I. A Study of Certain Floral Abnormalities in Nicotiana and their Bearing on Theories of Dominance

Orland E. White

When Mendel’s law was rediscovered, dominance was considered as essential and as important a principle as segregation. Further investigation soon demonstrated the phenomenon of "imperfect dominance," and still later studies led to a substitution of the "presence and absence" factor hypothesis for Mendel’s conception of contrasted character pairs. De Vries (1902), Bateson (1909), Davenport (1910), Castle and others lock upon dominance as an attribute of the factor or determiner, and according to the last two investigators, variation in dominance, at least in part, is the result of variable potency, or variation in the power of a determiner or factor to express itself in ontogeny. De Vries held the racially older characters to be dominant over the younger, a conception which the last ten years of experimental investigation has not upheld. On the other hand, East (1912) and Emerson (1912) think of dominance as a result of the activities of one or more specific factors, plus the modifications produced by the whole factorial organic complex (all the other factors concerned in the organism’s heredity) and by the external environment (climate, soil, etc.). In other words, under identical genotypical and external environments, the factor A would always give the same expression, no matter how often the experiment was repeated.

The chief value of the data which I have to present lies in its bearing on this important question of dominance. The abnormalities concerned are three in number, viz., petalody and pistillody of stamens and that peculiar form of corolla doubling to which de Vries and others...
apply the term catacorolla. The data on each are given in some detail, followed by a short discussion and summary.

The work was done in the Laboratory of Genetics, Bussey Institution of Harvard University, under the direction of Prof. E. M. East, for whose kindly interest and criticism, I wish to express my appreciation.

The material was obtained from various pure line cultures of *Nicotiana* species, which had been under observation for several years. All pure species used in this study bred comparatively true and no abnormal variations appeared in them, except in *Nicotiana langsdorffii grandiflora*, which was subject to petalody, and gave evidence of being a hybrid as it was heterozygous for yellow and blue pollen, the true form according to Comes (1899) having only blue pollen.

1. Petalody

This teratological character is an extremely common feature of garden flowers, and, as usually found, is variable even among the stamens of the same flower, *i.e.*, one stamen may possess it, or it may be present in two, three, four or all of them. On one stamen, the petal-like outgrowth from the filament, which constitutes the character, may be very small, while another filament in the same flower may show an anomalous enlargement from three to ten or twelve times as great. It presents its extreme form in the common double-flowered races of *Dianthus, Rosa, Prunus* and *Ranunculus*. The majority of gardeners as well as many scientists believe that such double-flowered races can be created from single-flowered varieties by selection. A very excellent treatment and historical résumé of this subject is given by de Vries (1906, Chap. 17) in which he produces historical proof that many of our common double-flowered races arose suddenly and in full possession of their peculiar character. His experimental studies led him to assign doubleness because of its variability, to the category of "ever sporting" characters. In many of our cultivated races, double-flowered plants quite faithfully reproduce themselves if they are fertile at all. The majority of these races have arisen as mutations, the causal factors of which are largely unknown. Among horticulturists the belief is prevalent that intense cultivation is responsible for the anomaly, but there are no data from controlled experiments to support such a belief. Peyritsch (Goebel 1900, I, p. 195) induced all degrees of doubling in the floral organs of
Cruciferae by artificial parasitization with Phytoptus, and, according to Hus (1908), Molliard caused the formation of double flowers by mechanical irritation. From these facts, one may conclude that double flowers may result from many different causes.

In Nicotiana, petalody arose in at least two dozen plants of four or five hybrid families on which observations were being made for other purposes. The pure species from which these hybrids were derived, while under observation for five years, never developed petalody. Further, this abnormal condition was never observed in F₁ hybrid generations, although thousands of flowers were examined.

Two of these abnormal plants were self-fertilized, and the progeny, grown under approximately the same environment as the mother plant, reproduced the character, showing it to be a hereditary and not an induced phenomenon. One of the races was derived from an F₂ segregate of N. langsdorffii × N. forgetiana. The expression of the character in the stamens was very variable. Table 1 gives a general idea of the extent of this variability among the different flowers of the mother plant. The progeny, over 100 in number, all possessed the abnormality. The throats of the corolla tubes in some plants were, however, almost packed with anomalous stamens; while in others, perhaps only a single stamen was malformed. An examination of the progeny plant by plant for differentiating characters showed that segregation in flower color, habit of plant, leaf shape, etc., had occurred, indicating that the mother plant was heterozygous for a large number of factors.

The other race of these anomalous stamen-bearing plants was derived from selfed seed of a plant which appeared to be N. langsdorffii grandiflora. The variability of the abnormal character is shown in Table 2. In 1912 under the same field conditions, 70 plants were grown from selfed seed of this mother plant. The inspection of these 70 plants showed the parent to have been homozygous in all its

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<th>Table 1</th>
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<tr>
<td>Number of affected stamens per flower</td>
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<td>Number of flowers</td>
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<th>Table 2</th>
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<tr>
<td>Affected stamens per flower</td>
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<tr>
<td>Number of flowers</td>
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grosser morphological features, excepting pollen color. Habit, foliage, height and floral characters were in all plants practically of the same type and no evidences of a difference in genotypical constitution were to be observed except for the case mentioned. The anomaly expressed itself to about the same degree in all 70 plants, and had I desired to begin selection work toward securing a double-flowering Nicotiana, one plant would have been as good a starting point as another.

Summarizing these facts, one finds that where the anomalous race was heterozygous in many characters, the expression of petalody was extremely variable; while in the race largely homozygous, practically no variation in the abnormality was noted.

2. Pistillody

This anomaly consists of the presence of small pistils in connection with the anthers. Sometimes these little pistils amount to no more than a style and a stigma; at other times, the anther or pollen-sacs may be partly changed into carpels and rudimentary ovules produced. Occasionally such ovules are fertile and produce seeds. An examination of the literature on the subject shows the character to be neither common nor rare. Usually it is so small and inconspicuous that it passes unnoticed, but in the opium poppy, it is showy and characterizes a distinct horticultural variety. *Papaver somniferum* var. monstruosum or var. polycephalum, as it is sometimes called, affords the material for a very interesting chapter on pistillody in “Species and Varieties, their Origin by Mutation” (de Vries, 1906, Chap. 13). The writings of Masters, DeCandolle, and Hofmeister also contain valuable information on this subject. Masters considered the anomaly to be an accidental phenomenon, while DeCandolle in his Prodromus described pistilloid wall flowers as a distinct variety. The pistilloid poppy is at least a century old, and was grown as a field crop in Europe, being especially valuable because its anomalous condition did not allow the capsule to open and scatter the seed. De Vries (1906, pp. 369–99) found these poppies, in respect to their chief peculiarity, very sensitive to environment, especially during the first two to five weeks of their seedling stages. By manipulating the soil conditions at the proper time, he was able to increase and decrease the anomalous expression. Plants almost normal and those extremely abnormal were produced in this manner. Selection had no permanent effect
on its expression. De Vries classified it as an "eversporting" variety. Although it was possible almost to destroy the character or inhibit the expression of its hereditary elements by modifying the environment, it was never absolutely eliminated by this treatment. In addition to the action of the external surroundings, internal factors must have had some part in making this an extremely sensitive character, because poppies, like corn, are cross-fertilized, and hence are more or less heterozygous, and, while the external conditions are no

![Nicotiana flower showing pistillody.](image)

**Fig. 1.** *Nicotiana* flower showing pistillody.

... doubt very important for the characteristic development of the anomaly, the eversporting condition one may ascribe at least partially to the effect of segregating genes.

The race of pistilloid *Nicotianas* with which I experimented originated from the guarded seed of a single anomalous mutant which was discovered among the segregates of an F₂ generation from *N. langsdorffii* × *N. alata*. Two or three hundred of these F₂ plants
from the same cross were grown, but no other pistilloid mutant was found among them. The plant was designated (-2-1A) and in all subsequent experiments will be known under this number. Over 110 of its flowers were examined, all of which showed the character in each stamen, although there was considerable quantitative variability. No semblance of an ovary in connection with the pistilloid stamens was found in these -2-1A flowers, although this occurred in its descendants. Cuttings of the mutant were made, and selfed seed procured from which 90 offspring were obtained, 72 of which reproduced the character in all faithfulness, and were in all apparent respects like the parent. Eleven of the progeny developed flowers with only two or three or at most four pistilloid stamens, and in these, the anomalous pistils were much smaller than those of the original (-2-1A) or of its 72 offspring. Seven of these offspring entirely lacked pistilloid stamens. At first, such a state of affairs was very puzzling, as the possibility of technical error was not taken into consideration. However, there were sap-colored flowers among the progeny, which was
very surprising, inasmuch as the hybrid family had contained only cream and white-flowered plants even to the grandparental generation. Table 3 shows the ratio of white to colored plants and their stamen character.

<table>
<thead>
<tr>
<th>Color</th>
<th>Pistillody</th>
<th>Pistillody not fully expressed</th>
<th>Normal</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>White</td>
<td>71</td>
<td>10</td>
<td>7</td>
<td>81</td>
</tr>
<tr>
<td>Colored</td>
<td>1</td>
<td>1</td>
<td>7</td>
<td>90</td>
</tr>
</tbody>
</table>

When I found that some of the progeny with sap-colored (magenta, etc.) flowers possessed pistilloid stamens, I was more puzzled than ever, because I had already found it to be completely recessive in the crosses I had made. When the conception of dominance and recessiveness as characteristics, not of the unit "character" or factor alone, but of the latter plus the effect produced upon it by its internal (genotypical) and external environments, was brought to bear upon the problem, the explanation was simple, especially as 90 F₁ and 381 F₂ progeny of a cross between -2-1A and 321 (N. alata) had given nothing but white-flowered plants. During the winter I had been working with many colored-flowered F₂ segregates of N. forgetiana (314) X N. alata (321) and had not been careful enough about cleaning my pollenizing tools before selfing the flowers on the cuttings of the original (2-1A) mutant, and, as a result, a few hybrid seeds were produced. Pistilloid stamens in the colored-flowered plants were due to dominance, complete in one case and partial in the others, of the anomalous condition over that of the normal. In the other 7 progeny with colored flowers, the expected condition, i.e., the dominance of the normal, prevailed. Probably all 18 progeny belonging to the normal and intermediate classes were hybrid. Further experiments are in progress to determine this. The change in dominance is not thought to have any special connection with the color factors, but is interpreted in the same manner as the anomalous results secured in some of my unpublished studies on fasciation, viz.: the modifying influence of other factors. The 18 plants which were causing confusion had, in the majority of cases, a very different and distinct habit from the original pistilloid mutant, and this was especially true of the plants with colored flowers. The 72 or more pure abnormal (2-1A) progeny were very similar in habit, flower color and other characters, so much so that I
inferred that the parent plant (2-1A) had been largely homozygous in its genotypical constitution.

From the cross referred to above (2-1A X 321), 90 F₁ progeny were grown, all of which were intermediate in both habit and in size of floral organs, but absolutely normal as regards pistillody. Two of these were selfed and F₂ progeny grown. The results are tabulated in Table 4.

<table>
<thead>
<tr>
<th>Pedigree</th>
<th>Normal</th>
<th>Abnormal</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>(394 X 321) — 2 — 1A X 321 — 1</td>
<td>103</td>
<td>82</td>
<td>185</td>
</tr>
<tr>
<td>(394 X 321) — 2 — 1A X 321 — 2</td>
<td>152</td>
<td>42</td>
<td>196</td>
</tr>
<tr>
<td>Total</td>
<td>257</td>
<td>124</td>
<td>381</td>
</tr>
<tr>
<td>Expected</td>
<td>285.75</td>
<td>95.25</td>
<td>381</td>
</tr>
<tr>
<td>Deviation</td>
<td>-28.75</td>
<td>+28.75</td>
<td></td>
</tr>
</tbody>
</table>

One family (-2) gave a fair approximation to the 3:1 ratio, but the other had a large excess of abnormal segregates, which I am at present unable to account for, because the two families were grown from the same grandparental stock, and under the same external environment. Many other characters of a structural nature had segregated in this F₂ generation, and the variation in the expression of the anomaly was large. Many plants were as abnormal, and many much less so than the grandmother. Other abnormalities appeared, both in pistillloid and normal segregates. Split corolla tubes and 3- to 4-loculed ovaries were not infrequent. Some of the segregates, as well as a number of the pure line (?) progeny, possessed flowers with pistillloid anthers containing numerous small ovules. Where these occurred, the pollen-sacs were deformed, sterile, and usually the ovules were exposed, owing to hypertrophy of the anther-sac walls.

3. Catacorolla

This is not an uncommon anomaly, and hereditary races of it have long been known, e.g., hose-in-hose primula, and a garden variety of gloxinia, first described by Prof. E. Morren (see Masters, 1869, pp. 451-52, figs. 213-14). Catacorolla has been exceedingly well described by both Morren and Masters, so I shall not take the space here for a general detailed description, but confine myself to the form it takes in the particular race with which I worked. This race (4-1A) is descended from a single plant which possessed the catacorolla
peculiarity to a more marked degree than any other one of the 15 anomalous plants which appeared in a family of 50 F2 segregates from a cross between *N. langsdorffii* × *N. alata*. In fact, this hybrid family was derived from the same grandparental cross as that in which the pistillloid mutant occurred. Instead of a bud mutation occurring shortly after fertilization, as was probably the case with the homozygous pistillloid character (-2-1A), this catacorolla mutant (-4-1A) must have originally arisen as a change in the gametes of one or the other of the grandparental types or in the cells concerned in their ontogenesis, if we are to interpret the succeeding experimentally obtained results in accordance with our general knowledge of heredity. In the F2 generation grown from guarded F1 seed from a cross between two normal individuals occurred a segregation of 15 anomalous and 35 normal plants, making a ratio of 7 normal to 3 abnormal or 2.33 : 1. Supposedly the abnormals would have all bred true, for the one plant (-4-1A) which was selfed produced 20 progeny all of which faithfully repeated the parental peculiarities in respect to catacorolla, habits of growth, character of foliage, size and color of flowers, and color of pollen. It is not supposed that only one “altered” egg cell or pollen grain was necessarily produced in attempting to explain the place in ontogeny at which this mutation arose. Possibly many were formed as the result of a prematuration mutation, but if such were the case, and if they united with unaltered gametes, the resulting seeds possibly were not planted, or if planted, only one F1 plant of this sort chanced to be included in those selfed for further propagative purposes.

Catacorolla in this race is typical of the anomaly as it appears in other plant species. Petalloid segments are produced outside the ordinary corolla, and partially adhere to it, these segments having colored outer and plain green inner surfaces. In other words, the normal corolla appears to have been separated at some time during its ontogeny into five segments. Later when these fused to produce the normal gamopetalous *Nicotiana* flower, the union appears not to have taken place through the careful growing together of the edges of each segment, but on the contrary, to have been brought about in such a manner as to leave a seam like that made by a tailor. At the point of union of two segments, there is a slight waste of material, and it is this which is reflexed back in the mature flower and gives the catacorolla effect. The segment then is really a piece of left-over petal. In some flowers, the petaloid segments are not united with the normal
corolla except at their bases, and, in such cases, other factors have interfered and effected a distinct separation. The anomalous character, then, is the result of imperfect fusion of the corolla segments in ontogeny. This theory is further supported by the relation that exists between the number of normal corolla lobes and the number of extra-corolla segments. Table 5 shows the character of this relationship in 28 flowers taken from the original parent (-4-1A).

**Table 5**

<table>
<thead>
<tr>
<th>Number of segments per flower</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of flowers</td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>9</td>
<td>5</td>
<td>3</td>
</tr>
</tbody>
</table>

*Fig. 3. “Catacorolla.” Nicotiana flowers from the parent plant of the -4-1A race, showing variation in the expression of the anomaly.*
A more extended investigation from the standpoint of anatomy and morphology is necessary before such a theory can be demonstrated as a truth. The fact that six extra-corolla segments are sometimes present can be explained by supposing that two segments sometimes result from a single "seam." The size of these segments varies from a slender, thread-like structure to one as broad as the normal lobe. In some flowers they fuse and produce a supernumerary corolla. This variability is characteristic of the race as a whole, i.e., some plants are not more variable than others, so that the character may be said to be eversporting only in the sense that a single plant may possess both very abnormal and slightly abnormal flowers.

Several series of hybridization experiments are in progress, but they have reached only the F₁ stage. The most interesting of these experiments relates to a study of the dominance and recessiveness of catacorolla. In addition to the selfed seed produced by the parent
(-4-1A) plant, a large amount of "open field" seed was gathered from it. Thousands of hybrid F2 segregates of various crosses such as N. forgetiana X N. alata and N. alata X N. langsdorffii were grown in the same field, and in the same year as the -4-1A parent. These were all normal in respect to catacorolla, excepting the 15 plants already mentioned. Cross-fertilization was more favorable to the production of seed on this one (-4-1A) selection than self-fertilization. This means that the open field seed would produce largely hybrid F1 plants. One hundred and sixty-two plants grown from this seed gave 43 homozygous 4-1A progeny and 119 hybrid F1 progeny, the latter representing almost as many different F1 combinations as there were individuals. As a consequence, they were extremely variable in almost every taxonomic feature,—in habit, height, foliage; in flower color, size and shape; in pollen color, and in many other less prominent characters. Sixty of the 119 were colored, and 59 were white. Some of the flowers were as small as those of N. forgetiana, while others were as large as those of N. alata. Fig. 4 is an attempt to show something of these differences in flower size, as well as in the variability of the catacorolla character. Each flower represents a single plant. The F1 variation in the expression of the catacorolla was remarkable. Supposedly each of the 119 plants represented a different genotypical complex, and hence one would, on the conception of dominance supported by East, expect a great deal of variability. Table 6 shows the results of classifying the whole 162 progeny by color and by their expression of the anomaly.

<table>
<thead>
<tr>
<th>Color</th>
<th>4-1A Pure Homozygote</th>
<th>Hybrids</th>
<th>Normal</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>White</td>
<td>43</td>
<td>33</td>
<td>26</td>
<td>102</td>
</tr>
<tr>
<td>Colored</td>
<td></td>
<td>11</td>
<td>49</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>43</td>
<td>44</td>
<td>75</td>
<td>162</td>
</tr>
</tbody>
</table>

Those classified as normals showed absolutely no expression of the character.

Guarded crosses were made between the -4-1A and -2-1A strains. The genotypical constitutions were very difficult, as each had a distinct growth habit, leaf size, etc. About 150 F1 plants were grown in the same field and under approximately the same conditions as the other "catacorolla" cultures. In this cross, the F1 expression of catacorolla was intermediate, with a fluctuation towards complete
dominance of the normal, although never approaching that state. The pistillody was absolutely recessive.

4. Discussion and Summary

1. Nicotiana plants showing petalody were selfed and progeny grown from them. In one race the abnormal character was extremely variable, some plants showing a large expression, other plants showing it only to a slight degree. This race varied in many other characters, proving the mother plant to have been very heterozygous. In another race, the abnormality was reproduced in all the progeny to the same degree as in the mother plant. With the exception of pollen color, no variation in other characters occurred in this race.

2. Pistillody originated as a discontinuous variation and was inherited in the same manner, crosses with the normal in one case giving in F2 a progeny closely approximating a simple 3:1 ratio. In two hybrid F1 families, it was completely recessive, while in what appears to be another hybrid F1 family, it is wholly dominant. The first two families differ from the last family in a large number of characters, as the ancestry of the latter involves another species.

3. The catacorolla race of Nicotiana originated from a discontinuous variation. When crossed with normal races, the F1 progeny were either intermediate in character or absolutely normal, though the individual F1 progeny from each cross showed no variation among themselves. Great variation existed between the different pollen parents of many of these F1 individuals.

As a whole, the data secured from hybridizing races of normal plants with those possessing the three abnormalities discussed above support the view that dominance and recessiveness are not in any way attributes of the factor or "character" in itself, but are the result of the factor expression plus the modifying influence of the environment, whether genotypical or external (soil, climate, etc.). The variability in the expression of catacorolla in the 119 F1 plants of -4-1A crossed with the 119 different normals is strong supporting evidence that this conception of dominance is the most tenable of those recently advanced by geneticists.

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