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ON THE ATTACHMENT OF NON-HOMOLOGOUS CHROMOSOMES AT THE REDUCTION DIVISION IN CERTAIN 25-CHROMOSOME DATURAS

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There are now at least three classes of 25-chromosome Daturas which have been more or less thoroughly studied, both by breeding experiments and by microscopical examination of their chromosomes. Of these, the main class, the *primaries*, come directly from triploids, or from non-disjunction in diploids; they give normally only diploids and primaries like themselves in their progenies; the different groupings of the chromosomes in their trivalents (Fig. 1) are those which would result in random assortment of three homologous chromosomes; they show triploid inheritance of genes in the trivalents, in the two or more cases which have been extensively investigated; non-disjunction is apparently no more abun-

FIGURE 1

Three trivalents of the primary $2n + 1$ mutant, *Rl*, with the extra chromosome in set I. The configurations are: (1) chain of three, (2) open V, and (3) ring and rod. These were drawn with the camera from iron-acetocarmine preparations.

FIGURE 2

Three trivalents of the secondary $2n + 1$ mutant, *Sg*, with the altered chromosome in set I. The configurations are: (1) closed V, (2) ring and rod, and (3) another closed V.

dant than in diploids; and non-homologous chromosomes have not been found attached to one another at the maturation divisions.

The second class of 25-chromosome Daturas, the *secondaries*, occur, as exceptions, in the offspring of the corresponding primaries (and of diploids and, of course, other primaries), they give normal diploids, secondaries like themselves, and the corresponding primaries, in their progeny; the groupings of the chromosomes in their trivalents (Fig. 2) point to one chromosome of the three having two homologous ends (and consequently being probably composed of two homologous halves), so that assortment is not at random; diploid inheritance of genes in the trivalent occurred in the one case investigated;[1] non-disjunction is no commoner than in diploids; and non-homologous chromosomes have not been seen connected.[2] Notwithstanding that one of the three chromosomes of the trivalent differs from the other two, measurements show that the chromosomes of the secondaries do not differ appreciably in size from those of their primaries.

In the third class of 25-chromosome Daturas, only one, *Wy*, has been as yet sufficiently investigated, both as to its breeding and its chromosomes, to allow deductions to be drawn (although some significant data have also been obtained with regard to *Hg*). The following statements then relate, primarily at least, only to *Wy*. This 25-chromosome mutant of the third class occurs in the offspring of a primary, *Pn* (which came from a *Pn* after being crossed with the *B* race of *Datura Stramonium*,[3]); *Wy* gives in its progeny, diploids, *Wy* and *Pn;* in the groupings of the three chromosomes which belong to set IX one of the three is often (in that form of *Wy* which was examined with the microscope) attached to one of the large chromosomes of bivalent I; and thus would not give free assortment nor triploid inheritance; notwithstanding this, the form of *Wy* tested by breeding showed triploid inheritance; non-disjunction was not more abundant than in diploids (but was common in *Nb*); and, as already stated, the non-homologous chromosomes, I and IX, were frequently united.

Hence there are apparently two forms of *Wy;* one which gives triploid inheritance, and one which should give approximately diploid inheritance.

The *Wy* trivalent was, in all cases seen in metaphase, an open V (although one ring and rod was seen in late prophase), but the ring and rod trivalent has been seen in the more or less parallel mutant *Hg*, which also had M-shaped chains of 4 or 5 chromosomes, groupings not yet identified with certainty in *Wy*, though they probably do occur. The trivalents observed and measured in *Wy* were 13 cases of two of the largest chromosomes, set I, forming an unequal V with one of the *Pn* chromosomes of set IX, which latter is only half the size of chromosomes I. This small chromosome was always at one free end of the V, never in the middle. Also there were two cases of an open V of three chromosomes of set IX. Lastly one case was measured where a V consisted of two small chromosomes of set IX, and one large chromosome of set I at a free end of the V.

From the measurements which have been made, it can be concluded that the chromosomes of sets I and IX in *Pn*, *Rl*, and *Wy*, are of the same sizes.

A working hypothesis which may be seen to fit most or all of the facts so far discovered is that in the ancestry of the B diploids there has been segmental interchange between two non-homologous chromosomes. In plants, such segmental interchange probably occurred between two non-homologous chromosomes in the ancestry of *one species* of Stizolobium (Mucuna).[5,6] In crosses between this species and three allied species and varieties, dwarf mutants with peculiar leaves appeared in F_2, in the proportion of about 0.5 per cent.[7,8] Similarly *Wy* might appear in the F_2 of crosses of normal and B diploids. The F_1 plants of the Stizolobium crosses were semisterile, as were also the F_1 plants of the crosses of normal and B diploids in Datura.

The following are the chief points that must be included in any working hypothesis:

(1) The tertiary mutants *Wy* and *Hg* have 25 chromosomes, as counted in the second metaphase.

(2) They show commonly 11 bivalents and one trivalent at the first metaphase.

(3) Non-homologous chromosomes in two particular sets (I and IX in *Wy*) are often or usually combined into trivalents (quadrivalents or quinquevalents). (See Figs. 3 and 4.)

FIGURE 3

Three trivalents from the tertiary $2n + 1$ mutant, *Wy*. The large chromosomes are from set I, while the small one comes from set IX, and is the altered chromosome (9).

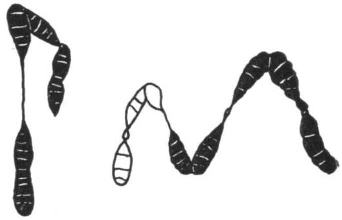

FIGURE 4

Three configurations from the tertiary $2n + 1$ mutant, *Hg*. The large chromosomes belong to set I, and the smaller ones (shown in outline) perhaps to set VI.

(4) In such trivalents the two chromosomes of one set are always together (that is, not separated by a non-homologous chromosome).

(5) Thus the single chromosome of the other set is connected by one end only with the non-homologous bivalent. (Fig. 3.)

(6) Sometimes the three chromosomes of the one set (IX in *Wy*) form a trivalent.

(7) Only one chromosome of the three is ever connected with non-homologous chromosomes.

(8) The open V is the common configuration of the trivalents, but the ring and rod also occur.

(9) The triangle or closed V does not occur.

(10) The three chromosomes (in set IX) are equal in size to the three chromosomes of the primary *Pn* (set IX).

(11) There is no perceptible difference in size or shape between the three chromosomes of set IX in *Wy*.

(12) Thus one of the chromosomes of set IX, in *Wy*, has one end normal, and attracting its fellow of set IX; while the other end is changed so that it attracts one of the ends of chromosome I.

(13) This could have been brought about by segmental interchange, at the constriction of chromosome IX; one-half of this chromosome interchanging with an equal length of chromosome I, in the ancestry of the B diploids.

In addition to these facts, the following data from the pedigreed cultures have to be reckoned with by any hypothesis.

(1) *Pn* may give *Wy* after crossing with the B strain, but without such crossing does not.

(2) Some *Wy* plants throw *Pn*.

(3) Some *Wy* plants give triploid ratios for genes in the chromosomes of set IX.

(4) *Pn* crossed twice by B diploids may give ratios, for genes in the trivalents, which show increase in the number of recessives.

(5) *Rl* after crossing with B diploids, may give ratios for genes in the IX bivalent, which are different to the ordinary diploid ratios.

(6) Crosses between the normal and B strains have given F_1 plants with 50 per cent of the pollen and ovules aborted.

A detailed working out of the hypothesis has shown that both the chromosomal and the cultural data fit the hypothesis tolerably well in most points, though there remain a few seeming exceptions (see note at end of paper). Since this hypothesis fits these facts, it may well be employed until a better is found.

Of the other $2n + 1$ mutants which apparently more or less resemble *Wy*, in the configurations of their chromosomes, viz., *Hg*, *Nb*, *Pk*, *Dv* and *X*; *Hg* has been partially studied (Fig. 4). Its largest chromosomes are larger than No. I. The meaning of this is as yet unknown.

NOTE.—All our primaries as well as the majority of our secondaries have been obtained in a purple-flowered race secured from Washington, D. C., which has been designated Line 1. When these mutants have been rendered heterozygous for certain white lines (called A whites), secured from various sources, they have all thrown disomic ratios; except *Pn* which has thrown trisomic ratios, since the genes for purple and white are located in the *Pn* chromosome. When these same Line 1 mutants are rendered heterozygous for certain other white lines (called B whites), abnormal ratios are thrown by *Rl* and by *Pn* if the latter appears to have the constitution Pp_2. The mutant *Wy* has occurred in the offspring of parents heterozygous for Line 1 and B whites; but never in the offspring of Line 1, of A whites, nor of parents heterozygous for Line 1 and A whites. Crosses between Line 1 and three different B whites have given F_1 plants with normal pollen and ovules.

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REDDISH—A FREQUENTLY "MUTATING" CHARACTER IN DROSOPHILA VIRILIS

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The body-color character "reddish" used in the experiments described below was first found in one of five identical pair matings which were back crosses involving several autosomal characters. Half of the males and none of the females from this pair mating were reddish, indicating that reddish is a sex-linked recessive character and that the parent female was heterozygous for it. Later experiments confirmed this interpretation.

Behavior of Reddish in Crosses with Yellow.—In appearance, reddish is very similar to the sex-linked character yellow body-color which has been known for a long time in Drosophila virilis.[1] Reddish, however, can be easily distinguished from yellow by its brighter color and still better by the color of hairs and bristles which is gray on yellow flies and yellowish on reddish flies.

Because of its similarity to yellow the first cross made with reddish was the cross between reddish and yellow, for the purpose of testing the