[9] These PROCEEDINGS, **4,** 1918 (364–370).

[10] Compare the argument from here on with that on pages 337–339 of my paper, "Concerning simple continuous curves," *loc. cit.*

[11] Mazurkiewicz, S., *loc. cit.*, p. 123.

[12] Cf. Hahn, H., *Wien. Ber.*, **123,** 1914 (2433).

[13] Janiszewski, S., "Sur les continus irreductibles entre deux points," *J. l'Ecole Polytech.* **16,** 1911–1912 (79–170).

[14] Mazurkiewicz, S., *loc. cit.*, p. 129.

THE REDUCTION DIVISION IN HAPLOID, DIPLOID, TRIPLOID AND TETRAPLOID DATURAS

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It is probable that the number and nature of the chromosomes which the zygotic cell of a flowering plant has received from the sperm nucleus and the egg-cell will account for most of the inherited qualities of the resulting plant. Hence an important time in the life history of such a plant is the brief period when the parental contributions to the gametes are being distributed. This period comprises the first division in the mother-cells of the pollen.

In the ordinary diploid Datura, there are visible, at late prophase and metaphase of the first division, 12 pairs of chromosomes, among which at least 6 sizes may be made out.[2] Usually, the two chromosomes of a pair are joined at both ends (diagram 1, middle of second column); but not uncommonly they are connected at one end only,[7] and rarely they are separate. The two members of each pair are, of course, of the same size; the formula for the bivalents being $L_2 + 4l_2 + 3M_2 + 2m_2 + S_2 + s_2$. In the haploid Datura[3] (diagram 1, first column) which has only one group of 12 chromosomes, the chromosomes are usually straight, and single, not in pairs; the size formula being $L + 4l + 3M + 2m + S + s$. In the triploid plants there are 36 chromosomes,[6,9] which form 12 sets of three connected chromosomes each,[8,2] the formula for the trivalents being $L_3 + 4l_3 + 3M_3 + 2m_3 + S_3 + s_3$. Usually there is one pair of chromosomes joined at both ends, as in the diploid plants, with the third chromosome attached by one end to one of the junctions (diagram 1, middle of column 3). Not uncommonly, however, there is a Y-shaped arrangement of the chromosomes, or the 3 chromosomes are joined end to end to form a usually hook-shaped rod. (The two forms at the bottom of column 3 are rare.) Occasionally one (or more) of the single chromosomes or chromosome pairs remains isolated, which is also a not infrequent occurrence in triploid Cannas.[1] In the true tetraploid Daturas, before the first division in the microspore mother-cells, the 48 chromosomes are in 12 sets with 4 connected chromosomes in each,[5] the formula for the quadrivalents being, $L_4 + 4l_4 + 3M_4 + 2m_4 + S_4 + s_4$. (Sometimes one or more pairs, or single chromosomes, remain unconnected.) A common arrangement is that of two pairs, the members of which are connected at both ends, and the pairs secondarily joined at one of these connections, the planes being sometimes at right angles (diagram 1, center of column 4). The two pairs are also often folded to-

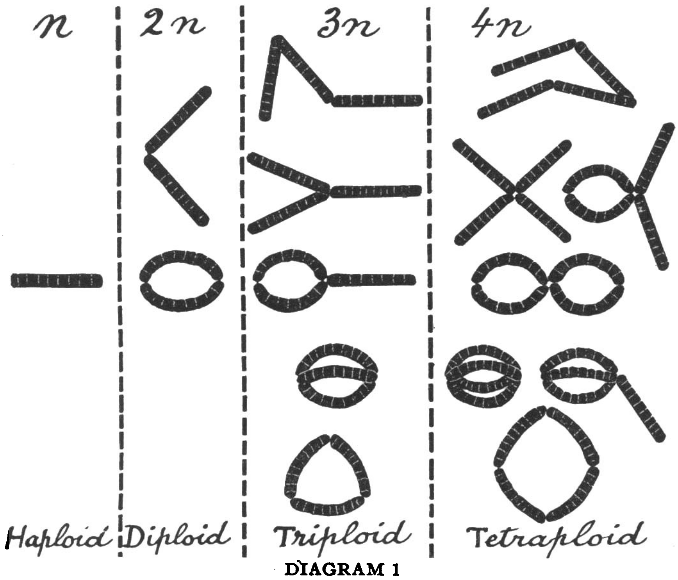

DIAGRAM 1

Arrangement of the chromosomes at the late prophase and early metaphase of the first division in the pollen-mother-cells of Datura Stramonium. (*Column 1*)—Straight chromosome of the haploid plant. (*Column 2*)—In the center, the ordinary pair of two bent chromosomes. Above, the V-shaped arrangement. (*Column 3*)—In the center, the ordinary form of a ring with an attached rod. Above, the less common Y-shaped arrangement, and the not uncommon hooked form. Below are two rare combinations. (*Column 4*)—In the center, the double ring, or figure of 8, the rings of which are often in different planes. Below this, to the left, the combined rings. The other forms are not so common.

gether so as to form a double hoop (diagram 1, column 4, below and to the left of the middle). The other forms are not so conspicuous or not so common.

In the first division in the pollen-mother-cells of the haploid plant, each chromosome moves, apparently by chance, in one or the other direction; so that two groups of 6 + 6, 5 + 7, 4 + 8, etc., are usually formed. After the second division, the resulting nuclei may have 1, 2, 3, 4, 5, etc., chromosomes each. When the cytoplasm has divided, microcytes,[2] or small microspores with deficient numbers of chromosomes, are formed. These diminutive pollen-grains with less than 12 chromosomes apparently lose their cytoplasm and perish.[3] In the diploid Datura, the two chromosomes of each pair pull apart in the usual manner, remaining for some time connected by their ends (diagram 2, column 2). When they have separated

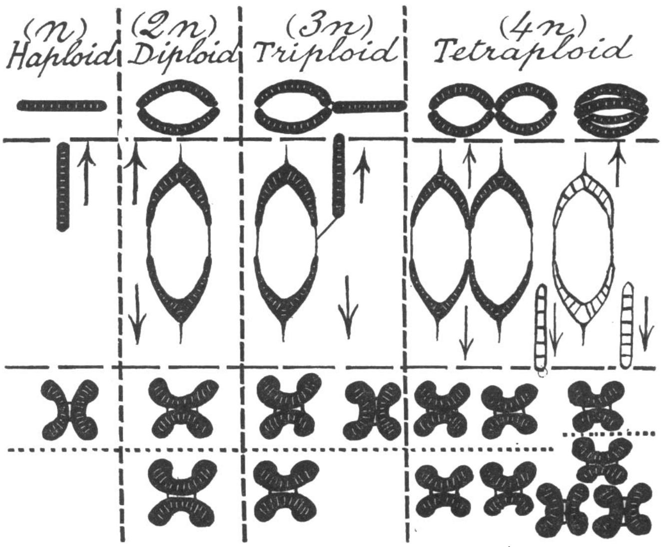

DIAGRAM 2

Arrangement of the chromosomes in the pollen-mother-cells of Datura Stramonium; *line 1*, at the late first prophase; *line 2*, at the late first metaphase or early anaphase; *line 3*, at the metaphase of the second division. (*Column 1*)—Each chromosome of the haploid plant moves in one or the other direction. It splits longitudinally before the second metaphase, the halves being shaped like bent dumb-bells, and the whole forming a pseudo-tetrad, of which there are 1 to 11 in the second-metaphase groups. (*Column 2*)—The chromosomes of each pair in diploid plants move in opposite directions, with about one exception in 2000 cases. They thus form second-metaphase groups of 12 split chromosomes each. (*Column 3*)—The two paired chromosomes of the ordinary trivalent separate regularly, and the odd chromosome goes in either direction, forming second-metaphase groups with from 12 to 24 chromosomes each. (*Column 4*)—The two pairs which usually compose a quadrivalent often separate regularly, giving two chromosomes to each pole. But in about one quadrivalent in 36, the chromosomes probably separate as 3 to 1. Thus, less than three-quarters of the second metaphase groups have 24 chromosomes.

the longitudinal split for the second division becomes obvious. Nondisjunction is normally rare, one case (comprising 3 adjacent cells) having been noted in 500 pollen-mother-cells at normal temperatures. In the pollen-mother-cells of triploid Daturas, the two paired chromosomes of each set usually move towards opposite poles as in diploid plants; and the third chromosome, which was laterally connected, moves to either pole, as in the haploid Daturas. The resulting distribution has been shown[2] to be closely comformable to the laws of chance. Whether non-disjunction is present or not in the triploid plant cannot be told from the chromosome distribution. In the true tetraploid Daturas, two chromosomes, out of the double pair forming a figure of 8, have been seen passing towards one pole, and the other two towards the other pole (diagram 2, column 4). But in one quarter and more of the pollen-mother-cells this regular distribution does not occur with regard to all of the 12 quadrivalents. In one (or more),

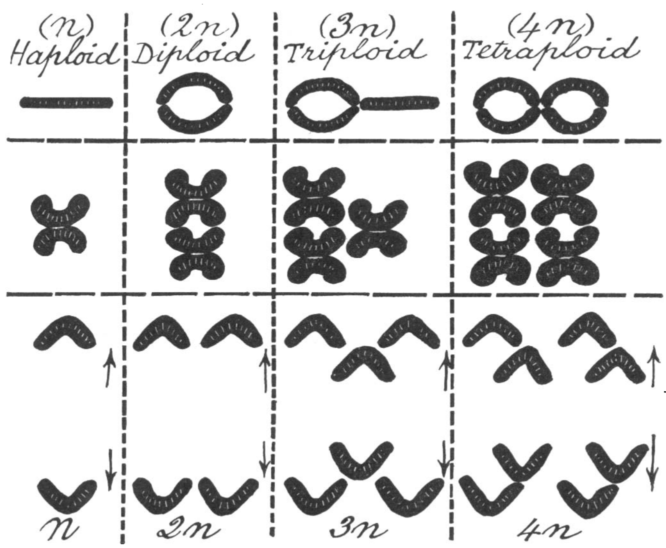

DIAGRAM 3

The results of non-reduction in the pollen-mother-cells of Datura Stramonium. (*Column 1*)—The 12 chromosomes of the haploid plant divide longitudinally, forming pseudotetrads. These separate, as at the second metaphase, forming two pollen-grains with 12 chromosomes each. (*Column 2*)—The 12 bivalents apparently form two pseudotetrads each. These divide, as in the second anaphase, giving rise to two pollen-grains with 24 chromosomes each. (*Column 3*)—Two pollen-grains result, with 36 chromosomes each. (*Column 4*)—Two pollen-grains are formed from each pollen-mother-cell, having 48 chromosomes each.

quadrivalents in such cases of non-disjunction, three chromosomes go to one pole, and one to the other pole. This is known by the results of the division, which give 23 + 25 (or 22 + 26, etc.) chromosomes, instead of 24 + 24, in more than one quarter of the cells. This non-disjunction would occur for the individual quadrivalents, by calculation, in slightly less than three per cent of the possible cases. (The figure in outline in diagram 2, column 4, serves merely to indicate the result, the details being as yet unobserved.) The lower part of column 4, diagram 2, shows the longitudinally split chromosomes prepared for the second division; the total numbers in the mother-cell being on the one hand 24 + 24, and on the other hand either 23 + 25, 22 + 26, 21 + 27, or in one case, 20 + 28.

In non-reduction, the chromosomes at the metaphase, instead of having a reduction division, divide longitudinally, and the two halves separate as in the normal second division, the first (reducing) division being omitted. This frequently occurred in the haploid Daturas examined, and the resulting pollen-grains, with 12 chromosomes each, appeared to constitute the full-sized and unaborted pollen-grains of the haploid plant.[3] In normal diploid Daturas, non-reduction, so far as yet noted, is rare, except after cold; double-sized pollen-grains being formed, presumably with 24 chromosomes each. In triploids, non-reduction has been seen[2] to occur fairly frequently, and the resulting pollen-grains have 36 chromosomes. In true tetraploids, non-reduction is rare, but a 48 + 48 division has been observed in the pollen-mother-cells; and giant pollen-grains of double volume, containing presumably 48 chromosomes, have been seen.

Pollen-mother-cells (microsporocytes) at the reduction division have a volume of cytoplasm, nearly proportional to the number of complete haploid groups of chromosomes which they contain.[4] The following measurements of Datura pollen-mother-cells, between the late first prophase and the second metaphase, show this.

Kind of plant	Number of pollen-mother-cells	Diameters found	Diameters calculated
Haploid..........	100	1.00	1.00
Diploid..........	100	1.32	1.26
Triploid..........	40	1.43	1.44
Tetraploid........	100	1.69	1.59

The fourth column gives the cube roots of 1, 2, 3, and 4. The diameter of the mother-cells in the tetraploid plant is about 6 per cent above the calculated figure.

Summary.—(1) The homologous chromosomes at the late prophase and the metaphase of the first division in the pollen-mother-cells of diploid, triploid, and tetraploid Daturas are connected by their ends.

(2) No chromosomes are connected in the haploid Datura.

(3) There are, as usual, 12 pairs of connected chromosomes in the diploid plant, the connection occurring usually at both ends.

(4) There are 12 trivalents in the triploid plant, there being usually two chromosomes connected at both ends, and one laterally attached, with one free end.

(5) There are 12 quadrivalents in the tetraploid plant; the usual arrangement being two pairs, the component chromosomes of which are joined at both ends, and the pairs connected with one another at one or both junctions.

(6) Non-disjunction, under ordinary conditions, is rare in the diploid, but of regular occurrence in the tetraploid plant, in which it happens in more than one quarter of the pollen-mother-cells.

(7) Non-reduction, at normal temperatures, is rare in the diploid, triploid, and tetraploid, but apparently of regular occurrence in the haploid plants. In this way pollen-grains with the somatic numbers of chromosomes are produced.

(8) The volume of the cytoplasm in the pollen-mother-cells, at the reduction division, is closely proportional to the number of haploid groups of chromosomes present in the cell.

[1] Belling, J., 1921, "The Behavior of Homologous Chromosomes in a Triploid Canna," these PROCEEDINGS, **7**, 197–201.

[2] Belling, J., and A. F. Blakeslee, 1922, "The Assortment of Chromosomes in Triploid Daturas," *Am. Nat.*, **56**, 339–346.

[3] Blakeslee, A. F., J. Belling, M. E. Farnham, and A. D. Bergner, 1922, "A Haploid Mutant in .... Datura Stramonium," *Science*, **55**, 646–647.

[4] Marchal, El., et Em., 1909, "Aposporie et Sexualité chez les Mousses," *Bul. Acad. Roy. Belgique* (Classe des Sciences), **9–10**, 750–778.

[5] Marchal, El. et Em., 1911, "Aposporie et Sexualité chez les Mousses," *Ibid.*, **12**, 1249–1288.

[6] de Mol, W. E., 1921, "Over het voorkomen van heteroploide varieteiten van Hyacinthus orientalis L., in de Hollandshe kulturen." *Genetica*, **3**, 97–192.

[7] O'Neal, C. E., 1920, "Microsporogenesis in Datura," *Bul. Torrey Bot. Club*, **47**, 231–241.

[8] Osawa, I., 1920, "Cytological and Experimental Studies in Morus, with Special Reference to Triploid Mutants," *Bul. Imp. Sericult. Exp. Sta. Japan*, **1**, 317–369.

[9] van Overeem, C., 1922, "Über Formen mit abweichenden Chromosomenzahl bei Oenothera," *Beih. z. Bot. Centralbl.*, **B39**, Abt. 1, Heft I, S. 1–80.

THE VARIATION AND INHERITANCE OF MILK CHARACTERS

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In 1919 the writer spent a year as a guest of Count F. Ahlefeldt-Laurvig at Tranekjaer Castle, Denmark. He had there the opportunity to study daily the remarkable herd of dairy cattle on the manor. The 700 cows are managed and fed uniformly and on a strictly commercial basis. The composition of the herd is unique. It contained originally two breeds, Red Danish dairy cattle and Jersey Cattle. Twenty years ago, Count Ahlefeldt proposed to the Experiment Station of the Royal Veterinary and Agricultural College at Copenhagen to use his herd for a series of experiments to investigate through an extensive control of feeding, growth,