CENTROMERIC BEHAVIOUR OF THE UNIVALENTS IN TWO *PHALARIS* HYBRIDS

By D. L. HAYMAN*

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Summary

The hybrid between *Phalaris coerulescens* ($2n = 14$) and *P. minor* ($2n = 28$) usually forms seven bivalents and seven univalents at the first metaphase of meiosis. The univalents are derived from *P. minor*. The centromeres of the seven univalents do not divide at the first anaphase, but neocentromeres in distal parts of the chromosomes assume control of their movement. These neocentromeres move towards opposite poles, between which the univalents become stretched. Formation of the cell wall causes breakage of the univalent bridges. Fusions may occur between fragments or between broken ends of sister chromatids in a fragment. Neocentric activity occurs only infrequently at the second anaphase.

This pattern of univalent behaviour is characteristic of this particular genome.

The hybrid between *P. tuberosa* ($2n = 28$) and *P. minor* ($2n = 28$) has several univalents at the first metaphase. Some of these may show misdivision of the centromere at both divisions of meiosis, and occasional neocentric activity distally in the chromosomes. Usually the centromeres of the univalents divide normally.

I. INTRODUCTION

The movement of chromosomes on to, and of daughters away from the equatorial plane during cell division, is normally a reaction between the spindle and the centromere. The centromere has a special cycle of division at meiosis, remaining undivided until anaphase of the second division. At the first division of meiosis the two centromeres in the chromosomes of a bivalent co-orient.

Centromere behaviour at meiosis is modified for chromosomes which are univalents. They cannot co-orient, but may congress on the equator after the bivalents have disjoined. The centromeres of univalent chromosomes which have congressed usually divide at the first division. The daughter chromosomes do not congress at the second division and may enter a T II group or be left out and form a micronucleus. If a univalent fails to congress, it may be included in one polar group at T I when the centromere divides normally at the second division, or be left to form a micronucleus.

While this represents the usual pattern of behaviour, the centromeres of univalents may misdivide, as has been described previously (Upcott 1937; Sears 1952). Misdivision occurs in one of the *Phalaris* hybrids discussed in the present paper.

* Department of Genetics, Waite Agricultural Research Institute, University of Adelaide.

In a number of instances, regions of the chromosome other than the centromere have assumed control of anaphase movement on the spindle after congression. Such regions may be conveniently referred to as neocentromeres (Rhoades 1952). In *Zea mays* (Rhoades and Vilkomerson 1942; Rhoades 1952), in *Secale cereale* (Kattermann 1939; Müntzing and Prakken 1942), and in *Elymus weigandii* (Vilkomerson 1950) this behaviour concerns bivalent chromosomes. Only univalent chromosomes are affected in an asynaptic *Secale* (Prakken 1943), in *Bromus* hybrids (Walters 1952*a*, 1952*b*, and unpublished data), and probably in an asynaptic *Pisum* (Koller 1938), in a haploid *Godetia* (Håkansson 1940), and in a *Pennisetum* hybrid (Krishnaswamy and Raman 1953).

With the possible exception of the *Pennisetum* hybrid, the true centromeres divide after the neocentromeres have moved some distance towards the spindle poles.

Both the hybrids to be described in the present paper exhibit neocentric behaviour. In one of them the centromeres do not divide, so leading to bridges at the first anaphase of meiosis.

II. Materials and Methods

Dr. E. M. Hutton's *Phalaris* hybrids (Hutton 1953) were made available for examination.

Whole panicles were fixed in Bradley's (1948) fixative, which consists of four parts of chloroform, three parts of ethanol, and one part of glacial acetic acid, and stored in a refrigerator until used. Meiosis was examined using iron-aceto-carmine squashes made permanent by the method described by Darlington and La Cour (1947).

The somatic chromosome number of *P. tuberosa* L. and *P. minor* Retz. is 28, that of *P. coerulescens* Desf. is 14. The chromosomes of all three species have median or submedian centromeres. Meiosis and mitosis are normal. *P. minor* has seven large and seven small bivalents at M I, *P. coerulescens* has seven small bivalents, and *P. tuberosa* has 14 bivalents which exhibit a range in size.

III. Results

(*a*) *Meiosis in* P. coerulescens × P. minor

Pachytene chromosomes are long and crowded, and paired and unpaired chromosomes cannot be traced completely. At M I the chromosomes are most frequently associated as seven bivalents and seven univalents (Plate 1, Fig. 1). The seven univalent chromosomes are conspicuously longer than the other 14 and are readily identifiable from M I onwards. They are evidently derived from *P. minor*. The mean chiasmata frequency per cell of the seven bivalents calculated on 143 cells is $14{\cdot}40 \pm 0{\cdot}08$. This indicates a considerable degree of homology.

The seven large univalents may take part in other configurations at M I. They form three types of rod bivalent, one of which has a chiasma between

relatively inverted segments. In addition, a linear trivalent is common. This consists of two small chromosomes with a large one in a terminal position.

At A I, all the bivalent chromosomes disjoin and pass to the poles. Their behaviour is normal and is not discussed further.

(*b*) *The Behaviour of the Univalents at the First Meiotic Division*

The univalents not included in polar nuclei at A I congress in the equatorial plane (Plate 1, Fig. 2). Their chromatids fall apart but remain attached at the undivided centromeres. Distal parts of the chromatid arms become directed towards the poles, the univalents coming to lie axially rather than transversely in the spindle (Plate 1, Fig. 3). The types of univalent orientation are shown in Figure 1. Two chromatid arms may be directed towards each pole (Figs. 1*a* and 1*b*) or one chromatid arm may be directed to one pole and three to the other (Fig. 1*d*). Univalents have been seen in which one or more of the chromatid arms appear to remain passively in the equator and contrast sharply

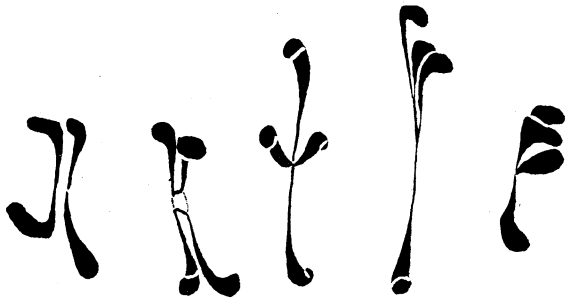

Fig. 1.—*P. coerulescens* × *P. minor*. Univalents at A I showing neocentric activity. × *c.* 1500.

with those that have moved poleward (Fig. 1*e*). Usually, however, all arms of all univalents that have congressed are affected, although the activity of the neocentric regions, presumed to be responsible for this orientation, varies so that one arm may be more stretched than the others (Figs. 1*c* and 1*d*).

The ends of the affected chromatid arms are always reflexed suggesting a subterminal location for the neocentromeres (Plate 1, Figs. 3 and 4). As the univalents are morphologically similar, no one chromosome is identifiable from cell to cell. Comparisons of the length of proximal stretched, and distal unstretched segments of an arm are difficult to make reasonably accurately. Thus it has not been possible to demonstrate a constant location for the neocentromeres in each particular chromosome. However, sister arms normally correspond in appearance.

In some univalents it was possible to trace the chromatids through the centromere and to see that when two chromatid arms pass to each pole they may be either sisters or non-sisters (Figs. 1*a* and 1*b*). The number of univalents

with three arms directed towards one pole and one toward the other pole, varies between cells. Where there are two such chromosomes in the same cell, the three arms may or may not be directed towards the same pole. It appears therefore, that the influence of the neocentromeres on the orientation of the univalents is irregular, and that sister neocentromeres do not always disjoin from one another. There are three arrangements of the arms of the congressed univalents: (i) all four arms directed to one pole, (ii) three arms directed to one pole and one to another, (iii) two arms directed to each pole. If the distribution of the arms under the influence of the neocentromeres is random, the frequencies of these three classes will be given by the sum of the appropriate terms in the expansion of the binomial expression $(\frac{1}{2} + \frac{1}{2})^4$, namely $\frac{1}{8}$, $\frac{1}{2}$, and $\frac{3}{8}$ respectively. Identification of class (i) is uncertain. When this class is ignored and the chromosomes in the other classes counted, 98 chromosomes are of class (ii), and 149 are of class (iii). The numbers expected in these classes, assuming random orientation are 141 and 106 respectively. There is a highly significant departure from expectation, χ^2 being 30·7 for 1 degree of freedom.

It appears that the chromatid arms tend to go in pairs. This is probably due to initial orientation on the metaphase plate and also to repulsion between chromatid arms.

Univalents may be included in a polar group by the greater activity of one of the sets of neocentromeres, perhaps assisted by initial displacement from the equatorial plane. No first division cells were seen where the neocentromere of one chromatid exerted sufficient activity to draw three opposing chromatids over the midpoint of the cell.

At the end of A I, from one to seven univalents lie stretched across the cell. The average number is between four and five. The median portion of the stretched chromatids near the equator of the spindle tends to become very slender. Some breakage by actual tension may occur at this stage, but most, if not all the breakage observed later, is due to the formation of the cell wall.

The precise sequence of events leading to cell wall formation is somewhat uncertain and may be variable. When there are a number of univalent bridges, both polar groups and the univalents are frequently enclosed in the one nuclear membrane. As the cell wall forms, the cytoplasm appears to withdraw on either side. The presence of a group of univalent bridges between the polar groups apparently prevents the withdrawal of the cytoplasm in the centre of the cell, while the cytoplasm all around the univalents is cleared (Plate 1, Fig. 5). Pressure from the cell wall formation appears to be exerted at the centre of the cell on the univalent bridges, compressing them so that there is a slender waist. Further wall development usually results in breakage of the univalents (Plate 1, Fig. 6).

The stretched univalents sometimes prevent the formation of the cell wall so that a restitution nucleus is formed. Cells with 21 chromosomes at each pole have been observed at A II. Their frequency makes it unlikely that they were derived from areas of tetraploid tissue, no evidence of which has been seen in any of the first division cells.

Even after cell wall formation is completed, chromosome connections between the cells may persist for some time. Where only one or two univalents lie across the cell, the formation of the cell wall proceeds unimpeded.

(*c*) *Univalent Behaviour at the Second Meiotic Division*

The effects of univalent breakage on second division configurations are summarized in Figure 2, which includes all the types which have actually been observed.

The most obvious products of univalent breakage are chromosomes with three arms (type V) or with three normal arms and a small fourth arm (type IV). Acentric fragments (types I, II, and IV) are very frequent. Dicentric chromosomes (type II) have been observed in only a few cells. They could also be due to the inversion pairing mentioned previously.

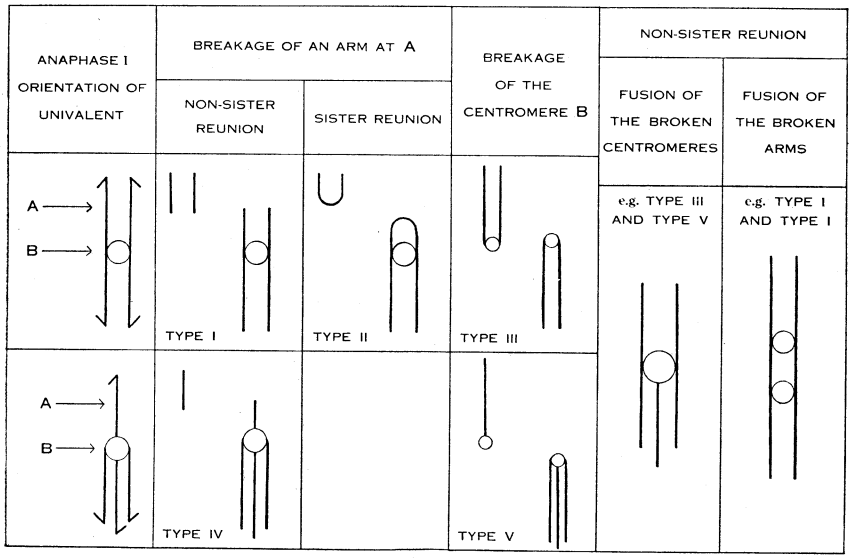

Fig. 2.—*P. coerulescens* × *P. minor*. Diagrams of the products seen at second division after univalent breakage and reunion at the first division.

Occasionally a remarkable multi-armed chromosome was seen. The number of arms varied from five to eight and in some cases was perhaps more. The chromosome arms were of similar size and were usually grouped radially about a central non-staining region (Plate 1, Figs. 8 and 9). In some cells it was evident that the structure had two or three centromeres lying close together, but in other cells two or three centromeres could have been fused together. It is believed that these multi-armed chromosomes are the result of fusion between the broken ends of chromatids or broken centromeres, which arose when univalent bridges compressed together were broken by the cell wall at T I. The fate of these chromosome bodies is uncertain but they appear to form micronuclei.

Figure 3 shows a pollen mother cell at late A II, the seven chromosomes in outline at each pole being those derived from the seven bivalents. The other chromosomes are those derived from the seven univalents. Those labelled *A*, *B*, and *C* are chromatids from unbroken univalents which were included in a polar group at the first division, and which have divided normally at A II. The *D* chromosomes are the result of type III breakage. The *E* chromosomes are

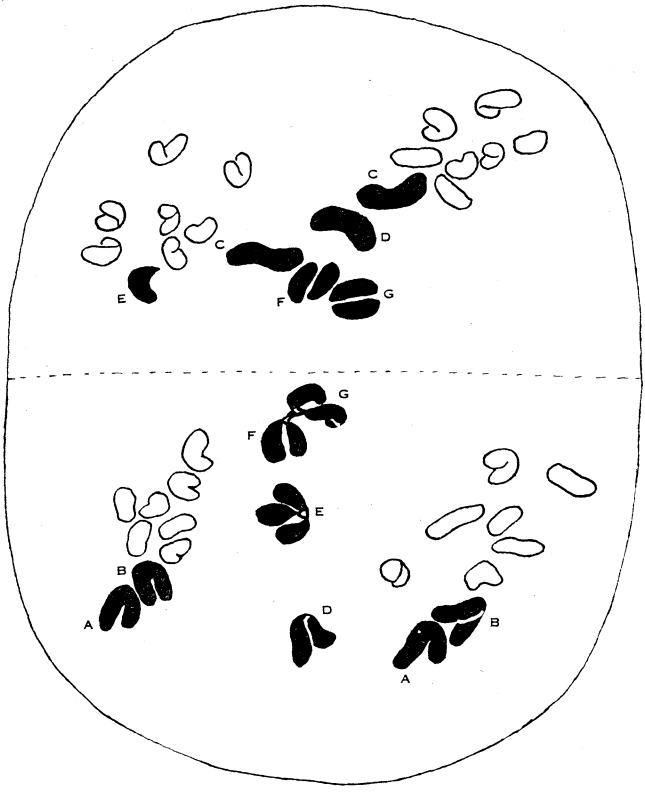

Fig. 3.—*P. coerulescens* × *P. minor*. Pollen mother cell at A II showing breakage and reunion products of the univalents. × *c.* 1200.

the result of type IV or type V breakage, the breakpoint being adjacent to the centromere. The *F* and *G* chromosomes are the result of type I breakage. Instead of fusion between sister chromatids, fusion has taken place between adjacent centric fragments of non-sister chromosomes (cf. Fig. 2). The four acentric chromatid arms of *F* and *G* remain inert on the other side of the plane of first division.

Those univalents included unbroken into one of the polar groups at T I disjoin normally at A II. There is no appearance of neocentric activity in these chromosomes, nor in those which belong to type I. Some of the products (types III, IV, and V) of univalent breakage at the first division remain behind

at the second when the normal chromosomes have disjoined, and behave in various ways. Type III chromosomes are the only ones which display neocentric activity at the second division, and not all such chromosomes show it. The neocentromeres appear in both arms and the chromosome may lie axially in the cell with one arm extended to each polar group (Plate 1, Fig. 7). These chromosomes are usually included in one of the daughter nuclei presumably through the greater activity of a particular neocentromere, or rarely such chromosomes remain between the polar groups to be broken by the second division cell wall. Rarely both chromosome arms are directed towards one pole and the true centromere towards the other pole (Fig. 4). Thus the broken centromere

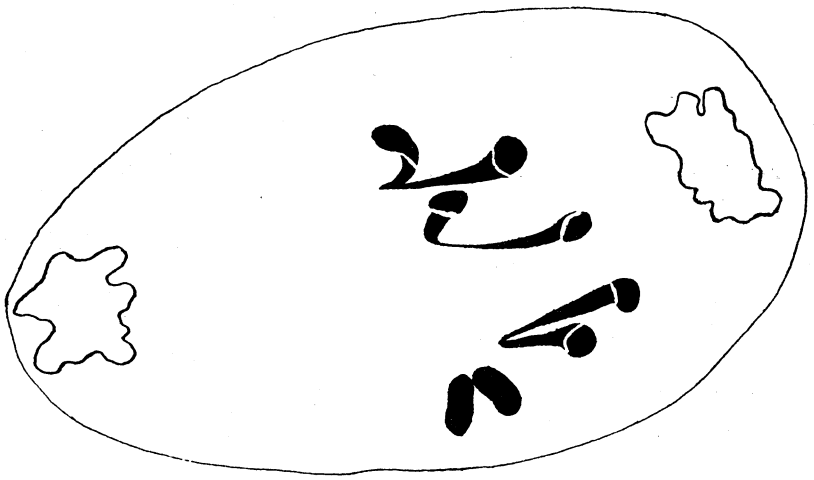

Fig. 4.—*P. coerulescens* × *P. minor*. A II showing joint activity of centromeres and neocentromeres in three univalents. Two acentric fragments are present. × *c.* 3000.

of these chromosomes is not inert as it was in the first division. When type III chromosomes do not show neocentric behaviour, they frequently divide, or misdivide, at the centromere. The exact nature of this division depends on the non-homology or homology of the chromosome arms, and presumably both occur.

The centromeres of type V chromosomes do not divide at the second division, and the chromosome remains in the middle of the cell. Type IV chromosomes were not observed at A II.

Very few pollen grain divisions were observed as most of the pollen grains failed to survive long enough to divide. Consequently, the later behaviour of the broken chromosomes could not be traced.

(*d*) *Meiosis in* P. tuberosa × P. minor

The association of the chromosomes is very variable at M I. Linear trivalents occur in 90 per cent. of the cells and there are between eight and nine univalents on the average per cell. The univalents vary considerably in size and no one chromosome could be identified as derived from a particular parental

species. The behaviour of the bivalent and multivalent chromosomes at meiosis is normal, and when they have disjoined at A I, varying numbers of univalent chromosomes congress at the equatorial plane. The various types of behaviour of the univalents with their corresponding frequencies are given in Table 1.

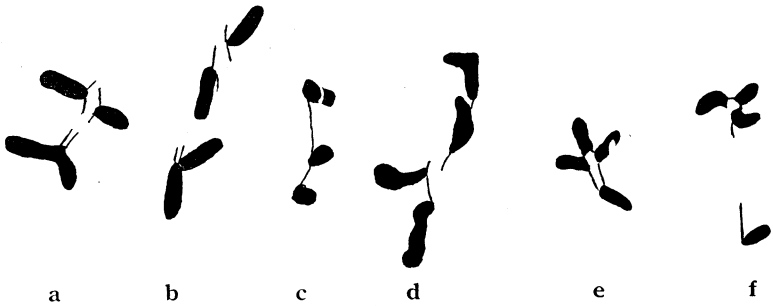

Fig. 5.—*P. tuberosa* × *P. minor.* Univalents showing various types of misdivision of the centromere. × *c.* 1300.

Misdivision of the centromere occurred in 20 of the 38 A I cells examined. Only one or two chromosomes in a cell misdivided, rarely more, and these included both large and small univalents. Three types of misdivision were observed (Fig. 5). The first involved separation of one chromatid arm from the centromere (Figs. 5*e* and 5*f*). The second type followed normal division of the centromere, the centromere of one of the daughter chromosomes divid-

TABLE 1

BEHAVIOUR OF UNIVALENT CHROMOSOMES AT MID-ANAPHASE I IN THE HYBRID *P. TUBEROSA* × *P. MINOR*

Centromere Fails to Divide	Centromere Divides Normally		Centromere Misdivides		Total
Neocentric Activity	Neocentric Activity	No Neocentric Activity	Neocentric Activity	No Neocentric Activity	
No. of univalents: 23	110	101	18	12	264
Per cent.: 8·6	41·7	38·5	6·8	4·5	

ing transversely to give two telocentric arms (Figs. 5*a*, 5*b*, and 5*c*). The third type of misdivision resulted in four telocentric arms (Fig. 5*d*) presumably by an extension of the second type, whereby the centromeres of both daughter chromosomes misdivide. Thin non-staining connections were visible between some of the misdivided centromeres. All these features have been observed by other workers. Misdivision of the centromere of single chromosomes was seen in 16 out of 50 A II cells.

Neocentric activity at the first division was observed in both large and small univalents and occurred in 90 per cent. of the cells examined. The range in appearance of the chromosomes with neocentromeres (Fig. 6) was greater than in the hybrid *P. coerulescens* × *P. minor* (Plate 1). Usually the end of the chromatid arm directed towards the spindle pole was rounded. No thin attenuated ends of the chromosomes like those in *Bromus* hybrids (Walters 1952*b*) were observed. Frequently only some of the chromatid arms of a univalent were affected. It could not be decided with any certainty whether sister arms were directed towards the same pole or not. Usually the centromere of the univalents divided normally after the neocentromeres had acted. Univalents which had misdivided, frequently showed neocentric activity in the telocentric and metacentric arms. Thin faintly-staining connections similar to those seen in the misdividing univalents, were sometimes present between univalents whose centromeres had apparently divided normally, and which had shown neocentric activity.

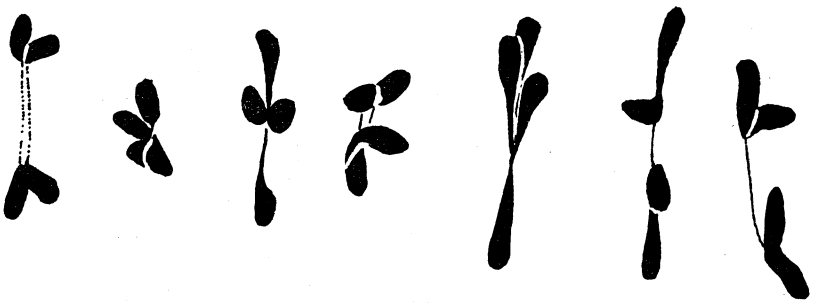

Fig. 6.—*P. tuberosa* × *P. minor*. Univalents at A I showing neocentric activity. × *c.* 3000.

At the second division of meiosis neocentric activity of the chromatid arms was observed in 15 of the 50 A II cells examined. Various types of orientation result from this activity (Plate 1, Fig. 11), with distal or terminal regions of the chromosome arms leading towards the poles. No cell was seen where both arms of the same univalent were directed towards the same pole.

Thirty per cent. of the T I cells examined possessed micronuclei. These were entirely absent from the hybrid first described. The micronuclei appear to be derived from univalents and telocentrics which failed to reach the polar groups.

IV. Discussion

Cell wall formation appears to be retarded or inhibited by several univalents stretched across the cell in *P. coerulescens* × *P. minor*. A similar obstruction of cell wall formation has been described in *Triticum* hybrids (Thompson 1931). The complete prevention of cell wall formation is rare in the *Phalaris* hybrid, even when there are a large number of univalents.

The bridges which usually lie across cells are chromatid bridges, and are broken by the cell wall. Dr. O. H. Frankel has suggested to me that the essential difference in action on cell wall formation between chromatid bridges and univalent bridges resides in the position of the centromere. Possibly it is the univalent's centromeres lying in the middle of the cell which impede, and occasionally prevent, cell wall formation.

The multi-armed chromosomes observed at the second meiotic division in *P. coerulescens* × *P. minor* are unique. They may be the result of reunion during the interphase, after chromosome breakage at cell wall formation at the first division. They are different from diplochromosomes (White 1935), which have eight chromatids with a single centromere.

It is evident that chromosomes at the second division which lie axially in the cell and show neocentric activity of the distal parts of the chromatid arms are not instances of misdivision of the centromere. Upcott (1937) and Sanchez-Monge (1950) have supposed similarly orientated chromosomes to be undergoing transverse division of the centromere.

The common feature of the neocentric activity shown by the univalents of the *Phalaris* hybrids and the previously reported examples, is the presence of lagging univalents at meiosis in which neocentric activity may occur.

There is no evidence of a visible "activator" of neocentric activity such as the abnormal chromosome 10 in *Zea mays*. The particular condition which evokes neocentromere activity may be either a genetic unbalance, or an alteration of the spindle by the centromeres of the disjoined chromosomes as suggested by Darlington (1937).

In *Zea* and less definitely in *Secale* it has been shown that there are constant locations in the chromosomes for the neocentromeres, and that their loci are heterochromatic. Although there is no evidence for the heterochromatic nature of the neocentromeres in the *Phalaris* hybrids, the constancy in appearance and behaviour of the univalents in *P. coerulescens* × *P. minor* strongly suggests a constant location and a common structure of the neocentromeres. The difference between the degree of neocentric activity in these two hybrids may then be the result either of genotypic differences or of structural differences or a combination of both.

The acentric fragment derived from the inversion occasionally seen in *P. coerulescens* × *P. minor* has not been observed at A I. Hence Rhoades's (1952) observation that the true centromere is essential for the functioning of the neocentromere in *Zea* has not been capable of test in this material.

While the large univalents in *P. tuberosa* × *P. minor* cannot be assigned with any certainty to either parent, it is significant that univalent bridges occur in this hybrid, similar to those seen in the first hybrid. It is not unreasonable to suppose that these univalent bridges are derived from the large chromosomes of *P. minor* and that the centromeres of this particular genome have a particular pattern of response to the univalent condition. This supposition is favoured by the behaviour at A I of the occasional univalents in allopolyploid *P. coerulescens* × *P. minor*. The large univalents derived from *P. minor* behave like those in the undoubled hybrid. The small univalents from *P. coerulescens*, how-

ever, do not show this extreme abnormality. Further, the univalents in an asynaptic *P. coerulescens* behave normally.

The loss of that property by which the centromeres lead chromosome movement is correlated with irregularities in the division of the centromere in the univalents of the *Phalaris* hybrids, in a *Bromus* hybrid (Walters 1952*a*), and apparently in a *Pennisetum hybrid* (Krishnaswamy and Raman 1953). The complete failure of the centromere to divide is an extreme form of these irregularities.

V. Acknowledgments

I should like to thank Dr. E. M. Hutton of the Division of Plant Industry, C.S.I.R.O., who made the material available to me.

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ADDENDUM

Bosemark (1954) has described the behaviour at meiosis of accessory chromosomes in *Festuca pratensis*. These chromosomes are largely heterochromatic. Where a number of univalent accessory chromosomes were present at A I, "difficulties" in their division were occasionally observed. This led to frequent univalent bridges with the chromatid arms apparently directed towards the poles. Groups of such bridges resulted in the formation of restitution nuclei. The general behaviour of these accessory chromosomes resembles that of the univalents in *P. coerulescens* × *P. minor*, and may well be open to a similar interpretation.

EXPLANATION OF PLATE 1

Figs. 1-9.—*Phalaris coerulescens* × *P. minor*. Figs. 10 and 11.—*Phalaris tuberosa* × *P. minor*.

Fig. 1.—M I with seven bivalents and seven large univalents.

Fig. 2.—Early A I with six univalents in the equatorial plane.

Fig. 3.—A I showing five univalents with intercalary regions of the chromatids drawn towards the poles.

Fig. 4.—Later A I showing the univalents stretched between the poles.

Fig. 5.—T I with univalent bridges undergoing compression by the formation of the cell wall.

Fig. 6.—Later T I. The cell wall has nearly broken the univalent bridges.

Fig. 7.—A II showing one chromosome lying axially under the influence of the neocentromeres.

Fig. 8.—A II with a five-armed chromosome, and three large and seven small chromosomes in each polar group.

Fig. 9.—A II with an eight-armed chromosome and a univalent.

Fig. 10.—A I showing univalent chromosomes moving to the poles under the influence of neocentromeres.

Fig. 11.—A II with three univalents showing neocentric activity and two showing none.

CENTROMERES IN *PHALARIS*