING (1944, 1945, 1946) in *Secale*.

The suggestion of the Cil-chromosome in subcompactoids being produced by misdivision and non-disjunction seems quite in harmony with the genetic analysis of the B-series segregates. The most frequent elimination of misdivided C-univalents is, according to table 4 found in series III. This one also gives the lowest frequency of subcompactoid segregates (ÅKERMANN and MAC KEY, 1948, unpublished). Series I is intermediate both with regard to elimination of misdivided chromosomes and to subcompactoids in het speltoid segregation, while series II is quite reverse to series III. The elimination of the misdivided C-chromosomes follows the total number of C-univalents excluded. The occurrence of misdivision is observed in about the same frequency in the three series. The comparatively rare segregation of subcompactoid out of B het speltoids ($<0.1\%$) may be explained by the high degree of elimination of Ctl-or Cil-chromosomes and by a low functioning capacity of the $20 + Cil$ pollen. This last assumption is quite in harmony with the low fertility of subcompactoid and compactoid plants.

As Ctl-chromosomes seem quite seldom observed in the progeny of B het speltoids, the telomitic Ctl-fragment surely has a rather high capacity of non-disjunction at the pollen mitosis. Such a supposition is quite in agreement with the observations of HASEGAWA (1944) and MÜNTZING (1945) at pollen mitosis of rye with extra fragment chromosomes. The investigations of MÜNTZING may also give an explanation why the fourth possible type, an isochromosome with a double Cts-arm, never has been observed as could be expected in accordance with the mechanism suggested in connection with the origin of subcompactoids. He found (1946) that the small iso-fragment, primarily originated from the short arm of the standard fragment, showed no evidence of non-disjunction, while the large iso-fragment, derived from the long arm of the standard fragment, has a very high ability of postmeiotic non-disjunctions. The conditions are, however, not quite the same as in the present case.

According to the misdivision observed and the distribution and elimination of the C-chromosome found at the different meiotic phases of a B het

speltoid the following types of pollen grains (or more correct generative pollen nuclei) may be formed:

1. — (20)
2. — (20 + C)
3. — (20 + Cts)
4. — (20 + Ctl)
5. — (20 + Cil)
6. — (20 + 2 C)

The behaviour of the C-univalent during meiosis and the probable origin of the different types of pollen grains are schematically illustrated in the diagram. The composition of the centromere is presumed to be in accordance with the ideas recently put forward by ÖSTERGREN (1947). According to the doubleness in the chromosomal spindle fibre bundle attached to the centromere, he considers that the actively mobile component of the centromere is the proximal heterochromatin corresponding to the number of chromatid arms present.

If the same types of female gametes are produced, asitis very probable, the formation of the different types segregated from B het speltoids would be as follows:

♀ \ ♂	20	20 + C	20 + Cts	20 + Ctl	20 + Cil	20 + 2 C
20	40 B hom sp	40 + C B het sp	40 + Cts ?	40 + Ctl B het sp	40 + Cil Subnormal	40 + 2 C Normal
20 + C	40 + C B het sp	40 + 2 C Normal	40 + C + Cts C het sp	40 + C + Ctl Subnormal	40 + C + Cil Subcomp.	40 + 3 C Subcomp
20 + Cts	40 + Cts ?	40 + C + Cts C het sp	40 + 2 Cts C hom sp	40 + Cts + Ctl ?	40 + Cts + Cil ?	40 + 2C + Cts ?
20 + Ctl	40 + Ctl B het sp	40 + C + Ctl Subnormal	40 + Cts + Ctl ?	40 + 2 Ctl Subnormal	40 + Ctl + Cil Subcomp.	40 + 2C + Ctl ?
20 + Cil	40 + Cil Subnormal	40 + C + Cil Subcomp.	40 + Cts + Cil ?	40 + Ctl + Cil Subcomp.	40 + 2 Cil Comp.	40 + 2C + Cil Subcomp.
20 + 2 C	40 + 2 C Normal	40 + 3 C Subcomp.	40 + 2C + Cts ?	40 + 2 C + Ctl ?	40 + 2 C + Cil Subcomp.	40 + 4 C Comp.

As can be observed, several of the possible segregates have not yet been found but these unknown types have certainly a very low propability of arising and perhaps some of them may be one of the types that LINDHARD found as segregates in his B-series, namely, the perennis, the dwarf normal, the dwarf speltoid or the late maturing type.

The authors think that it is also posible that the appearance of the subcompactoids directly in normal *Tr. vulgare* may be due to a misdivision

of one of the C-univalents that occasionally are found in normal wheat. The observation of subcompactoids in C-series may be given a similar explanation.

For a confirmation of the non-disjunction really occurring, further investigations devoting special attention to the pollen mitosis will be necessary.

SUMARIO

En el presente trabajo se estudia el comportamiento del cromosoma C en la meiosis de los trigos espeltoides heterocigóticos de la serie B. Se dedica una atención especial a la distribución de los cromatidios del univalente en la segunda telofase meiótica y a la formación de micronúcleos en las tétradas.

Se observan casos de misdivisión del cromosoma univalente C, tanto en la primera como en la segunda telofase meiótica, más frecuentemente en la última.

Se supone que esta misdivisión es el mecanismo por el cual aparecen trigos espeltoides de la serie B con un cromosoma Ctl en lugar del cromosoma C normal.

Los cambios de la serie B a la C, observados previamente por otros autores, pueden también ser explicados por la misdivisión del cromosoma C. En este caso la serie C se caracterizaría por un cromosoma Cts procedente de la misdivisión.

Se puede explicar el origen de los subcompactoides a partir de la serie B por una misdivisión del cromosoma C seguida de no-disyunción, en la mitosis del polen, de los dos cromatidios procedentes del brazo mayor del cromosoma C. El nuevo isocromosoma formado, sería incluido en el núcleo generativo en la mayoría de los casos.

La aparición de subcompactoides en algunos espeltoides heterocigóticos de la serie C y aun directamente en trigos normales, puede ser explicada por un mecanismo análogo.

Como consecuencia de la formación de nuevos cromosomas por misdivisión, se explica la complicada segregación que presentan los trigos espeltoides heterocigóticos de la serie B.

LITERATURE CITED

BELLING, J. and A. F. BLAKESLEE

- 1924 The configurations and sizes of the chromosomes in the trivalents of 25-chromosome *Daturas*.-*Proceed. National Acad. Sciences*, **10**: 116-120.

DARLINGTON, C. D.

- 1939 Misdivision and the genetics of the centromere.- *Jour. Genetics* **37**: 341-364.
1940 The origin of isochromosomes.- *Jour Genetics* **39**: 351-361.

DARLINGTON, C. D. and P. T. THOMAS

- 1941 The activity of inert chromosomes in Shorgum. - *Proc. of the Royal Soc. of London* **130**: 127-150.

HÅKANSSON, A.

- 1932 Zytologische Studien an compactoiden Typen von *Triticum vulgare*. *Hereditas* **XVII**: 155-196.
1940 Die Meiosis bei verschiedenen Mutanten von *Godetia Whitneyi*. *Lunds Univ. Ars.* **2**: 3-37.
1940 Die Meiosis bei haloiden Pflanzen von *Godetia Whitneyi*. - *Hereditas* **XXVI**: 411-429.

HASEGAWA, N.

- 1934 A cytological study on 8-chromosomes Rye. - *Cytologia* **6**: 68-77.

HILLARY, B. B.

- 1940 Uses of the Feulgen reaction in cytology. - II - New techniques and special applications. - *Bot. Gaz.* **102**: 225-234.

HOLLINSHEAD, L.

- 1932 The occurrence of unpaired chromosomes in hybrids between varieties of *Triticum vulgare*. - *Cytologia* **3**: 119-141.

HUSKINS, C. L.

- 1928 On the cytology of speltoid wheats in relation to their origin and genetic behaviour. - *Jour. Genetics* **20**: 103-122.
1946 Fatuoid, speltoid and related mutations of oats and wheat. - *Bot. Rev.* **12**: 457-514.

HUSKINS, C. L. and JANE D. SPIER

- 1934 The segregation of heteromorphic homologous chromosomes in Pollen Mother Cells of *Triticum vulgare*. - *Cytologia* **5**: 269-277.

KOLLER, P. C.

- 1938 Asynapsis in *Pisum sativum*. - *Jour. Genetics* **36**: 275-305.

LEVAN, A.

- 1942 Studies on the meiotic mechanism of haploid Rye. - *Hereditas* **XXVIII**: 177-211.

LINDHARD, E.

- 1922 Zur Genetik des Weizens. Eine Untersuchung über die Nachkommenschaft eines im Kolbenweizen aufgetretenen Speltoidmutanten. - *Hereditas* **III**: 1-90.
1923 Fortgesetzte Untersuchungen über Speltoidmutationen. Begranungskomplikationen bei Compactum-Heterozygoten. - *Hereditas* **IV**: 206-220.
1927 Über Ährendichte und Spaltungsmodi der Speltoidheterozygoten. - *Kung. Vet. Landb. Aarsskr.* **1927**: 1-37.

LOVE, R. M.

- 1938 A cytogenetic study of white chaff off-types occurring spontaneously in Dawson's Golden Chaff winter wheat. - *Genetics* **23**: 157.

MÜNTZING, A.

- 1944 Cytological studies of extra fragment chromosomes in rye. - I - Iso-fragments produced by misdivision. - *Hereditas* **XXX**: 231-248.
- 1945 Cytological studies of extra fragment chromosomes in rye. - II - Transmission and multiplication of standard fragments and isofragments. - *Hereditas* **XXXI**: 457-477.
- 1946 Cytological studies of extra fragment chromosomes in rye. - III - The mechanism of non-disjunction at the pollen mitosis. - *Hereditas* **XXXII**: 97-119.

NILSSON-EHLE, H.

- 1917 Untersuchungen über Speltoidmutationem beim Weizen. - *Botaniska Notiser* **1917**: 305-329.
- 1920 Multiple Allelomorphe und Komplexmutationen beim Weizen. - *Hereditas* **I**: 277-311.
- 1921 Über mutmassliche partielle Heterogamie bei den Speltoidmutationen des Weizen. - *Hereditas* **III**: 25-76.

NISHIYAMA, I.

- 1931 The genetics and cytology of certain cereals. II - Karyogenetic studies of fatuoid oats with special reference to their origin. - *Jap. Jour. Genetics* **7**: 49-101.

ÖSTERGREN, G.

- 1947 Proximal heterochromatin, structure of the centromere and the mechanism of its misdivision. - *Botaniska Notiser* **1947**: 176, 177.

RHOADES, M. M.

- 1938 On the origin of a secondary trisome through the doubling of a half-chromosome fragment. - *Genetics* **23**: 163-164.
- 1940 Studies of a telocentric chromosome in maize with reference to the stability of its centromere. - *Genetics* **25**: 483-520.

UCHIKAWA, I.

- 1941 Genetic and cytological studies of speltoid wheat. II - Origin of speltoid wheat. - *Mem. Coll. Agric. Kyoto Imperial Univ.* **50**: 1-64.

UPCOTT, M.

- 1937 The external mechanics of the chromosomes. - VI - The behaviour of the centromere at meiosis. - *Proceed. Roy. Soc. of London, Series B*, **124**: 336-361.

PLATES

PLATE I

Chromosome complement of B het speltoid

PLATE I

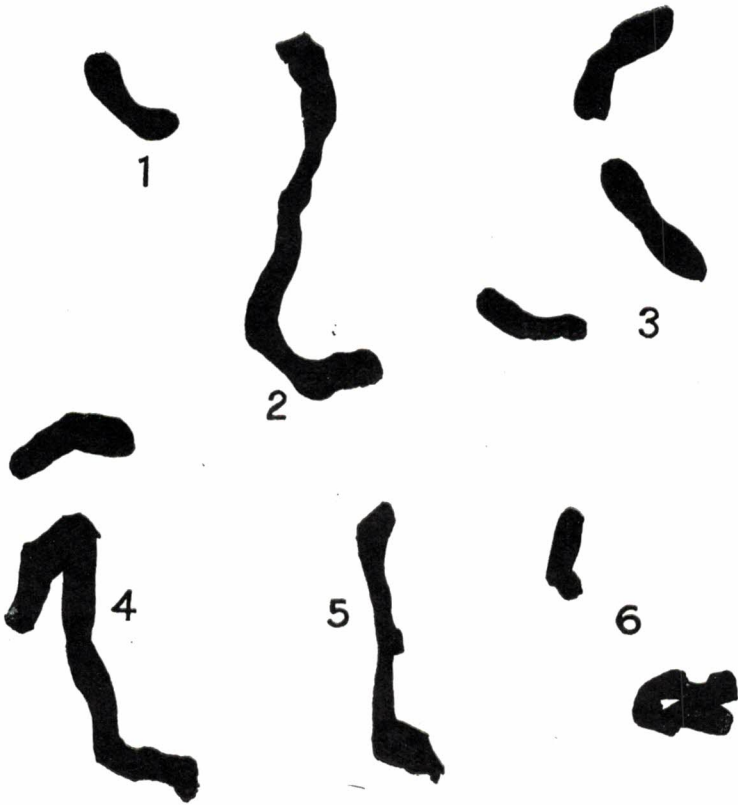


0.01 m.m.

PLATE II

Figs. 1-4 from B het speltoids.-Fig. 1, univalent.-Fig. 2, a trivalent including the C-chromosome.-Fig. 3, three univalents in the same plate.-Fig. 4, a tetravalent and an univalent in the same plate.-Figs. 5-6 from subcompactoids.-Fig. 5, a heteromorphic bivalent.-Fig. 6, the Cil-and C-univalent.

PLATE II



0,01 mm.

PLATE III

Figs. 7-9, metaphase I of het speltoid (not all the bivalents are visible). - Fig 7, 20 II + 1 I. - Fig. 8, 19 II + 3 I. - Fig. 9, 19 II + 1 III. - Fig. 10, metaphase I of subcompactoid, showing 20 II + C + Cil.

PLATE III

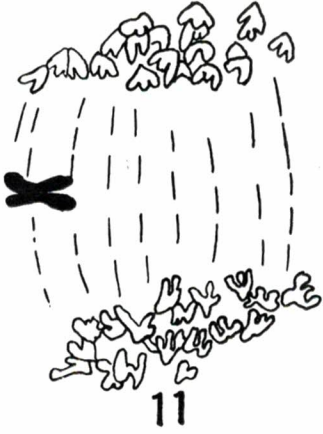


0.01mm.

PLATE IV

Figs. 11-16, PMC's of B het speltoids. - Fig. 11, splitting of the C-univalent at anaphase I. - Fig. 12, normal telophase I. - Fig. 13 misdivision of the C-univalent at telophase I. - Figs. 14-16, nondisjunction of the univalent-halves at telophase I.

PLATE IV

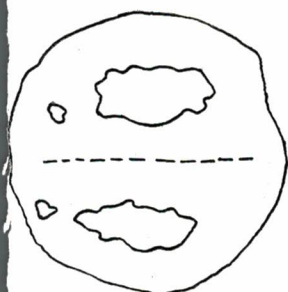


0.01 mm.

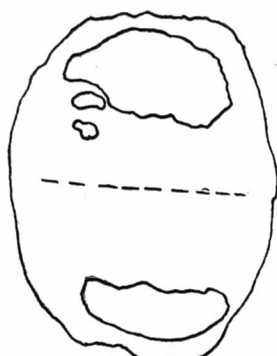
PLATE V

Figs. 17-25, PCM's of B het speltoids. - Figs. 17-18, micronuclei distribution in dyad cells. - Fig. 19, normal metaphase II. - Fig. 20, metaphase II showing a misdivided C-univalent. - Fig. 21, C-halves at metaphase II and anaphase II. - Fig. 22, telophase II showing a misdivided C-univalent. - Fig. 23, normal telophase II. Figs. 24-25, misdivision at telophase II.

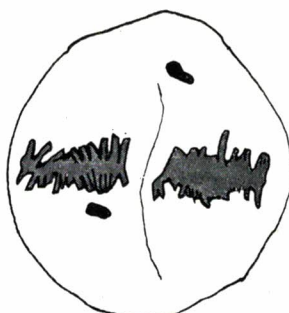
PLATE V



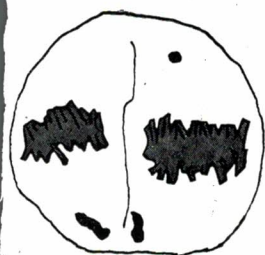
17



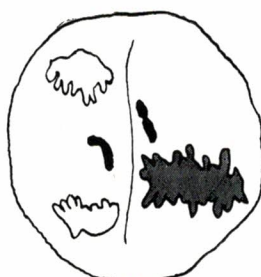
18



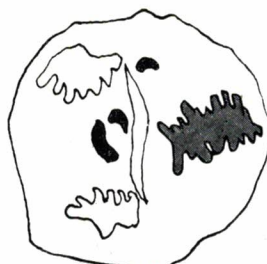
19



20



21



22



23



24

0.01mm.



25

PLATE VI

Figs. 26-34, PMC's of B het speltoid. - Figs. 26-27 misdivision at telophase II. - Fig. 28, formation of micronuclei at late telophase II. - Fig. 29-34, tetrads showing different possibilities of micronuclei formation.

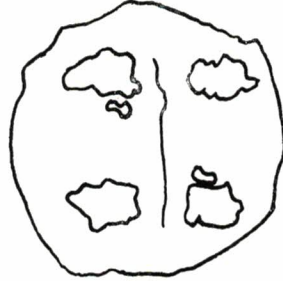
PLATE VI



26



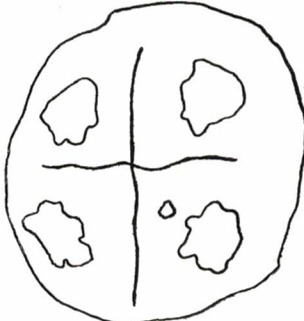
27



28



29



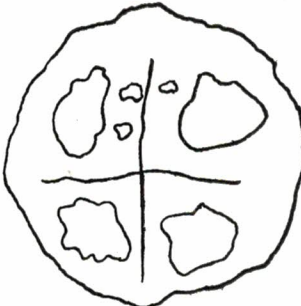
30



31



32



33



34

0.01mm.

PLATE VII

Diagram showing the behaviour of the C-univalent and the probable origin of the different types of pollen grains in B het speltoids. At telophase II only one of the poles is taken into consideration in order to avoid the diagram becoming too complex.

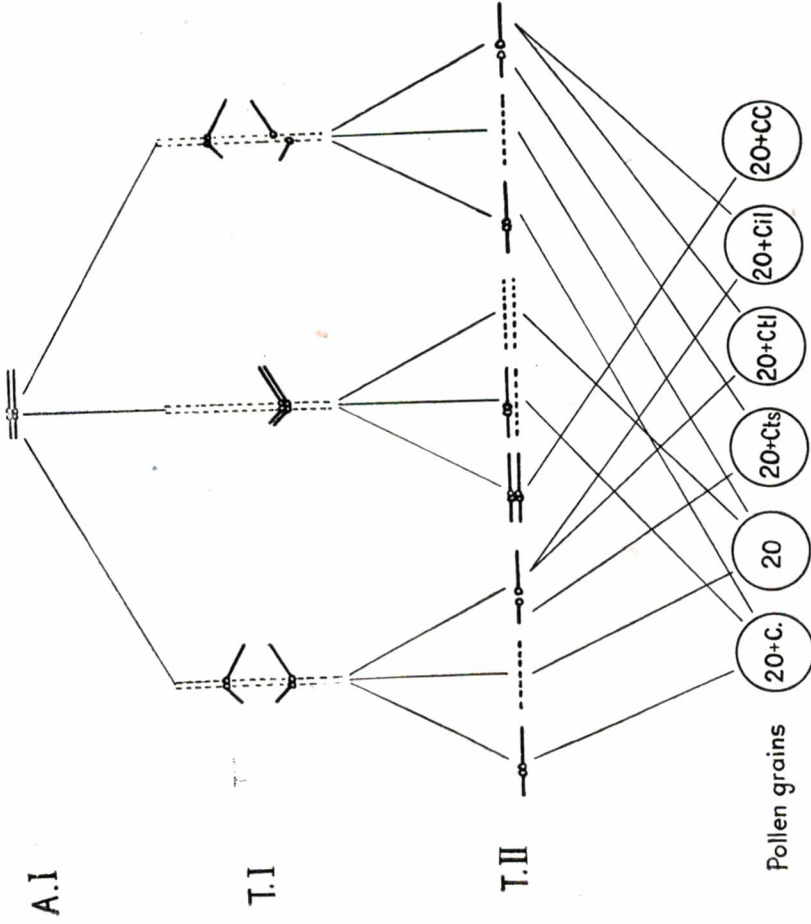


PLATE VIII (microphotographs)

Photos 1-3, metaphase I of B het speltoids. - Photos 1-2, 20 II + 1 I. - Photo 3, 19 II + 1 III. - Photo 4, metaphase I of subcompactoid showing 20 II + C + Cil. - Photos 5-11, B het speltoids. - Photo 5, anaphase I. - Photo 6, telophase I. - Photo 7, interkinesis. - Photo 8, C-halves at metaphase II and anaphase II. - Photo 9, misdivision at telophase II. - Photos 10-11, tetrads showing micro-nuclei resulting of the misdivides univalent.

PLATE VIII

