Segmental Interchange in *Pisum* II

By

Eva R. Sansome

John Innes Horticultural Institution,
London

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Introduction

The present paper is a continuation of a study of the cytogenetics in *Pisum sativum*, the garden pea.

An association of 6 chromosomes which frequently takes the form of a "figure-of-eight" has been described in a previous paper (E. Richardson Sansome 1932). On the assumption that only homologous parts of chromosomes normally pair at meiosis, certain predictions were made from the cytological observations regarding the genetical behaviour of the plant having the association of six chromosomes. The present paper deals with some of the progeny of this plant. The observations are in accordance with the predictions, and are therefore taken to afford genetical proof of the occurrence of segmental interchange or reciprocal translocation between otherwise non-homologous chromosomes as the result of crossing-over in an interstitial homologous segment. Since the paper describing the "figure-of-eight" was sent to the press, two other papers have appeared in which a precisely similar configuration has been described, in *Datura* (Bergner and Blakeslee 1932) and Maize (Brink and Cooper 1932). In both cases the breeding behaviour of the plant having this configuration was according to expectation.

General Observations

The root tips of fourteen of the offspring of 227¹/₃₁, the plant having a "figure-of-eight" of six chromosomes, were examined cytologically. Two were found to be trisomics, the rest were diploids. The occurrence of trisomics was expected since many second division plates of the parent plant had 8 chromosomes. Metaphase plates

from the root tips of the two trisomics $354^5/_{32}$ and $354^{11}/_{32}$ are to be seen in Fig. 1.

Fig. 1. Somatic metaphases from the root tips of two trisomics, (a) plant $354^5/_{32}$, (b) plant $354^{11}/_{32}$. $\times 3750$ ca.

The Trisomics. The trisomic plants were, on the whole, slower growing and longer in maturing than their sister plants. The foliage was finer than that of the sister plants, the leaves being narrower. The peduncles also had strongly developed paired bracts. Both trisomics showed these characters, but as there was considerable variation among the sister plants none of the characters mentioned could be used as a positive means of identifying trisomics. However, trisomics could be definitely distinguished from the diploids by an examination of their pollen. Fig. 2 shows pollen grains of (a) a fertile plant, (b) a trisomic and (c) a partially sterile plant. The trisomic pollen is distinguished from the rest by having a number of tetrahedral grains mixed with the usual oval grains. The tetrahedral

Fig. 2. Photomicrograph of pollen grains mounted in cotton blue solution. (a) of a fertile plant, (b) of a trisomic plant showing unstained aborted grains and a mixture of oval and tetrahedral grains, (c) of a three-quarter sterile plant. $\times 70$.

grains are in excess of the oval grains, but no counts of statistical value of the two types have yet been made. The tetrahedral pollen grains may represent the $n+1$ grains, the oval the n grains. If so, the excess of tetrahedral over normal grains may be related to the structural hybridity of the trisomics as disclosed by the cytological observations. An extra chromosome may replace deficiencies brought about through non-disjunction in a chromosome ring and therefore structural hybrid trisomics may sometimes have an excess of viable $n+1$ over n gametes. Tetrahedral pollen grains have been reported in trisomic *Oenothera*s by Lutz (1917) and Gates (1923) but these authors do not mention the presence of normal grains also. If the tetrahedral pollen grains do represent $n+1$ grains, they ought to be found in small numbers in the pollen of the three-quarter sterile sister plants which resemble the parent. It is intended to examine such pollen for these grains when opportunity occurs. They may be a valuable diagnostic feature of the trisomics, but may of course be associated only with the presence of one particular chromosome or chromosome segment.

Segregation of $227^1/_{31}$. The association-of-six forming plant, $227^1/_{31}$, segregated for the factors A, for coloured or white flower, M, for marbling of the testa, R for round or wrinkled cotyledons and Pl for black or light hilum. As however only 14 plants survived, the actual numbers have no genetical significance.

Sterility. Of the diploid plants, three were fertile on both male and female sides, 4 were found to be half-sterile from ovule and pollen counts; one was classified as half-sterile on pollen counts alone and one on ovule counts alone. Three, or possibly 4 plants were found to be three-quarter sterile on both male and female sides. Of the three-quarter sterile plants $354^3/_{32}$ gave pollen counts of 1201 aborted to 412 good pollen grains, which is a ratio of 74.48:25.52, and $354^{12}/_{32}$, another three-quarter sterile, gave 558 aborted ovules to 208 good ovules, a ratio of 72.84:27.16.

The percentage of aborted ovules in the trisomics has not been established. First counts of pollen showed about 25% of aborted grains in both plants, but later counts showed as much as 58% of aborted pollen. Since however the later flowers were all attacked by thrips it is possible that the earlier counts are the more correct. The percentage of ovule failures could not be recorded because of the poor setting, the latter being partly due to the fixing of a large number of flower buds for cytological examination.

Cytological Examination

Methods. Young flower buds were fixed in Carnoy for about 30 seconds and then transferred to La Cour's fixative 2B for from 12–24 hours. Sections were cut at 20μ and stained by Newton's gentian-violet method. The drawings were made with a Zeiss camera lucida 1.5 mm. objective and a $\times 30$ eyepiece at an initial magnification of about 6000 diameters.

Observations. Some of the offspring of $227^1/_{31}$, the association-of-six forming plant, numbered $354/_{32}$, $356/_{32}$ and $357/_{32}$ respectively, were studied cytologically. Of these, $357^1/_{32}$ and $354^8/_{32}$ were found to have an association of four chromosomes at meiosis, $354^4/_{32}$ had seven pairs and $354^{12}/_{32}$ had an association of six chromosomes like the parent plant. Of the two trisomics, one, $354^5/_{32}$, was studied in detail, but only a few good divisions were obtained in the case of the other, $354^{11}/_{32}$.

Fig. 3 *a, b* shows two metaphase plates from $354^{12}/_{32}$, showing the association of six chromosomes. Since this closely resembles that found and described in the parent plant $227^1/_{31}$ (E. R. Sansome 1932) it is not necessary to give a full account of it. However, Fig. 3 *b* is interesting as it shows chiasmata on both sides of the attachment

Fig. 3. Late metaphases of first reduction division, (a) and (b) from $354^{12}/_{32}$ showing an association of 6 chromosomes and 4 bivalents and (c) from $354^4/_{32}$ showing 7 pairs.

In (b) a 2:4 separation of chromosomes is shown. $\times 3750$ ca.

constriction in one of the pairs of chromosome segments, probably the D segments (see Fig. 5). A similar configuration was found in 227¹/₃₁. Fig. 3 *c* shows an early anaphase complement from the plant 354⁴/₃₂. Seven pairs of bivalents are formed regularly in this plant, in agreement with the fact that it is fully fertile.

The plants 357¹/₃₂ and 354⁸/₃₂ showed similar configurations at metaphase, so only the former has been extensively illustrated. The half-sterile, 357¹/₃₂, has five bivalents and an association of four chromosomes at meiosis. The association of four generally takes the form of a figure-of-eight, as the result of one pair of continuously pairing segments having chiasmata on both sides of the attachment constriction (see Figs. 4 *d, g, h, i*). Terminalisation in this case results in the movement of chiasmata towards the ends of the chromosomes at one side of the attachment constriction, and on the other, towards the point where the homology changes. Such a "figure-of-eight" is not strictly comparable with that found in association of six or more chromosomes, in which two chromosomes each pair with three different chromosomes.

The configuration is not always constant in appearance (see Figs. 4 *h* & *j*) but the type seen in Fig. 4 *j* occurs most frequently. The differences between the two types may be due to different degrees of terminalisation or to the presence of chiasmata on both sides of the attachment in different chromosomes. Fig. 4 *i* indicates that two pairs of chromosomes have their points of attachment sufficiently removed from the parts of change of homology to allow of chiasmata being formed, occasionally, between the attachment constriction and that point. That the point of contact which gives the "figure-of-eight" appearance is an actual chiasma or interchange of partner amongst the chromatids is shown by Fig. 4 *d*, in which the chromatids can be seen opening out of the chiasma at early anaphase. It is proposed to call this chiasma the "median chiasma" for convenience in description. Open rings are occasionally observed as the result of failure of formation of the median chiasma (see Fig. 4 *e*). Similarly chains are found, presumably as the result of failure of chiasma formation in one pair of segments in addition to failure of the median chiasma (see Fig. 4 *f*) and "necktie" configurations as the result of failure of a chiasma in one pair of end segments (Fig. 4 *k*). The association of four found in 354⁸/₃₂, which is identical in appearance with that shown by 357¹/₃₂, is illustrated in Figs. 4 *g* & *j*.

Fig. 4. Meiosis in the new association-of-four forming plant (*a*) early anaphase showing non-disjunction in the association of four, (*b*) and (*c*) association of four disjoining, (*d*) early anaphase showing chromatid non-disjunction in the association of four, (*e*) ring of four showing non-disjunction, (*f*) chain of 4 showing non-disjunction, (*g*) ring of showing non-disjunction and 5 bivalents, (*h*) association of 4 with chiasmata on both sides of the attachment constriction in 2 chromosomes, (*i*) association of 4 with chiasmata on both sides of the attachment constriction in 4 chromosomes, (*j*) early anaphase showing chromatid non-disjunction in the association of 4, (*k*) association of 4 with 2 ends unpaired. *g* and *j* from $354^{8/32}$, the rest from $357^{1/32}$. $\times 3750$ ca.

Relationships of the new association of four chromosomes

The possible occurrence of plants having four different types of association of four chromosomes amongst the offspring of the association of six was predicted. These associations of four with the segments lettered in accordance with the diagram of the association of six, see Fig. 5, are

- (1) AB.BC.CXD.DXA
- (2) AXE.EF.FD.DXA
- (3) CXD.DF.FE.EXC
- (4) AXE.EXC.CB.BA

Of these (1) and (4) are expected to form figure-of-eight configurations whenever chiasmata are formed in the X segment, whereas the other two should not form such configurations. The ring of four chromosomes formed when the Thibet line is crossed with normal lines often takes the form of a figure-of-eight (E. R. Sansome, 1932), although this was not at first recognised. Such a configuration is illustrated for comparison beside a figure-of-eight obtained from $357^{1/32}$ in Fig. 5. It will be noticed that the two configurations differ, that from $357^{1/32}$ being the bigger and having two "Querarme" (Håkansson) caused by the presence of interstitial chiasmata whereas the other figure-of-eight has only one. Therefore if the lettering given to the figure-of-eight of six chromosomes is followed, the new ring of four must be AB.BC.CXD.DXA, with "Querarme" in the B and D segments, and the ring formed when the Thibet line is crossed with normal lines, AXE.EXC.CB.BA with a "Querarm" in the B segment only. The Thibet-normal ring was originally given the formula AB.BC.CD.DA, but as this does not correspond with the formula given to the association of six it is considered advisable to change the formula of the Thibet-normal ring to AXE.EXC.CB.BA. If this is done then the formula of its parents must be AB.CXE.DF and BC.AXE.DF for the chromosomes with which the experiments are concerned. The formulae of the parents of the plant having the association of 6 chromosomes must be AB.CXE.DF and BC.AXD.EF, adopting the lettering of Fig. 5 a. The T line being common to the association of four and the association of 6 must have the formula AB.CXE.DF. The formula of the N line which forms the AXE.EXC.CB.BA ring with the T line must therefore be AXE.BC.DF whereas the formula of the K line which

forms the association of six with the T line must be BC.AXD.EF. These formulae differ from those previously given to the three lines, but since it has been found possible to link them up with the association of six, it is considered advisable to adopt formulae to correspond with the lettering given to the previously published diagram of the association of six. It is, perhaps, worth noticing that the partial sterility associated with the figure-of-eight is not due to the proportion of non-disjunction but to the fact that the figure-of-eight

Fig. 5. (a) Diagram of the association of six (after E.R.S. 1932). (b) drawing of an association of four from the cross $T \times N$ lines. $\times 3750$ ca. (c) drawing of a new association of 4 from $357^{1/32}B$. $\times 3750$ ca. The drawings are lettered to correspond with the diagram.

can never show complete disjunction but generally shows half-disjunction or chromatid non-disjunction. Two of the four gametes resulting from chromatid non-disjunction will be balanced and viable and the other two will be unbalanced and non-viable. Bergner, Satina and Blakelee (1933) give a diagram illustrating the results of chromatid non-disjunction in an association of four chromosomes. It is interesting to note that such configurations in *Datura* are associated with 50% pollen abortion, whereas simple rings generally show little or no abortion owing to their regular orientation. Disjunction may be affected by the relative sizes of the chromosomes, the position of

Fig. 6. Meiotic metaphase from the trisomics. *k* and *l* from $354^{11}/_{32}$, the rest from $354^5/_{32}$. $\times 3000$ ca.

the attachment constriction and the presence or absence of interstitial chiasmata. The last-mentioned is probably the most potent factor (Darlington 1933). However, a configuration with chiasmata on both sides of the attachment constriction in one pair of chromosome segments must always lead to chromatid non-disjunction and if such configurations are formed regularly they must therefore be associated with 50% gametic abortion.

Trisomics. Only one trisomic, $354^5/_{32}$, was studied in detail, since very few clear metaphases were obtained of $354^{11}/_{32}$. The extra chromosome is variable in its behaviour. It may be unpaired or it may pair up with some of the other chromosomes in various configurations. Figs. 6 *a*, & *b* show a ring of four chromosomes, 5 bivalents and a univalent. Fig. 6 *c* is similar except that chiasma formation has failed in one of the segments of the association of 4 chromosomes, with the consequent production of a chain instead of a ring. From these figures it is clear that $354^5/_{32}$ is a structural heterozygote as well as a trisomic. Fig. 6 *f* shows a chain of five chromosomes and 5 bivalents, indicating that the extra chromosome is homologous at one end with one of the chromosomes in the ring. In Fig. 6 *g* an association of 5 is observed in which the extra chromosome is united with two of the chromosomes in the ring by a triple chiasma. Fig. 6 *d* shows a ring of four chromosomes, a chain of 3 and 4 bivalents. Here the extra chromosome is pairing with one of the bivalents, presumably at the opposite end from that at which it sometimes pairs with the association of 4. Thus the extra chromosome is also partly homologous with one of the bivalents. This assumption is substantiated by the branched chain of 7 chromosomes illustrated in Fig. 6 *h*. The extra chromosome forms a triple chiasma with the group of 4 at one end and is united with a chain of 2 at the other. The data indicate, therefore, that $354^5/_{32}$ is a ring-of-four forming heterozygote with an extra chromosome, homologous in part with one pair of segments in the ring and in part with one of the pair of chromosomes. Fig. 6 *k* taken from $354^{11}/_{32}$ shows an association of 5 chromosomes and 5 bivalents and Fig. 6 *l* from the same plant shows a group of 3 and 6 bivalents.

Discussion

The occurrence of plants forming an association of four chromosomes would not ordinarily be expected amongst the progeny of a

ring-of-six forming hybrid. In the absence of interchange of segments between chromosomes not completely homologous, such a hybrid would be expected to produce two kinds of viable gametes only, corresponding in chromosome structure to the gametes received from the parents. These gametes should produce on fertilisation three types of zygotes, one resembling each of the parents in chromosome structure and forming 7 pairs of chromosomes at meiosis, the third resembling the ring-of-six forming hybrid. However, configurations observed in the ring-of-six forming hybrid led to the prediction of four types of viable n gametes (E. R. Sansome 1932) with the possible formation of 4 types of structural homozygotes showing normal pairing and complete fertility, 4 types of structural heterozygotes with associations of 4 chromosomes and half sterility, and 2 types with associations of 6 chromosomes and three-quarter sterility. Since association-of-four-forming types have been observed, the predictions based on cytological observations may be said to have been verified genetically. The predictions were based on the observation of configurations which could only have occurred as the result of segmental interchange between chromosomes homologous interstitially but terminally non-homologous, if the generalisation be accepted that only homologous parts of chromosomes pair. This segmental interchange was held to have occurred as the result of crossing-over in the homologous interstitial region. The observation of association-of-four forming plants in the progeny of association-of-six forming plants is thus a confirmation of the above generalisation. McClintock (1932 and private communication) has observed in maize a pachytene pairing of non-homologous chromosome parts. However, we do not yet know how far crossing-over with chiasma formation and metaphase pairing can result from such non-homologous association. Certainly, the metaphase pairing of non-homologous parts cannot be a regular phenomenon and since the "figure-of-eight" configuration on which this work is based is observed in about 78% of the cases studied, it cannot be said to be due to the pairing of non-homologous segments. The chance pairing of non-homologous chromosomes has been held to be one of the methods by which segmental interchange between non-homologous chromosomes can occur—such pairing is not believed to be due to any attraction between non-homologous chromosomes but rather to the lack of any definite repulsion. Thus if two chromosomes are homologous except for short interstitial segments, pairing between

these segments may be brought about as the mechanical result of the pairing of the homologous regions. Catcheside (1932) has expressed this idea but carries it still further, believing that allelomorphs have no attraction for one another but are merely paired because of the pairing of the identical genes on either side of them. At present there is no evidence as to whether attraction is exercised only by identical genes or whether allelomorphs have the same, a graded or no attraction.

Recently, the cytology and breeding behaviour of plants having a figure-of-eight involving 6 chromosomes has been described for *Datura* (Bergner and Blakeslee 1932) and Maize (Brink and Cooper 1932). In the case of *Datura*, Bergner and Blakeslee found that the *Stramonium-ferox* hybrid had a "figure-of-eight" of 6 chromosomes besides 2 rings of 4, and 5 bivalents. They describe the configuration as "a circle of four to which a bivalent is attached by its humps." However, there is little doubt that the configuration is strictly similar to that in *Pisum*, being more difficult to interpret on account of the small size of the chromosomes. When the *Stramonium-ferox* hybrid was back-crossed with *Stramonium* the association of 6 was generally broken up. It was only recovered once amongst 30 plants. Instead, two types of circles of four distinguishable by the different sizes of their chromosomes were recovered, one of them being a figure-of-eight. These results are explained by Bergner and Blakeslee on the basis of crossing-over in the interstitial segments of the association of six chromosomes. However, if random formation of the four types of gametes takes place the association of 6 ought to be recovered in 25% of the back-crosses with one of the parent types. Its recovery only once in 30 plants may be a matter of chance or it may indicate that the viable crossover gametes are found more frequently than the viable non-crossover gametes.

Brink and Cooper on crossing semisterile-1 and semisterile-5 obtained amongst the progeny of the cross, plants which had an association of 6 chromosomes at meiosis and showed 75–85% of pollen abortion. Semisterile-1 involves an interchange between the P-br and b-lg chromosomes, whereas semisterile-5 involves an interchange between the P-br and Y-Pl chromosomes. The two interchanges do not involve corresponding portions of the P-br chromosome—the region between the two points of interchange on the P-br chromosome being called the interstitial segment. The genes br and f are located on this segment, which is about 25 crossover units long. A pachytene

figure which shows complete pairing is illustrated, the six arms of the complex radiating from the ends of the interstitial segment. Two fertile derivatives of an association-of-six forming hybrid were tested and one was found to be normal, the other, the double interchanged type. The occurrence of such fertile types was predicted as the result of crossing-over in the interstitial segment and the authors point out that the two fertile derivatives tested must have resulted from combination between crossover gametes of the two respective kinds. The three fertiles from the *Pisum* association of six have been crossed with the Normal, the Thibetan and the K lines, in order to test their chromosome structure. It is hoped that one of them may be of the double-interchanged type, giving an association of 6 with the normal line. The *Pisum* data are insufficient as yet to show whether the four possible types of viable gametes are formed at random, but the ratio of 3 fertiles: 6 semi-steriles: 4 three-quarter steriles is very close to the 1:2:1 ratio expected on a random formation of gametes. The results in *Datura*, Maize and *Pisum* indicate that chromosome interchanges with other chromosomes may take place at different points on the same chromosome. Thus on crossing two lines with interchanges involving one chromosome with two others, a figure-of-eight of six chromosomes is formed by the pairing of an interstitial segment of two non-adjacent chromosomes from different parents. Darlington (1933) has shown how the formation of such interstitial segments may account for the building up of complexes in *Oenothera*. The fact that the behaviour of the figure-of-eight was predicted on Belling's segmental interchange theory and that no results incompatible with that theory have been obtained afford very strong support to the theory. Darlington (1931) on the basis of the observation of a figure-of-eight in *Oenothera* explained the formation of half-mutants and mass-mutants as the result of crossing-over in homologous interstitial segments in otherwise non-homologous chromosomes. The results in *Datura*, Maize and *Pisum*, in which viable gametes with new structural combinations have been shown to arise from such a figure-of-eight, strongly support Darlington's suggestion.

The occurrence of trisomics in the progeny of structural heterozygotes as the result of chromosome non-disjunction has been reported in maize amongst the progeny of semi-steriles. Håkansson suggested the possibility that it might occur in *Pisum*, as the result of observation of second metaphases with eight chromosomes

(Håkansson 1929). The association of 6 chromosomes, however, showed a greater proportion of such metaphases and it is not surprising that trisomics in *Pisum* should first be discovered amongst the progeny of such a plant. It is now clear that trisomics in *Pisum* are viable and it is probable that they may be found amongst the progeny of simple rings of four, although in much smaller numbers than amongst the progeny of association of six-forming plants.

Since the origin of the trisomics is known, it seems worth while to consider the type of trisomics likely to arise as the result of non-disjunction in the association of six chromosomes. For purposes of discussion, one particular chromosome, for example EF, may be taken to be the extra one. Since the extra chromosome gametes taking part in the formation of the trisomic must have arisen as a result of non-disjunction at both ends of the EF chromosome, it must have had the constitution AB.CXE.EF.FD or BC.AXE.EF.FD. Such a gamete would have the chance of meeting with any one of the four types of viable n gametes produced, which may be represented as follows: AXD.BC.EF, AB.CXE.DF, AB.CXD.EF, and AXE.BC.DF. The zygotic combinations of which the first type of $n+1$ gamete is capable are therefore

These combinations will give as the maximum chromosome association at meiosis, (1) a "figure-of-eight" of 6 chromosomes with an extra chromosome attached to form an association of 7 chromosomes, (2) a bivalent and two pairs linked by the extra chromosome to form an association of 5 chromosomes, (3) a bivalent and a ring of four chromosomes with the extra chromosome attached to form an association of 5 chromosomes and (4) a ring of four chromosomes linked to two paired chromosomes by the extra chromosome to form an association of 7. The possible zygotic combinations if the $n+1$ gamete had the alternative constitution would be precisely similar.

There are, therefore, two possible types with a maximum association of 5 chromosomes, (2) and (3), and two with a maximum

association of 7 chromosomes, (1) and (4). Trisomics of type (2) should be distinguishable from trisomics belonging to class (3) by the occasional occurrence of 7 closed bivalents and 1 univalent in the former type and the absence of closed rings of four, which should be fairly frequent in type (3). Types (1) and (4) are differentiated by the fact that type (1) will form closed rings of 6 but never closed rings of 4, whereas (4) will form closed rings of four regularly and never closed rings of 6. Actually, the four types of trisomics may be considered as being (1) a double-interchange heterozygote, forming an association of 6 chromosomes with one of these chromosomes duplicated, (2) a structural homozygote with an extra chromosome pairing up with two bivalents, (3) a single-interchange heterozygote, forming an association of four chromosomes with an extra chromosome composed of two of the segments in the ring, and (4) a single-interchange heterozygote forming a ring of four chromosomes with an extra chromosome partly homologous with two of the chromosomes in the ring and partly with a bivalent. In the case of $354^{5/32}$ the evidence is sufficient to show that the trisomic belongs to class (4). Unfortunately, there are not sufficient data to classify $354^{11/32}$ with certainty, but Fig. 6 *k* shows that it must belong to Group 3 or 4, and Fig. 6 *l* in which the extra chromosome seems to be attached to two apparently homologous chromosomes indicate that the plant actually belongs to Type 4 also. It is not yet known which of the chromosomes is in excess in the trisomics, or whether the trisomics have the same or different extra chromosomes. It seems probable from a consideration of the drawings that the extra chromosome is one of the smaller chromosomes DF or EF and since they might reasonably be expected to show non-disjunction more frequently than the larger chromosomes, it is quite probable that the two plants have the same chromosome in excess.

Summary

Some of the progeny of the previously described hybrid with an association of 6 chromosomes were studied cytologically.

Two plants were found to be trisomic and structurally hybrid, one showed normal bivalent pairing and was fertile, one had an association of six and was three quarter sterile, like the parent plant, and two had a new association of 4 chromosomes. The relationship

between the new association of 4 and the original association of 6 is discussed.

The frequent observation of "figure-of-eight" configurations in the association-of-six forming hybrid led to the prediction that plants with associations of four would occur amongst its offspring. Since the present observations fulfil these predictions, they afford genetical evidence that segmental interchange between otherwise non-homologous chromosomes has occurred as the result of crossing-over associated with chiasma formation in an interstitial homologous segment.

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