

with so few individuals tested. Aside from these two mutations from this treated capsule and three or four mutations which occurred in F_1 's from a haploid, we have not yet determined any gene mutations in *Datura Stramonium*. There were tested by selfing about 400 individual parents in the F_2 or later generations from the haploid 1A without discovering a single gene mutation.

Following treatment with radium emanation, we have obtained in the offspring from a single capsule—(a) 17.7 per cent chromosomal mutants (chiefly non-disjunctional forms³), a much higher percentage than ever obtained from untreated capsules, the average for over 15,000 offspring being 0.47 per cent; (b) a new compound chromosomal type, Nubbin; (c) two new gene mutants out of 18 individuals tested.

It is our belief that for most, if not for all, of these three types of results, the radium treatment may be held largely responsible.

* Brooklyn Botanic Garden Contributions, No. 49.

¹ Gager, C. Stuart, "Effects of the Rays of Radium on Plants," *Mem. New York Bot. Gard.*, 4, 1-278, 1908. Results also presented before Sect. G, A. A. A. S., Jan., 1907.

² Stein, Emmy, "Ueber den Einfluss von Radiumbestrahlung auf Antirrhinum," *Zeitschr. Indukt. Abstamm. Vererb.*, 39, 1-15, 1922. Also *Ibid.*, 43, 1-87, 1926.

³ Cf. Mavor, James W., "The Production of Non-Disjunction by X-Rays," *Science*, 55, 295-297, 1922.

THE CHROMOSOMAL CONSTITUTION OF NUBBIN, A COMPOUND ($2n + 1$) TYPE IN DATURA¹

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Nubbin is one of the mutant types of the Jimson Weed (*Datura Stramonium*) which has been shown² to have a single extra chromosome. It was found in 1921 among the offspring of a plant which had been treated

TABLE I
OFFSPRING OF NUBBIN, PINCHED AND HEDGE FROM SELFINGS OR FROM BACK-CROSSES
LINE 1. GARDEN RECORDS. FIGURES IN PARENTHESES REPRESENT PERCENTAGES
UNRELATED TYPES IN OFFSPRING NOT SHOWN

TYPES	NO. OF PARENTS	TOTAL	?	$2n$	NB	PH	BK	HO	EC	RL
Nubbin	7	1226	5	668	424	58	9	36	14	...
1923-26				(54.5)	(34.6)	(4.7)	(0.7)	(2.9)	(1.1)	...
Pinched	4	561	13	339	...	180	10	...	1	8
1924-26				(60.4)	...	(32.0)	(1.8)	(1.4)
Hedge	3	689	6	541	121	11	5
1924-26				(78.5)	(17.6)	(1.6)	(0.7)

by Dr. C. Stuart Gager with radium emanation (cf. preceding paper) and has not appeared spontaneously since. Its parent was a normal ($2n$) diploid in line 1 which had been inbred by selfing for nine generations.

Like other ($2n + 1$) forms, Nubbin does not breed true, being not at all transmitted through the pollen and transmitted through the egg cells to considerably less than the 50 per cent theoretically possible. It differs from the other ($2n + 1$) forms in the types which it throws in its offspring as shown in figure 1, in which arrows point to capsules of the types of offspring produced.

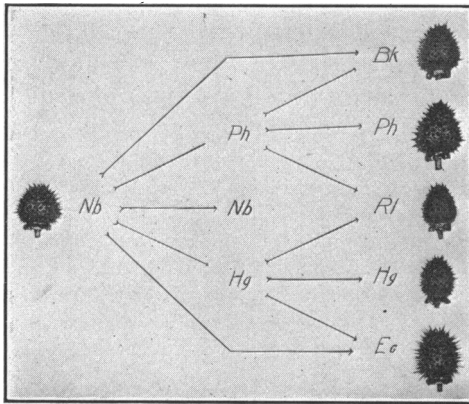


FIGURE 1

Diagram with capsules illustrating the breeding behavior of Nubbin, Pinched and Hedge.

The normal ($2n$) offspring are omitted from the diagram. Nubbin (Nb) regularly throws Nubbins but in addition two other new types with single extra chromosomes, Pinched (Ph) and Hedge (Hg) which have never appeared spontaneously in our cultures. Nubbin also throws a few of the primary ($2n + 1$) types, Buckling (Bk) and Echinus (Ec). Pinched throws Pinched, Buckling and the primary ($2n + 1$) Rolled (Rl) while Hedge throws Hedge, Echinus and Rolled. Table 1

gives the offspring of Nubbin, Pinched and Hedge within line 1.

From the breeding behavior we may conclude that Nubbin cannot be a primary ($2n + 1$) form (5, 6) in which the extra chromosome is similar in makeup to the other two members of the set since (a) primary types do not regularly throw other specific mutants and (b) primaries are regularly thrown by triploids while Nubbin is not. Furthermore, Nubbin cannot be a secondary of the ordinary type since secondaries throw their own primaries alone in any regular proportions.

Buckling bears the same relation to Pinched that Echinus does to Hedge. Buckling and Echinus are both thrown by Nubbin and hence bear the same relation to Nubbin.

Could the occurrence of Pinched and Hedge be explained in some other way, the fact that Nubbin throws both Buckling and Echinus might lead us to consider it a double mutant, Echinus-Buckling, with an extra chromosome in both the Echinus and in the Buckling set. Even if the chromosomal counts could allow Nubbin to be considered a ($2n + 1 + 1$) mutant, the proportion of types in its offspring is unlike that from a double

mutant. In the progeny of Echinus-Buckling, diploids, the two ($2n + 1$) types and the double type average a rough approximation to a 6:2:2:1 ratio. Echinus-Buckling throws fewer double mutants than it does the simple mutants—Echinus and Buckling—while Nubbin throws more Nubbins than it does Buckling or Echinus types.

From figure 1 it will be seen that although Nubbin itself does not throw Rolled, it is related in some way to Rolled through the fact that both the reciprocal mutants, Pinched and Hedge, throw Rolled. Pinched and Hedge are also morphologically related reciprocally to the two secondaries of Rolled, as will be shown later. Nubbin is related to Rolled in still another way through its behavior when heterozygous for "B" whites. It has been pointed out that when all the primary ($2n + 1$) types are rendered heterozygous for certain white-flowered lines, called "A" whites

Strawberry BUCKLING Maple

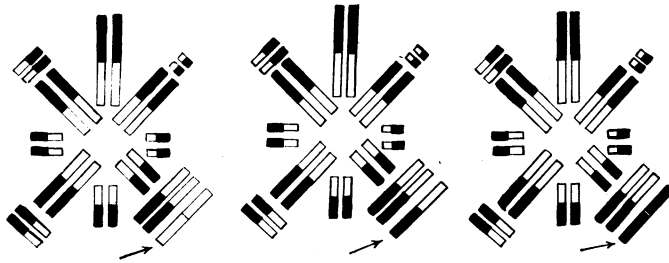


FIGURE 2

Chromosomal diagrams of types in the Buckling group. Buckling is the primary, Strawberry one of its secondaries and Maple probably the other secondary.

the mutant type Poinsettia alone gives trisomic ratios in its offspring, indicating³ that the factors for purple and white are located in the Poinsettia chromosome. When, however, these same primaries are heterozygous for certain other white lines called *B* whites, trisomic ratios are thrown by Rolled as well as by Poinsettia. The responsibility for the ratio abnormalities has been traced to the Rolled chromosome⁴ and a hypothesis in explanation has been offered by the cytological investigations of Dr. Belling.² It will be sufficient to state that Nubbin when heterozygous for *A* whites gives normal disomic ratios while, when it is heterozygous for *B* whites, it throws a considerable excess of whites in its offspring.

Before discussing the morphology of Nubbin, it will be necessary to point out some of the characteristics of the related types. The distinction between primaries and secondaries has been discussed in earlier publications.^{5,6}

The Buckling Group consists of the primary Buckling and of the secondaries Strawberry and Maple. The extra chromosome in Buckling is like the other two members of the Buckling set. In the secondaries, however, the extra chromosome is a double half chromosome. Speaking in terms of the conventionalized diagrams of figure 2, the extra chromosome of Strawberry is made up of two "white" halves while the extra chromosome of its complementary secondary is made up of two "shaded" halves. It is for this reason that in this as in other groups the primary is intermediate in characters between its two complementary secondaries, having extra both a white and a shaded half. The secondaries, on the other hand, are extreme in certain characters having the factors in one half chromosome doubled and the factors in the other half as in normal $2n$ plants. By taking stock of the peculiarities of the three types in this group we can learn what are the aggregate of factors not only in the whole Buckling chromosome but also in its two halves. Thus we conclude that the Strawberry half of Buckling contains factors tending to make the plant erect, and the leaves relatively narrow, while the Maple half of Buckling contains factors for spreading habit and broad leaves. The primary Buckling is intermediate in respect to all these characters as well as others not mentioned.

The Rolled Group consists of the primary Rolled and its two secondaries Sugarloaf and Polycarpic, while the *Echinus Group* consists of the primary Echinus and its secondary Mutilated.

Nubbin has distinctly dimorphic pollen due to lack of starch in half the grains as have also only Echinus and its secondary Mutilated. It must, therefore, possess in excess either an Echinus whole chromosome or its Mutilated half, in which the factor or factors for the dimorphism are located. If an extra whole Echinus chromosome is present, there must also be an extra whole Buckling chromosome since these two primaries have the same relation to Nubbin. This would make Nubbin morphologically the double mutant, Echinus-Buckling. The morphology as well as the breeding behavior shows that Nubbin cannot be Echinus-Buckling.

Since a whole extra Echinus chromosome is ruled out, Nubbin must contain the Mutilated half chromosome in excess since both Mutilated and Nubbin have dimorphic pollen. Nubbin is much more vigorous in growth than the mutant Mutilated which has as its extra chromosome two similar halves containing the factors for dimorphism. Hence, Nubbin can contain, at most, a single Mutilated half chromosome in excess, otherwise the plant would be more severely unbalanced. Possessing an extra half chromosome of Echinus, Nubbin should be expected to throw a certain proportion of this primary as does also the secondary Mutilated. We have apparently discovered the chromosomal component responsible

for the dimorphic pollen in Nubbin and for the relation which Nubbin bears to the primary Echinus. By a similar line of argument, taking into account the fact that the capsule of Nubbin most nearly resembles that of Strawberry, it can be shown that a single Strawberry half of the Buckling chromosome is in excess in Nubbin.

Morphologically, therefore, Nubbin seems to be $2n + \frac{1}{2}$ Mutilated + $\frac{1}{2}$ Strawberry. Its pollen dimorphism and thickish leaves come from the Mutilated component while its capsule shape and erect habit come largely from the Strawberry component.

In considering Nubbin to be morphologically $2n + \frac{1}{2}$ Mutilated + $\frac{1}{2}$ Strawberry, as we are forced to do, we have not explained the relation of Nubbin to Rolled nor to Pinched and Hedge. The Rolled chromosome has been determined by Dr. Belling to be distinctly the largest of the twelve⁷ and either half as well as the whole chromosome has a very distinct effect upon the appearance of a plant when present in excess. It seems clear that morphologically Nubbin does not contain an extra Rolled chromosome nor an extra half of this chromosome. A way out

of the difficulty may be found by a consideration of the morphology of the reciprocal types—Pinched and Hedge.

Pinched strongly resembles Sugarloaf, the secondary of Rolled, and less markedly Strawberry, the secondary of Buckling, and is judged to have in its extra chromosome the Strawberry half of the Buckling chromosome

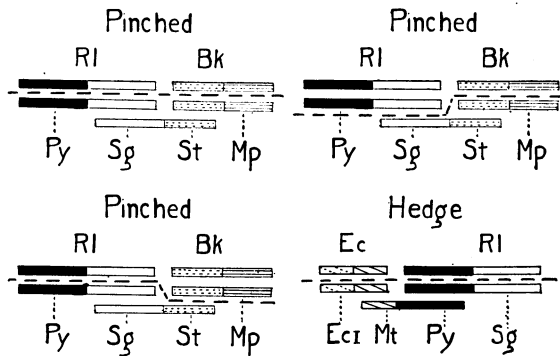


FIGURE 3

(a) above, left. Diagram of chromosomes in Pinched. The dotted line represents the disjunction at reduction which leads to the formation of $1n$ and Pinched eggs and pollen grains.

(b) lower, left. Dotted line represents disjunction leading to formation of $(n + 1)$ Buckling and $1n - 1Bk + \frac{1}{2}St \frac{1}{2}Sg$ eggs and pollen grains. The latter cells, since they lack a half of the Buckling chromosome, would probably die and be represented by aborted ovules and pollen grains.

(c) above, right. Dotted line represents the disjunction leading to formation of $(1n + 1)$ Rolled and $1n - 1RI + \frac{1}{2}St \frac{1}{2}Sg$ eggs and pollen grains. The latter cells die.

(d) lower, right. Diagram of Hedge. $Ec II$ is the half of the Echinus chromosome opposite to Mutilated. The dotted line represents the disjunction leading to formation of $1n$ and Hedge eggs and pollen grains. Rolled and Echinus eggs and pollen grains would be formed by a type of disjunction similar to that shown in figure 3, (b) and (c), for the formation of Rolled and Buckling gametes in the mutant Pinched.

joined to the Sugarloaf half of the Rolled chromosome, justifying the chromosomal formula $2n + \frac{1}{2}St \frac{1}{2}Sg$. Chromosomal diagrams are given for Pinched (Fig. 3) showing the probable method of disjunction leading to the formation of Buckling and Rolled egg cells and pollen grains.

Similarly Hedge shows resemblances to Polycarpic, the secondary of Rolled (complementary to Sugarloaf) and also to Mutilated, the secondary of Echinus. It is believed to have in its extra chromosome, the Mutilated half of the Echinus chromosome joined to the Polycarpic half of the Rolled chromosome justifying the formula $2n + \frac{1}{2}Mt \frac{1}{2}Py$ (Fig. 3).

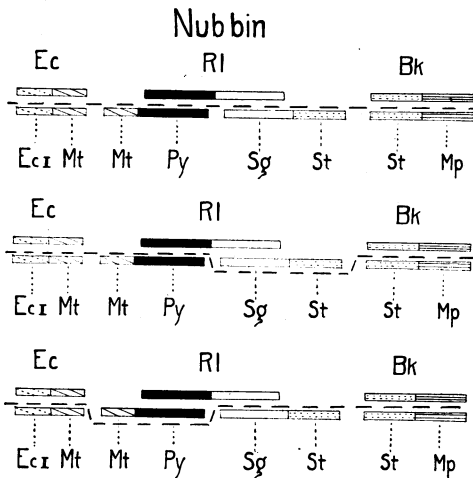


FIGURE 4

(a) Above. Diagram of chromosomes in Nubbin. The horizontal dotted line represents the disjunction which leads to the formation of In and Nubbin ($In - 1RI + \frac{1}{2}Sg \frac{1}{2}St + \frac{1}{2}Mt \frac{1}{2}Py$) eggs and pollen grains.

(b) Middle. The dotted line represents the disjunction which leads to the formation of Pinched and In ($In - 1RI + \frac{1}{2}Mt \frac{1}{2}Py$) eggs and pollen grains. The latter cells, since they lack the Sugarloaf half of the Rolled chromosome, would abort.

(c) Below. The dotted line represents the disjunction which leads to the formation of Hedge and In ($In - 1RI + \frac{1}{2}St \frac{1}{2}Sg$) eggs and pollen grains which latter cells would be expected to abort. Buckling and Echinus, but not Rolled, gametes could be formed by a type of disjunction indicated under Pinched and Hedge.

Nubbin may be considered to be compounded of Pinched and Hedge, having as extras both the Pinched and the Hedge compound chromosome (which together furnish the two opposite halves of the Rolled chromosome), and lacking a single whole Rolled chromosome. Morphologically, therefore, Nubbin should show no Rolled characters since it would possess the factors of only two Rolled chromosomes. Its chromosomal formula may be written $2n - 1RI + \frac{1}{2}St - \frac{1}{2}Sg + \frac{1}{2}Mt \frac{1}{2}Py$. Chromosomal diagrams (Fig. 4) are given for Nubbin, showing its probable constitution and the methods of disjunction that might lead to the formation of

Normal, Nubbin, Pinched and Hedge gametes.

Normal, Nubbin, Pinched and Hedge gametes.

For each Pinched and Hedge pollen grain formed by Nubbin, there could be expected an aborted grain. The fact that Nubbin shows about 13 per cent aborted pollen grains while Pinched and Hedge show only about 7 per cent⁸ is in agreement with the arrangement of chromosomes

shown in the diagrams and with the breeding behavior shown in table 1. The diagrams are also in accord with the attachment of non-homologous chromosomes shown by Dr. Belling² for Nubbin and Pinched and Hedge.

The only fact so far discovered which seems to be in conflict with our interpretation of the chromosomal constitution of Nubbin, Pinched and Hedge is the lack of strong pollen dimorphism in Hedge which is believed to contain in excess the Mutilated half of the Echinus chromosome. The majority of the chromosomes must favor starch production since in diploids and in all primary ($2n + 1$) types, except Echinus, all the pollen grains contain an abundance of starch. It is not unreasonable to assume, therefore, that the Polycarpic half of the Rolled chromosome may contain starch-favoring factors antagonistic to those in the Mutilated half of Echinus which are responsible for the reduction of starch.

The present paper presents in brief a method of analysis as well as contributes to the solution of a special problem in *Datura*. A fuller treatment of the subject will be given in another publication.

Reference has been made to investigations in progress as to the nature of "A" and "B" white lines. In addition certain lines when crossed together produce F_1 's with a definite proportion of aborted ovules and pollen grains.⁹ It is believed that responsibility for the peculiarities of these races may be laid to chromosomal changes similar to those which appear to have occurred in the production of Nubbin.

¹ Abstract of paper presented before the International Congress of Plant Sciences, Aug. 18, 1926, awarded the A. Cressy Morrison Prize No. II of the New York Academy of Sciences, December 20, 1926.

² Belling, J., and A. F. Blakeslee, 1926, these PROCEEDINGS, 12, 7-11.

³ Blakeslee, A. F., and M. E. Farnham, 1923, *Amer. Nat.*, 57, 481-495.

⁴ Blakeslee, A. F., 1924, quoted in *Yearbook of Carnegie Institution of Washington*, No. 23, pp. 24-27.

⁵ These PROCEEDINGS, 1924, 10, 109-116.

⁶ Belling, J., and Blakeslee, A. F., 1924, these PROCEEDINGS, 10, 116-120.

⁷ Belling, J., quoted in *Yearbook of Carnegie Institution of Washington*, No. 23, 1924, pp. 28-30.

⁸ Blakeslee, A. F., and Cartledge, J. L., 1926, these PROCEEDINGS, 12, 315-323.

⁹ In press, *Proceedings of International Conference on Flower and Fruit Sterility*.