THE STABILITY OF ISOCHROMOSOMES

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The karyotype of subcompactoid wheats consists of twenty one pairs of chromosomes of which twenty pairs are of the normal complement and one pair is formed by the so-called C chromosome, which in fact is also of the normal complement, and the isochromosome Cil (for nomenclature see HUSKINS, 1946). In a certain frequency of the P. M. C. the chromosomes C and Cil remain as univalents. This fact makes it possible to study the relative stability of the two centromeres, viz. the original one of the C chromosome and the one of the isochromosome. In the present paper a comparison is made between the frequencies of lagging and misdivision of above mentioned chromosomes during meiosis in order to get some idea of the stability of the isochromosomes. The identification of the C and Cil chromosomes at meiosis is rather easy as the normal chromosome is clearly heterobraquial, whereas the isochromosome is isobraquial.

For this study the anthers were fixed in acetic alcohol (1:3) and FEULGEN smear preparations were made. For comparing the behaviour of the C and Cil chromosomes 2 × 2 contingency tables were used.

OBSERVATIONS

In 238 P. M. C. studied, the C and Cil chromosomes were associated into heteromorphic bivalents in 36 cases (15.1 %) whereas in 202 cases they remained as univalents. When the isochromosome did not pair with the C to form the heteromorphic bivalent, it almost always formed a chiasma between its two arms, showing a characteristic configuration as is depicted in Figs. 1 *d-e*. Figs. 1 *a-c* show several instances of the heteromorphic bivalent.

The disjunction of the heteromorphic bivalent is normal, viz. the C chromosome to one pole and the Cil to the other. When they remain as univalents, the C'' and Cil'' at first ana-telophase as well as their daughter univalents C' and Cil' at second division, behave in exactly the same way as the C'' chromosome and its daughter univalent C' at meiosis in speltoid wheats of the B series which has been previously described (SANCHEZ-MONGE and MAC KEY 1948, SANCHEZ-MONGE 1950 *a* and *b*). Thus each univalent or daughter univalent may go to one or the other pole or undergo a- or p-misdivision (SANCHEZ-MONGE 1950 *a*).

Tables I and II give the frequencies of lagging and misdivision during ana-telophases of respectively the first and second meiotic division. In table II are also included the observations on the two telocentrics Ctl and Cts, which being produced by misdivision, can be sometimes observed at the second division.

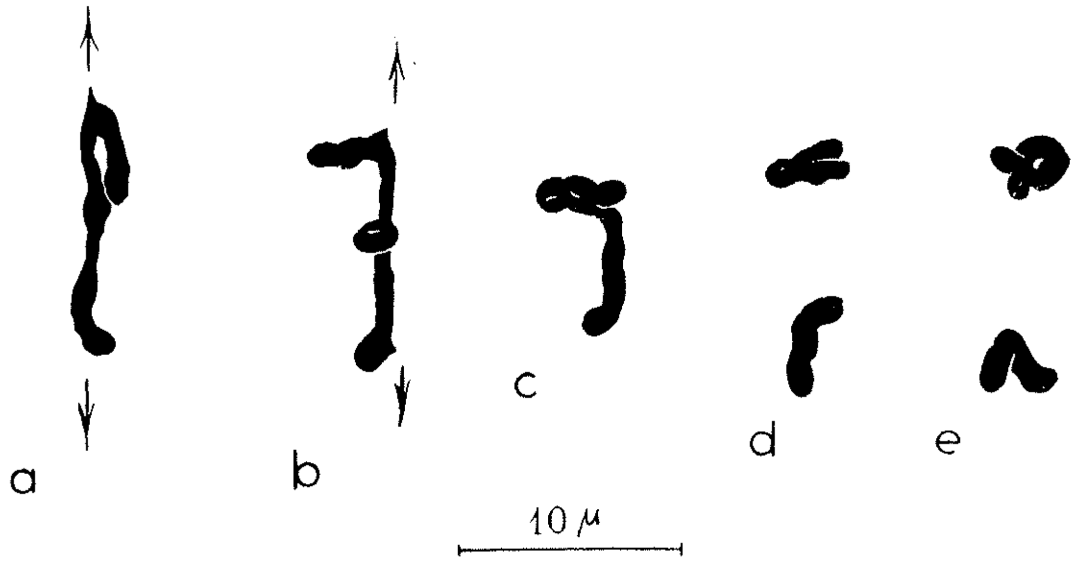

Fig. 1. First meiotic division of the subcompactoid wheat.— *a, b:* orientated heteromorphic bivalents, formed by a C'' and a Cil'' chromosome; *c:* non-orientated heteromorphic bivalent; *d, e:* the unpaired C'' and Cil'' of two cells.

TABLE I. *Frequencies of lagging and misdivision at first ana-telofase*

Chromosome	Lagging		P-misdivision		A-misdivision		Total misdivision		Total cell number
	N.°	%	N.°	%	N.°	%	N.°	%	
C''	94	30.72	—	—	—	—	—	—	306
Cil''	110	35.95	—	—	—	—	—	—	306
C''	—	—	4	4.00	2	2.00	6	6.00	100
Cil''	—	—	1	0.87	3	2.63	4	3.50	110

The χ^2 values obtained in the contingency tables for the frequencies of lagging and misdivision are respectively 1.8823 (0.1 > P > 0.2) and 0.7422 (0.3 > P > 0.5). Thus the difference is not significant. Several instances of normal separation and of a- and p-misdivision of the C and Cil chromosomes can be seen from figure 2.

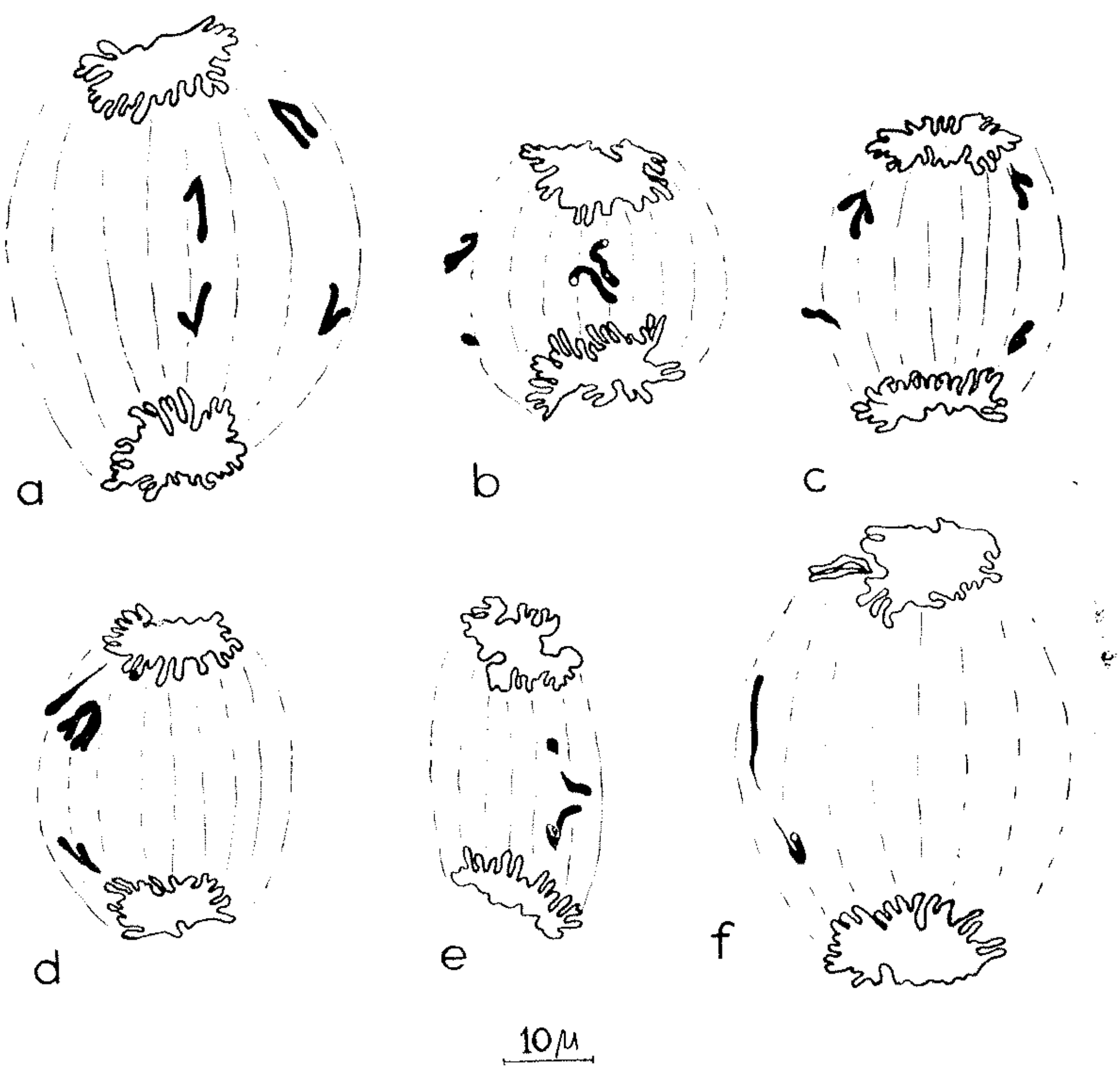

Fig. 2. First meiotic division of the subcompactoid wheat. — *a:* splitting and normal separation of the C'' and Cil''; *b:* a-misdivision of C''; *c:* a-misdivision of Cil''; *d:* a Ctl' arisen through a-misdivision of the C''; *e:* p-misdivision of the C'; *f:* p-misdivision of the Cil'.

TABLE II. *Frequencies of lagging and misdivision at second ana-telofase*

Chromosome	Lagging		P misdivision		A misdivision		Total misdivision		Total cell number
	N.°	%	N.°	%	N.°	%	N.°	%	
C'	52	73.23	10	14.08	3	4.25	13	18.33	71
Cil'	33	46.47	5	7.04	2	2.81	7	9.85	
Ctl'	6	8.45	—	—	—	—	—	—	
Cts'	2	2.82	—	—	—	—	—	—	

The χ^2 value for the difference in frequencies of lagging, obtained in the corresponding contingency table, is 10.5804, producing $P < 0.01$. This P value indicates a significant difference, while the frequency of lagging of the C chromosome is greater than that of the isochromosome. For the difference in the frequency of misdivision the values are 2.2821 and $0.1 < P < 0.2$; the difference is not significant.

Several cases of distribution of the C, Cil and Ctl to both poles as well as a beginning of the a- and p-misdivision of the C can be seen from Fig. 3.

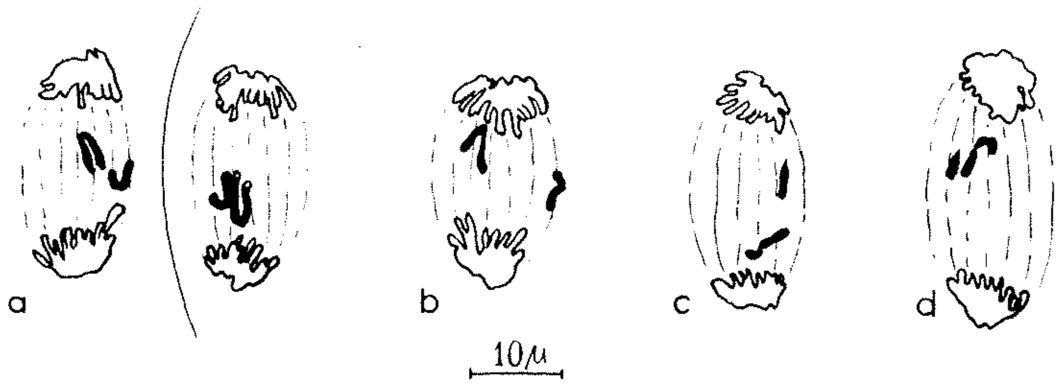

Fig. 3. Second meiotic division of the subcompactoid wheat. — *a*: dyad cell showing on one side the movement of the C' and Cil' to the same pole and on the other side the movement of each of them to opposite poles; *b*: half dyad cell showing a Cil' and the beginning of p-misdivision of the C'; *c*: half dyad cell with a C' and a Ctl' chromosome; *d*: half dyad cell with a Ctl' and a Cil' which is probably starting its p-misdivision.

DISCUSSION

The statistical analysis of our observations show evidently that the centromere of the isochromosome Cil is of normal strength and behaviour and as its frequency of misdivision does not differ significantly from that of the normal C chromosome, it is therefore apparent that *the instability of the centromere of this isochromosome is not due to its being an isochromosome but to the fact that it sometimes remains as a laggard in a certain frequency of the P. M. C.*

The normal behaviour of the centromere of the isochromosomes arisen through misdivision has been observed before by MÜNTZING (1946). He noticed it in both isofragments formed by the two arms of the standard fragment of *Secale*. The same author (1948) also studied the position of the normal chromosomes, the standard fragments and the isofragments at somatic metaphase. He arrived at the conclusion that the position of the isofragments indicated the normality of their centromere.

After the observations made by TJIO *and* LEVAN (1950) in various plant spp. of the centromere having 4 chromomeres, two for each chromatid, it is quite obvious that the centromere of the isochromosome must be formed by the reunion of the interchromomeric filaments which have been broken at misdivision. DARLINGTON and LA COUR (1950) too found in *Campanula* two types of telocentrics, some are stable and others are unstable, the latter being the ones which produce isochromosomes by secondary misdivision.

In the light of these observations the assumption can be made that the following types of telocentrics can be formed: Unstable telocentrics produced by misdivision of the centromere and stable telocentrics formed by whole arm deletion. The stable telocentrics can however also undergo misdivision and thus give rise to unstable telocentrics. The possible transformations of both types of telocentrics with the subsequent secondary changes are schematically represented in Fig. 4.

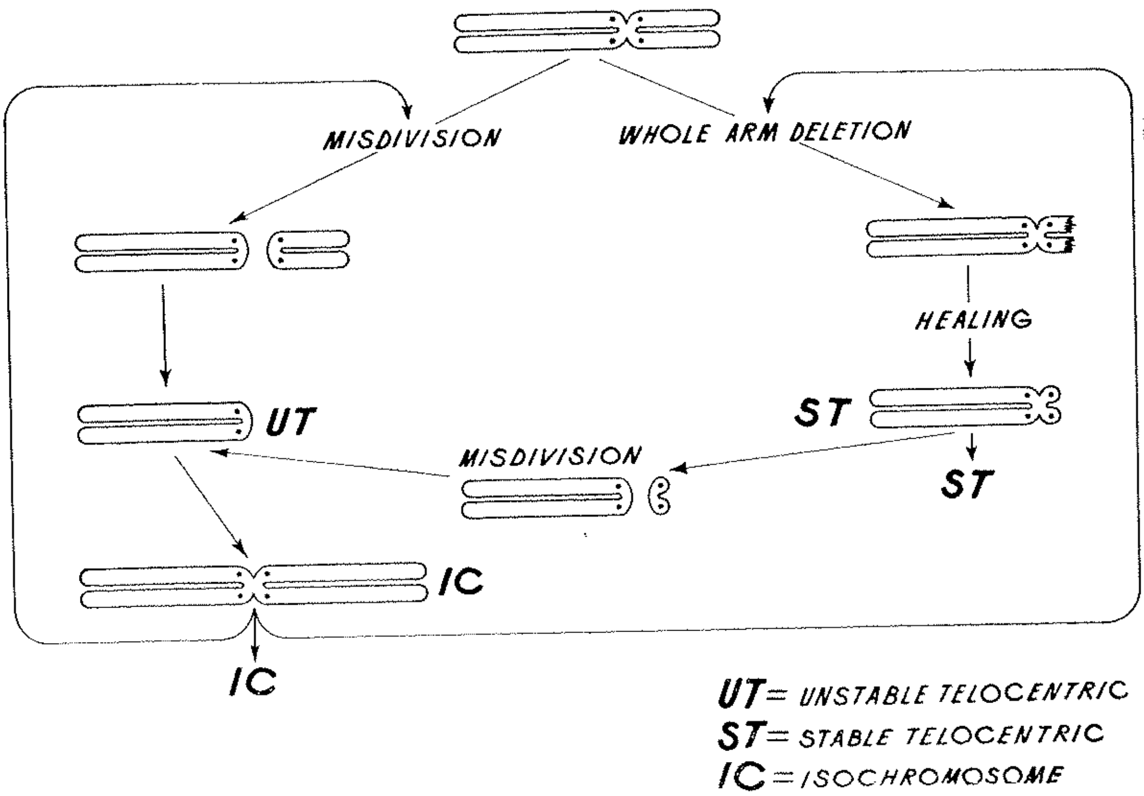

Fig. 4. Diagram showing the origin of the stable and unstable telocentrics as well as the origin of isochromosomes and the possible reciprocal transformations of one type into an other.

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SUMMARY

The relative stability of the centromeres of an isochromosome and its original chromosome has been studied in the meiosis of subcompactoid wheat. The statistical analysis of the observations show

that the isochromosome is provided with a centromere of normal strength and that its instability is due to its being an univalent and not to itself being an isochromosome. The possibility is suggested that there are two types of telocentrics: the stable telocentrics which arise through whole arm deletion and the unstable ones which are produced by misdivision and can be transformed into isochromosomes by secondary misdivision.

RESUMEN

(ESTABILIDAD DE LOS ISOCROMOSOMAS)

En la meiosis de un trigo subcompactoide se estudia la estabilidad relativa de los centrómeros de un isocromosoma y de su cromosoma originario por medio de la comparación de sus respectivas frecuencias de retardo y misdivisión.

El análisis estadístico de los datos indica que el isocromosoma está provisto de un centrómero de fuerza normal y que su inestabilidad se debe a que permanece como univalente en parte de las células madres de polen y no a que es un isocromosoma.

Seguramente existen dos tipos de cromosomas telocéntricos. Unos estables que se originan por la deleción completa de un brazo cromosómico y otros inestables formados a consecuencia de una misdivisión y que son los que pueden dar origen a isocromosomas por misdivisión secundaria.

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