small compared with the additive genetical effects; for the female progeny an adequate fit is obtained when no potence is specified so the character is under predominantly additive genetical control.

Returning to the results from the population cage, it is clear that some factor has caused the population mean to fall well outside the parental range, whilst at the same time the variance has declined. At any given time there are approximately 2000 flies in the cage so random genetic drift may be discounted. Mutation is very unlikely to produce such a rapid change. This suggests that natural selection has been responsible for reducing the population mean to an optimal level. That this level is so far away from the F_1 mean (which has maximum heterozygosity) demands an explanation other than heterozygote advantage.

A similar population ot 18° C. is currently being studied and considerable interest attaches to the outcome.

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THE CONSEQUENCES OF CROSSING-OVER IN PERICENTRIC INVERSIONS IN ACROCENTRIC CHROMOSOMES

P. E. BRANDHAM

Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey

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1. Introduction

THE meiotic events associated with heterozygosity for a paracentric inversion are by now very well known (Brown and Zohary, 1955; Darlington, 1965; Kreft, 1969), and the formation of a dicentric chromatid bridge with an accompanying acentric fragment at AI is the most familiar occurrence. Other events, which are usually less common, are (i) the formation of a chromatid loop and an acentric fragment, (ii) a double bridge with two fragments, and (iii) two loops with two fragments (Brandham, 1969). On the other hand, when an inversion is pericentric no bridges or loops are formed at AI; instead, chromatids are produced carrying certain deletions and duplications which, unless precise measurements are made, would be morphologically difficult to detect in metacentric chromosomes. When there is a marked difference in arm length of the original chromosomes duplicate/deletion chromatids produced by crossing-over in a pericentric inversion are clearly recognisable as small or large metacentric chromatids. These can, under certain circumstances suggest that iso-chromosomes have

been formed. Such was the conclusion of Giles (1943), working on *Gasteria maculata*, which has a bimodal complement of acrocentric chromosomes. He observed the production at AII of small and large metacentric chromatids from one of the four large bivalents, and interpreted their formation as being due to combinations of transverse and longitudinal misdivisions of the centromeres of the bivalent at or before MI and their subsequent reunion in various combinations to form iso-chromosomes.

Giles' work was recently given prominence by John and Lewis (1965), who considered it to be a novel mode of origin of iso-chromosomes that did not involve the prior occurrence of telocentrics by misdivision of univalents. They mentioned that part of Giles' observations could possibly be explained in terms of a pericentric inversion, but I believe that all of his results, both qualitative and quantitative, can be explained in this way, an alternative which is much simpler and more acceptable than Giles' rather cumbersome one, and which is discussed below.

2. Meiotic products of a pericentric inversion

In the account which follows the chromosome used as a model is heterobrachial, and has been given an arm length roughly corresponding to those found in *Gasteria* and other members of the Aloineae (Liliaceae) and considered by Giles. In such a model duplications and deletions produced during meiosis in a pericentric inversion heterozygote are readily seen.

As with a paracentric inversion, during the formation of a bivalent heterozygous for a pericentric inversion the inverted region of one chromosome forms a loop, and the whole chromosome is then able to pair with all parts of its homologue. Chiasmata may be formed anywhere within the loop, their number and position being influenced by the size of the inversion and by the position of the centromere within it. A single chiasma anywhere in the loop results in the production at AI of one dyad having three long arms and one short, and one having three short arms and one long. The presence of a second chiasma within the loop has various effects, depending on its position and on which chromatids are involved. The effects of 0, 1 or 2 chiasmata in different positions are illustrated at AI and AII of meiosis in fig. 1. The various AII quartets are in the same order and are given the same identifying letters as those illustrated by Giles (1943) and by John and Lewis (1965).

Fig. 1 shows that at AI it should be possible to recognise three types of segregation of long and short arms; (i) two long and two short arms in each dyad (types, A, D and E); (ii) three short arms and one long arm in one dyad, with the other complementary to it (type B); (iii) four long arms in one dyad, with four short in the other (type C). The structural relationships between the long and short arms in types A, D and E dyads will actually vary, some chromatids being the normal acrocentric types and some appearing to be "two iso-chromatids held together by the single centromere" (Giles, 1943, p. 514). This variability was suspected and even figured by Giles, but he was unable to distinguish them with certainty, and included all AI dyads having two long and two short arms in a single category.

The AI stages leading to the production of types B and C quartets are readily distinguishable, and good photographs of these were provided in Giles' plate 1F and 1G.

At AII, fig. 1 shows that three types of chromatids are produced. Some chromatids are of the same acrocentric type as the parent chromosomes, and may or may not contain the inversion. The remaining two types are metacentric and carry duplications and deletions. The short metacentric contains the inverted segment and two short arms, and lacks that segment of the long arm which was distal to the inversion. The long metacentric contains the

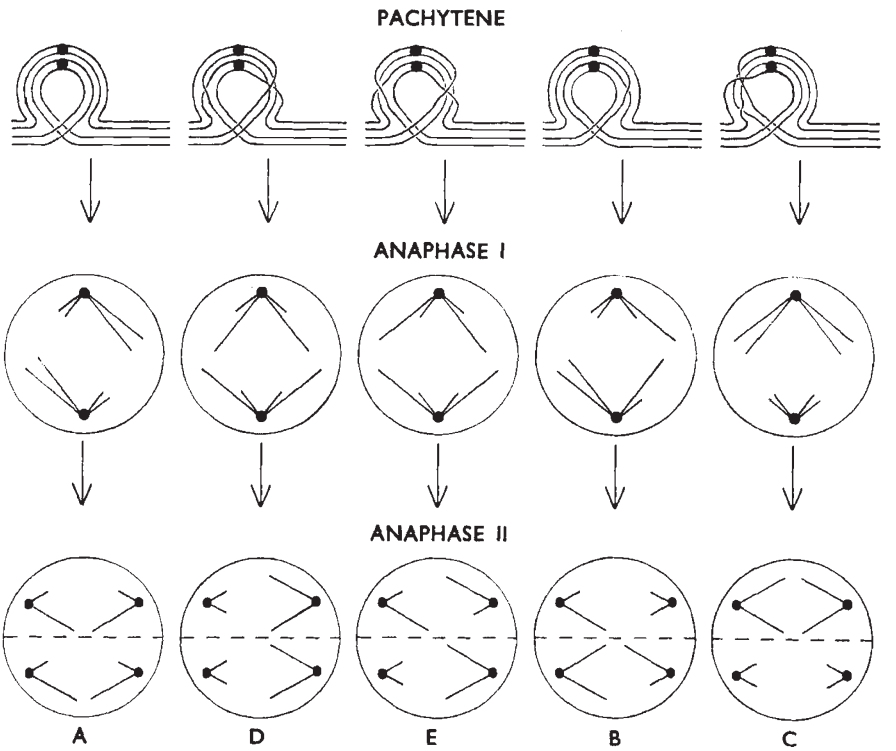

FIG. 1.—Diagram of the five types of configuration produced at AI and AII by different numbers and positions of cross-overs at pachytene in a pericentric inversion loop.

inverted segment and two long arms, and lacks the distal part of the short arm. Because of their deletions the metacentrics would seem unlikely to survive beyond the gamete stage, although they were observed at pollen grain mitosis by Giles.

3. DISCUSSION

The long and short metacentrics could possibly be interpreted as iso-chromosomes, particularly if the inversion is symmetrical about the centromere, and Giles in fact came to this conclusion when he observed them in *Gasteria*, proposing centric breakage and reunion to explain his observations. The five different types of AII quartet drawn in fig. 1 were observed by Giles, and formed the basis for his conclusions, but as is now quite apparent each quartet can be produced in theory as a result of the formation of up to two chiasmata in the inversion loop. The metacentrics produced by the inversion are morphologically the same as those figured by Giles, but are genetically different. They are not iso-chromosomes, the arms being homologous only in those regions distal to the inversion.

When the inversion interpretation of Giles' observations is considered, predictions can be made of the relative occurrence of the five quartet types A, B, C, D, E produced by combinations of various numbers and positions of chiasmata in the inversion loop and by the four possible types of cross-over which can occur at any chiasma (table 1). The ratios in table 1 are given on the assumption that the two chromatids which cross-over at a particular chiasma are randomised and are not influenced by the cross-over at a neighbouring chiasma.

TABLE 1

Theoretical values for the relative numbers of the five AII quartet types (fig. 1) produced by various positions of up to two chiasmata within a pericentric inversion

Number of chiasmata	Position of chiasmata	Relative occurrence of 5 AII quartet types				
		A	B	C	D	E
0	–	1	–	–	–	–
1	Anywhere in loop	–	1	–	–	–
2	Either side of centromere	$\frac{1}{4}$	–	–	$\frac{1}{4}$	$\frac{1}{2}$
2	Same side of centromere	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	–	–

When two chiasmata are on either side of the centromere in the inversion loop a two strand double cross-over gives type A, a three strand double cross-over gives type E and a four strand double cross-over gives type D. When the two chiasmata are on the same side of the centromere a two strand double cross-over gives type A, a three strand double cross-over gives type B, and a four strand double cross-over gives type C.

In *Gasteria* Giles found 19·1 per cent. A, 53·2 per cent. B, 7·1 per cent. C, 5·4 per cent. D and 15·2 per cent. E in a rather small sample of 184 cells at AII.

From the information given in table 1 it can be seen that a single chiasma in the inversion always produces type B quartets at AII, but that two chiasmata can produce any of the five types, depending on their position and on which chromatids are involved. Thus it may reasonably be predicted that type B will greatly exceed types C, D or E in frequency, even if the incidence of two chiasmata in the inversion is higher than that of one, unless the inversion is so big that the frequency of a single chiasma falls far below that of two. This would seem unlikely when approximately symmetrical pericentric inversions in acrocentrics are concerned. Table 1 also predicts that type E quartets should be more abundant than type D, because three strand double cross-overs are theoretically twice as common as four strand double cross-overs, assuming randomness of cross-over. Both of the above predictions are verified by Giles' quantitative data.

4. CONCLUSION

It is felt that Giles' explanation of apparent iso-chromosome formation at meiosis by centric misdivision and reunion in a bivalent is too complex to be acceptable, particularly since it is difficult to explain why the process should occur in one bivalent and not in the others. All of his qualitative and quantitative data can be satisfactorily explained far more simply on the basis of a pericentric inversion. I therefore suggest that his interpretation should be rejected in favour of the latter.

5. Summary

1. Chiasmata formed in a pericentric inversion loop in an acrocentric bivalent give rise to the production at AII of long and short metacentric chromatids which have one segment duplicated and one missing, also to acrocentrics which may or may not contain the inversion.

2. The metacentrics superficially resemble iso-chromosomes, but genetically they are not, the arms being homologous only in the distal regions. Observations of Giles (1943), who proposed iso-chromosome formation at meiosis by a process of centromere misdivision and reunion are more readily interpreted as being due to a pericentric inversion.

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BREEDING SYSTEMS IN *PLANTAGO*

M. D. ROSS

Department of Biology, Dalhousie University, Halifax, Nova Scotia

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1. Introduction

Paliwal and Hyde (1959) reported an association between the presence of an accessory or B chromosome and male sterility in a strain of *Plantago coronopus*. All the male steriles studied in their material had a single B chromosome, while all the hermaphrodites lacked B chromosomes. During a study of breeding systems in this genus, I obtained data which are difficult to reconcile with such an association. These data are given here, together with a brief survey of some of the breeding mechanisms found in this genus.

2. The situation in *Plantago coronopus*

Paliwal and Hyde's strain of *P. coronopus* (supplied by Professor Hyde) showed two types of male sterile, here called MS and Intermediate MS. The first type has minute anthers which are not exserted, or has small, slightly exserted indehiscent anthers. The Intermediate MS type has small exserted anthers producing very little or no pollen. This type is probably functionally male sterile. A minority of plants are intermediate between the male steriles and the hermaphrodites. The anthers are exserted, but produce