A GENETICAL ANALYSIS OF PINK DAFFODILS

A PRELIMINARY ATTEMPT

By EDGAR ANDERSON
(Missouri Botanical Garden)

and

EARL HORNBACK
(Oregon Bulb Farms)

One of the results of the extensive hybridization in the genus *Narcissus* has been the production of the so-called pink daffodil. Pink is scarcely an apt name for this new range of colors which was once characterized by the late Canon Engelheart as "pinky-citrony-buffy-apricotty-tawny-topazy-inside-of-a-melony colouring." The tint in question is a chancy thing. It is very much affected by the temperature at blooming time and needs cool weather to develop most completely. It is also one of those colors which change with time; it does not fade as the flower ages and is often most intense just before the bloom begins to wither. It is dependent too on how much yellow there is in the background. Even the strongest pink will produce no more than a buffy shading when yoked to a strong yellow. On a pure white background and under optimum conditions it can become a true light pink, almost the rosy shade of a bright grape juice which has been diluted with water.

Before discussing the genetic mechanism by which these lovely narcissi came into existence we must first of all turn aside and consider the complications of polyploidy. Many modern varieties of *Narcissus* are polyploids, tetraploids to be more precise, which means that their germ plasm, instead of being in sets of twos as were many of the old-fashioned varieties, is in sets of fours. We know for certain that King Alfred and some of its progeny are tetraploids and the size and breeding behavior of our other modern varieties suggest that most of them are tetraploids or close to it. Once such a break has occurred, there is a very strong tendency for polyploid varieties to be selected due to their greater size and better substance. Even though one breeds back to the old diploid varieties these may have a few exceptional giant pollen grains which will give tetraploid offspring from such a cross. These exceptions tend to be favored in various ways and the modern daffodil, like modern bearded irises, and modern wheat, is largely a polyploid assemblage, though like them, it came from diploid ancestors.

Polyploidy introduces a number of secondary complications into breeding systems. Its primary effect is usually to give a larger size and a heavier texture to the flower; the whole plant is usually a little more thick and robust, and the season of bloom is frequently lengthened. Polyploids, once they occur, are usually selected merely for this greater size and vigor, but as soon as one starts breeding from them, he finds that they possess a number of secondary peculiarities, some of which may be advantageous. Two of these will be considered here: New Intermediates, and Percentages of Recessives.

NEW INTERMEDIATES, PRODUCED BY POLYPLOIDY

In a diploid the genes are in pairs and for each gene we can therefore have only three types of plants. In Narcissi, for instance, pale yellow (Pa) vs. bright yellow (pa) is a single gene difference and pale is dominant over bright. A plant may have two doses of pale (Pa, Pa), it may have one of pale and one of bright (Pa, pa), or it may have two of bright (pa, pa). If pale is completely dominant over bright we can have only two kinds of color from this gene, the bright yellows and the pale yellows, and any further variation in the color will have to come from other genes which modify the tint in some further way, as for instance, by restricting it to the crown, or to the very edge of the crown. In tetraploids, on the other hand, the genes are in sets of four and we can have three possible types of intermediates instead of the one type of the diploids. One of these will have three doses of the recessive bright yellow and only one of the pale (Pa, pa, pa, pa). Few dominant genes will be strong enough to prevail against three recessives and this new balance will probably let through enough of the color to produce a light soft yellow, brighter than the old dominant pale but not so bright as the rich butter yellow of the recessive. This same increase in the possible kinds of intermediates will affect every other gene in the whole organism. As breeders learn to take advantage of the new system, polyploidy offers a wide range of soft intermediate shadings which were not possible in the original diploids. The last two decades have seen this phenomenon at work in the late bearded irises which were gradually worked over from their original diploid condition by hybridization with tetraploid species from Asia Minor. We are just now, in late bearded irises, beginning to get the various soft blendings of rose and brown and tan, of gold and white, which were made possible by the fact that tetraploids deal their hands four at a time instead of two. From the breeder's standpoint this greater complexity is an advantage; from the geneticist's point of view it is an added nuisance and makes it almost impossible to score segregating tetraploid families as exactly as had been done with the diploids. Haldane and his co-workers found that though with their experimental diploid strains of Chinese primrose they could score nearly every plant merely by inspection, and then confirm these scores by making breeding tests, no such precision was possible with the polyploids.

In the cross Tunis x Mrs. R. O. Backhouse there seem to be at least three readily recognizable genes, concerned with color and color distribution. The first is bright versus pale, as discussed above, and pale (Pa) is quite dominant. However, some of the Papapapa have a good deal of yellow. The results suggest that only the extremely bright yellows should be scored as being papapapa.

The second gene is a dominant gene (E) for restricting the color to the edge of the cup. It may be thought of as a very strong color suppressor which causes fading everywhere except the edge. It must originally have come in from the poets narcissus. E is not as fully dominant over e as Pa is over pa and it is more difficult to score this exactly.*

The third gene is P which is non-pink. Pink (p) is a recessive.

For each of these three genes there will be four possible types with one or more dominants. In the case of the pale, for instance, there will be PaPaPaPa, PaPaPapa, PaPapapa and Papapapa which will be pale, and there will be only one type (papapapa) which will be bright. For each gene, therefore, we can score a plant as being more or less dominant for that gene or else being recessive. Only from the breeding results can we be certain whether it has four, three, two or one doses of the dominant. Each plant was threfore scored as being Pa or pa, E or e, P or p. If we consider nothing but these three genes and their possible extreme combinations, we have the following eight types:

1. PaPE	5. paPE
2. PaPe	6. paPe
3. PapE	7. papE
4. Pape	8. pape

The colors of these will be as follows:

1. Dominant pale, non-pink, with an edge. In other words, a plant more or less like Tunis.
2. Pale, non-pink, but without the color restricted to the edge. In other words, a plant with a pale-yellow trumpet, the color evenly distributed.
3. Will have pink around the edge and will be a plant more or less like Mrs. R. O. Backhouse, but with a much stronger restriction of the color to the edge.
4. Will have the pink suffused all the way through, like Rosabella.
5. A bright yellow trumpet but fading out except at the very edge which will be intense yellow.
6. A typical bicolor with a bright yellow trumpet, bright yellow throughout.
7. Like number five but will have the capacity to produce pink. If it has a great deal of pink this will either have a wash of buff on the inside or the colored edge will have a buff tone. (Bright yellow will completely hide a weak pink although a very strong pink will produce an interesting buff tone in even the strongest yellow.)
8. A strong yellow trumpet, yellow throughout and if the pink is strong there will be enough pink to show through the yellow,

*(And it may be added parenthetically that it is never possible to score tetraploids exactly. In the case of the Chinese primrose, 99% of the diploid plants can be scored precisely. When these same stocks were raised into tetraploids the exact scoring could not be done even by such experts as Miss de Winton, who had spent twenty years scoring diploids. However, it can be done in a rough and fairly effective sort of way. The segregation in daffodils is as sharp as in anything known among tetraploids.)

particularly when one looks inside the crown. This is a new color in daffodils apparently and is one of the most interesting things coming out of this cross.

PROPORTIONS OF RECESSIVES IN TETRAPLOIDS

Another of the effects of tetraploidy is to reduce very greatly the expectations of getting pure recessives out of crosses. If, in a diploid, we cross a pure color with a pure breeding pale, in the second generation we expect one quarter pales. In a tetraploid there are a number of complications too technical to go into here, but in any case the percentage of recessives is very much reduced and on the simplest assumption we expect about 35 more or less pales to one pure color. It is also quite possible that only a portion of the progeny from this cross are polyploids. Even had both of the parents been pure tetraploids a few exceptional diploid progeny might be expected after species hybridization. Not until a careful cytological survey of modern daffodils has been completed can we be precise about such matters. Such a survey would not be difficult nor time-consuming with our modern short-cut methods.

Mrs. R. O. Backhouse is pure pink; it is therefore pppp. Tunis we know to carry pink though it does not show it. The chances are that it is either PPpp or Pppp, probably the former. If it is the former, we expect roughly about 5 non-pinks to 1 pink. The actual result from the first row in the nursery was 64 to 19, a ratio of about 3 or 4 to 1. Considering the difficulties described above, this is pretty close to what one expects. For the pale gene both Mrs. Backhouse and Tunis are pale, carrying bright yellow. If both were not carrying bright yellow it would not appear in the seedlings. Depending on how many doses of pale there are on either side we might get ratios all the way from 35 to 1 to 3 to 1. One of the most likely ratios expected would be something in the neighborhood of 11 to 1. On the assumption that Tunis has two doses of pale and that Mrs. R. O. Backhouse has one dose of pale, the actual ratio is 60 pale to 25 bright yellow. However, in this scoring all the doubtfuls, of which there were a great many, were scored as bright. If all the doubtfuls had been scored as pales the result would have been about 10 to 1.

The edge gene is the most difficult to score exactly. Tunis certainly has it and Mrs. R. O. Backhouse probably does not. The results obtained in the cross are 47 "edged" to 36 "no restriction." This is close to the 1 to 1 we would expect if Tunis has one dose and Mrs. R. O. Backhouse none. It is a reasonable guess therefore that the constitutions of these two varieties are as follows:

MRS. R. O. BACKHOUSE	TUNIS
Papapapa	PaPapapa
pppp	PPpp
eeee	Eeee

CONCLUSIONS

Whereas these results only apply specifically to the above cross, we may expect to find them holding generally among the large modern tetraploid daffodils. Pinks, bright yellows and suffused color are all recessives, Pink x a Pink will always give a pink, though there are many modifying factors affecting the degree of pink and a strong pink x a light pink may give a large percentage of plants which have the capacity for producing pink but do not show any. The hardest to produce will be the combination of all three recessives (pa, p, e) which will be a bright yellow trumpet showing its color throughout and with a strong buff tone on the inside. However, two of these crossed together should give nothing but combinations of the same general sort.

THE PINK DAFFODIL COMPLEX AND WHERE IT CAME FROM

The above discussion, although complicated by the occurrence of tetraploidy, is conventional genetics which concerns itself almost exclusively with single gene differences, such as color and color pattern. However, to the ordinary breeder these are relatively unimportant matters and what he needs to know is something about the entire germ plasm; what the plant is like as a whole, and on the whole what general kinds of combinations are going to be thrown. As has been previously shown,* in a series of technical papers, when crosses are made between distinctly different species, the total effect of the forces making for coherence of the things that went in together is very strong even after generations of breeding. These forces are of several kinds but they all work in the same direction and they mean in simple terms that we tend to get back out of the mass whole sets of characters which went in together in the first place. Rarely we may even get a throw back to one of the original species. We are, however, much more apt to get things which remind us only in part of one or the other of the species which went into the hybrid varieties. These forces of specific cohesion are so strong that we may even determine what the original combinations were even when they are unknown if we have large numbers of hybrids from controlled crosses to study.

In the hybrid of Tunis x Mrs. R. O. Backhouse an attempt was made to find out what the pink gene was tied up with. What was the general sort of complex that had put the pink into the pink daffodils? It has been obvious to everyone who bred daffodils that one of the ultimate sources of the pink daffodils must be the poets narcissi. They have the color restricted to the cup, usually to the very edge, and they alone, of all the original species, have a strong red pigment. The pinks, however, have a different shade of red; it is a weak ecru pink instead of a strong orange red and it does not fade with the age of the flower, whereas the colors of *N. poeticus* fade very perceptibly. The pinks as we know them must be the result of recombination. They inherit the quantity of pigment and its

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*Anderson, E. & W. B. Turrill, 1938. Statistical studies on two populations of *Fraxinus*. *New Phytol.* 372:160-172.

Anderson, Edgar, 1939. The hindrance to gene recombination imposed by linkage: an estimate of its total magnitude. *Amer. Nat.* 73:185-188.

Anderson, Edgar, 1939. Recombination in species crosses. *Genetics* 24:668-698, 15 fig.

distribution from *poeticus;* the peculiar tint must have come from elsewhere. Where might that have been?

The technique for investigating this subject is really very simple though it sounds complicated. Every plant was scored for flower color and measured for sepal length, sepal width, crown length, and then the degree of crimping of the crown was scored. This latter was merely put in three grades: 1. Strong with a very wavy edge, 2. Medium with a more

The above facts give us a picture of what the gene (p) might have come into the cross with. The species we are looking for has a long, narrow crown with a straight edge and narrow, poor quality perianth parts. The obvious answer to this is *Narcissus moschatus* Haworth. We now have a working hypothesis. The pink daffodils are recombinations of elements from *N. poeticus* and from *N. moschatus* or similar straight-edged white trumpets. From the former they inherited a red or red-bordered cup; from the latter they inherited the capacity to turn pigment (when present) into a pinky red which does not fade. There are various directions in which we may look for confirmatory evidence. After the above analysis had been made, *N. moschatus* was carefully examined in the field. We customarily think of it as a pure white daffodil but as it ages, although it has almost no pigment, what little it has appears first as a faint blush of pink or ecru which gradually deepens into a light purplish brown as the flower fades. This would seem to be the color we are looking for. To be sure, it shows most strongly in the perianth, rather than in the crown, but on the above hypothesis we are not looking for a pink-cupped daffodil; the amount and the distribution of pigment would have been brought in by *N. poeticus.* What we are looking for is the ability to use the pigment precursors to produce a pink which holds its color as the flower ages. Diagrammatically the recombination would have been somewhat as follows:

or less medium edge (for this set of plants of course they are all pretty much waved, due to the strong waving brought in by Tunis), and 3. Weak, which means an edge fairly straight and even. Each of these characters was then compared for the whole lot of hybrids and for the pinks alone. Let us take these up one at a time:

(1) Pink is linked with a straight edge. Among the strongly crimped there were only two pinks out of a total of 13 plants. Among the crimped there were two out of four plants.

(2) Pinks are linked with narrow sepals. Among the wide sepals there were only two pinks in fifteen. Among the narrow sepals there was one out of four.

(3) There is no linkage between sepal length and pink.

(4) There is a very slight linkage between a long crown and pink and this is much stronger if one considers a proportionately long crown.

(5) From observation it is also clear that pink is linked with a floppy, poor perianth and with a narrow crown instead of a wide, flaring one.

GENETICAL ANALYSIS OF PINK DAFFODILS

MOSCHATUS	POETICUS
Little pigment	*Much pigment
No pigment in crown	*Pigment restricted to crown
*Pigment pinkish, non-fading	Pigment orange-red, fading

MRS. R. O. BACKHOUSE (Recombination after several generations of breeding)

*Much pigment
*Pigment restricted to crown
*Pigment pinkish, non-fading

From the above diagram it is clear that we can no longer speak of the pink daffodils as tracing back to any one wild progenitor. To get sufficient pigment they must ultimately have a *poeticus* in their ancestry; to get the proper shade of pigment they must trace back to a straight-edged white trumpet such as *moschatus.* We can no more think of the poets as being potential pinks than we can of *moschatus* being a potential pink. The latter color is a real achievement, resulting from the recombination of genes from different sources.

On the above hypothesis *moschatus* x yellow trumpets could never lead to pinks without the introduction of *poeticus* blood, nor could *poeticus* x yellow trumpets without the gene "p" from *moschatus* or some such daffodil. Therefore we have two types of questions in scanning pedigrees to test the above hypothesis: (1) Do pink daffodils actually trace back to *Narcissus moschatus* and *N. poeticus?* (2) Are there any pinks which do not have *poeticus* in their ancestry or any which do not have *moschatus* or some such straight-edged white trumpet? Fortunately, many daffodil breeders have kept accurate records and we have evidence on these points. The answer to the first is clear; some of the pinks are known to trace back to both species and by more than one line. The second test is more difficult to answer in full. So far as we know, no pink daffodil has been produced from *moschatus* x yellow trumpets with no introduction of *poeticus,* or by yellow trumpets x *poeticus* without the inclusion of a straight-edged white trumpet. The fact that we have located no such pedigrees does not mean that none exists and we shall be glad to hear from any daffodil breeders who have evidence either for or against the above hypothesis.

The really critical observation in the above cross is that the gene "p" is linked with a straight rather than with a ruffled edge. *Poeticus* introduces so much ruffling, fluting, etc., that any gene which ultitmately came from that species should be tied up with a very unevenly edged crown, rather than the reverse.

These pedigrees complete the tests which may be applied to the hypothesis with the data at hand. Others could be suggested. One of the most obvious would be to cross a strong pink to *N. moschatus.* On the above hypothesis all the progeny should be potential pinks; some might have so little pigment as to be as white as *moschatus* or even whiter. It is quite possible that the rather dirty cast to the pink of *moschatus* is due to a dominant gene and in this case one would have to raise a second generation from the cross in order to achieve a soft, clear shade of pink.

One who has had some experience with species hybrids may learn at length how to predict the hybrid if both parents are known, or to characterize the unknown parent if the hybrid and the other parent are at hand. We can use this method to answer the following question. If something more or less like *N. moschatus* is active in the germplasm of the variety Mrs. R. O. Backhouse, what kind of an influence would have had to come in from the other side of the cross in order to produce Mrs. R. O. Backhouse? To answer this question we merely measure the two knowns and calculate the unknown on the simplest assumptions: For both *moschatus* and Mrs. R. O. Backhouse we measure the following 10 features with a ruler: length of stipe, length of pedicel, length of tube, length of sepal, width of sepal, length of petal, width of petal, length of crown, diameter of crown at base, diameter of crown at tip. For each one of these characters we then proceed to calculate the unknown "X." Since polyploidy will affect absolute dimensions we can work only with proportions. Consequently our calculations will show us only the proportions to be expected, not the actual sizes. In calculating the pedicel length of "X" we merely set up the equation:

$$\frac{\text{Pedicel length of } \textit{moschatus}}{\text{Pedicel length of Mrs. R.O.B.}} \qquad \frac{\text{Pedicel length of Mrs. R.O.B.}}{\text{Pedicel length of "X"}}$$

and solve for "X." Table One shows the actual measurements. To remove somewhat the complications of absolute size, the actual calculations were made by taking the sepal length of each variety as units and turning the absolute measurements into relative measurements. The 10 calculated measurements were then turned into diagrammatic form along with observations on the angle at which the flower is held, the twist of the perianth segments, etc. "X" in Figure 2 shows the kind of narcissus which would have to balance *N. moschatus* in order to produce Mrs. R. O. Backhouse. It is almost a further proof of the above hypothesis for it is very similar to the variety Will Scarlett, which is known to be one of the parents of Mrs. R. O. Backhouse, and is itself the result of hybridizing a yellow trumpet with *N. poeticus*.

In the same breeding fields with the cross Backhouse x Tunis were the progeny of two other crosses, Backhouse x Daisy Schaffer and Tunis x Daisy Schaffer. Since a set of parallel crosses of this sort gives an excellent check upon genetic hypotheses a random sample of each family was scored. Allowing for the complications expected in polyploid crosses the results checked very closely. The results are shown in Table 1 in tabular form.

SUMMARY

1. Since many modern varieties of *Narcissus* are tetraploid, the complications introduced by polyploidy must be considered in any genetic analysis of modern daffodils. Two of these are discussed: (a) the creation of new intermediate types, (b) lower frequency of recessives.

2. The cross Tunis x Mrs. R. O. Backhouse was analyzed genetically and the following gene pairs are described:

Pa (pale yellow) vs. pa (bright yellow)
P (orange red) vs. p (pink, non-fading)
E (color restricted to edge of crown) vs. e (color diffused through the crown)

3. In the above cross the recessive 'p' is linked with (a) a straight edged crown rather than a crinkly one, (b) narrow sepals, (c) proportionately long crown, (d) floppy perianth. These facts suggest that 'p' might have been introduced from *Narcissus moschatus* Haworth.

4. *N. moschatus* was examined and was found (under cool growing conditions) to fade to pale pink as the flower aged.

5. It is suggested that the pink daffodils are recombinations of characteristics derived from *N. poeticus* and *N. moschatus*. From the former they derive color in the cup and red pigment. From the latter they get the recessive gene 'p' which turns the pigment into a pinkish red which does not fade.

6. This hypothesis fits the known breeding results.

7. On the above hypothesis it is shown that something like *Narcissus* Will Scarlett would have to balance *N. moschatus* to produce a variety similar to Mrs. R. O. Backhouse.

8. A genetic analysis of the three crosses examined in detail is presented in tabular form.

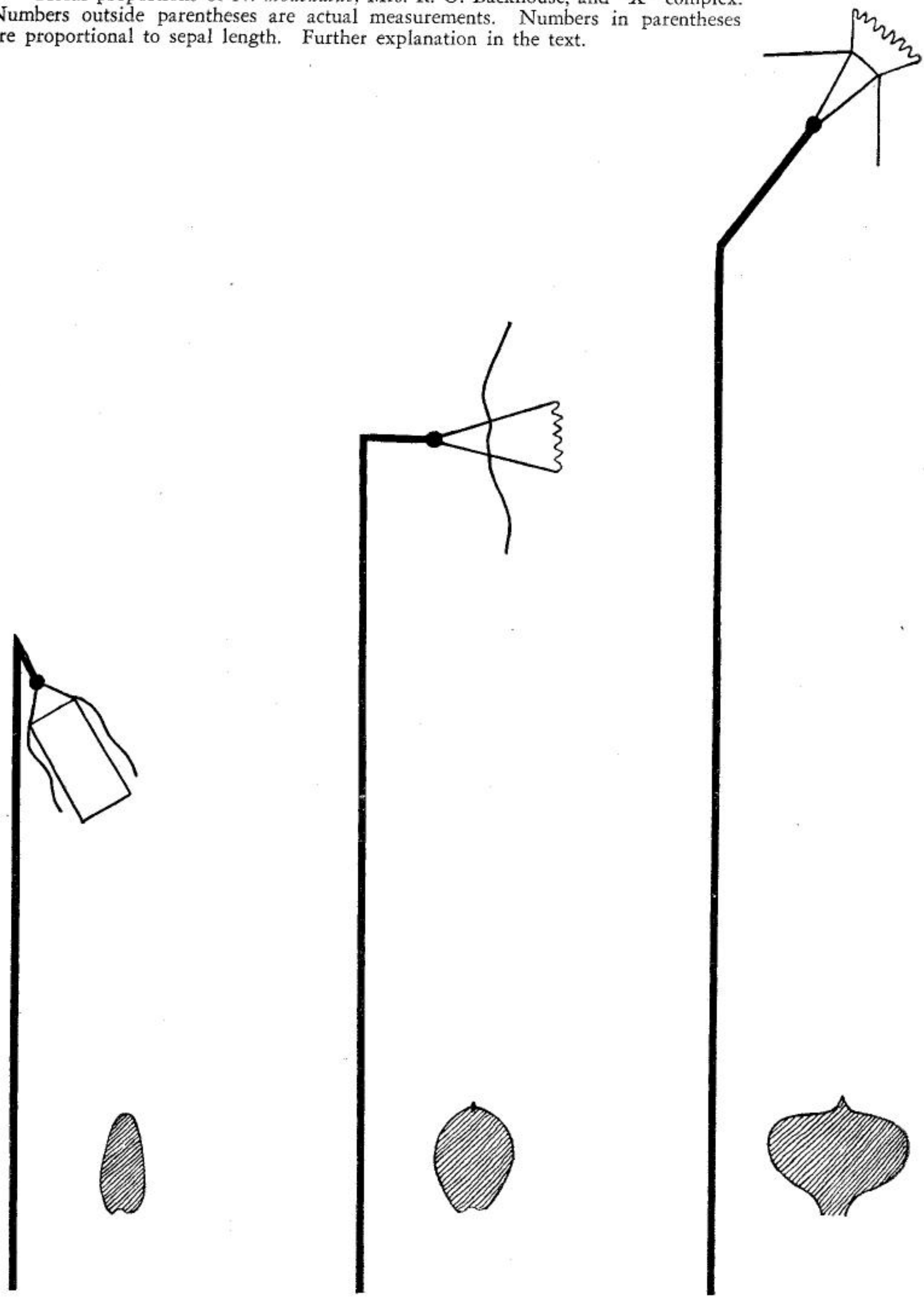
N. MOSCHATUS	MRS. R. O. BACKHOUSE	"X"	
16 (6)	35 (8)	11	stipe
1 (.4)	3.5 (.8)	1.6	pedicel
1 (.4)	2.5 (.6)	.9	tube
2.5 (1) x 1.0 (.4)	4.5 (1) x 3.4 (.8)	1 x 1.6	sepal
2.4 (1) x .8 (.3)	4.5 (1) x 2.9 (.7)	1 x 1.4	petal
2.9 (1.2)	3.2 (.7)	.4	crown length
1.2 (.5)	1.7 (.4)	3	diameter at base
1.2 (.5)	3.2 (.7)	9	diameter at tip

TABLE I

Summaries of flower color in crosses between Mrs. R. O. Backhouse, Tunis, and Daisy Schaffer:

Tunis x Mrs. R.O.B.	D.S. x Mrs. R.O.B.	Tunis x D.S.	
55	126	16	PaPE
17		7	PaPe
14			PapE
10			Pape
8	37	1	paPE
15		3	paPe
1			papE
			pape

Floral proportions of *N. moachatus*, Mrs. R. O. Backhouse, and "X" complex. Numbers outside parentheses are actual measurements. Numbers in parentheses are proportional to sepal length. Further explanation in the text.



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SUPPLEMENTARY OBSERVATIONS

Tunis x Mrs. R.O.B. When the yellows were scored in this cross, all the doubtful cases were considered to be bright yellow. The above results suggest that the scoring should have been the other way around and that all but very deep buttery yellows should be scored as Pa. These doubtful cases are probably Papapapa. Among the pinks there was fairly sharp segregation between those which had suffused color throughout and those in which the color is restricted to a ring in the center, at the base, or at the edge of the crown. Those with suffused color are in the minority. This is probably due to still further dominant genes for color restrictions that come in from *poeticus.*

D.S. x Mrs. R.O.B. In both this and the next cross there was a very small proportion of pure white trumpets with no color of any kind. There were eight in this cross and three in the next.

Of the bright yellows 31 were bicolors and 6 were yellow throughout. There is evidently another dominant gene for color restriction which we may call "B." It is noteworthy that all the *poeticus* genes for color suppression are dominant and the bright yellow trumpets are triple recessives being pa, e, b, on the above notation. In breeding for yellow trumpets, many bicolors and Leedsii should be possible parents but only trial can tell whether or not all three necessary recessives are being carried by any particular variety. The above results suggest that D.S. would give both bicolors and pure yellows when crossed with such varieties as King Alfred but that Tunis would give only bicolors.

Tunis x D.S. While there were no actual pinks in this cross there were a number of plants in which a more or less buffy pigment was deposited on the inside of the cup in the same positions as the pink colors of the sister cross. These are probably potential pinks, held down by the dominant 'P' introduced from D.S.