

Color Inheritance in Hybrid Freesias

W. P. MORGAN, Indiana Central College

The history of the commercial introduction of "*Freesia refracta alba*" and its hybrids was presented in previous papers. Although the popularity of the plant has declined in recent years, thousands of corms are produced each year in California and sold to northern florists for the production of cut flowers during January, February and March. The results presented here have been gathered over a period of years beginning in 1927 in a project mainly concerned with the commercial production of new varieties of Freesias. The hybridizing, selection, trial and early development of clones has been carried out in the greenhouses of Elder Brothers, Inc., at Indianapolis. More than 300 planned crosses have been made in a single season which has yielded more than 30,000 seedlings. Seedlings produce typical blossoms in their second season after which all but a few plants are destroyed. Corms of the new "varieties" are produced commercially in the vicinity of Oceanside, California where climatic conditions are favorable for the successful growth of Freesias and other plants of South African origin.

Early in this work it was recognized that many phases of the project would be clarified if specimens of the original species could be obtained. Through the help of Professor Robert Compton, Director of the Botanic Gardens at Kirstenbosch, Cape Province, and several South African amateur botanists, live specimens were imported. These included several species that were new to botanists. Corms of the "pink" species *F. Armstrongi* were collected from the same clump as that which supplied the type specimen (Fig. 2). Importance is attached to this item because most records of the development of colored freesia hybrids date from 1905 when corms of this species arrived at Kew Gardens in England. *Freesia Andersoniae* (Fig. 7), and *Hurlingii* (Fig. 3), were also used in this study. These two species have been described in recent years and were not available during the time that the hybridizers were developing the forms that have been introduced commercially. In addition to known species, collected specimens from remote localities differing from anything yet described were also supplied. Identification of these new forms was never made due to the untimely death of Dr. N. E. Brown whose revision of the Genus *Freesia* appeared in 1935.

All of the species may be crossed with many of the hybrids and all species would cross with one or more of the species. All species blossomed in the greenhouse during the months of January, February, and March which permitted crossing the last blossoms of the early species with the first blossoms of the latest species. In addition to supplying material for the study of the inheritance, these species have contributed many

new characters to the genetic complex associated with hybrid freesias. This includes genes for the production of at least two new types of fragrance, new blooming dates, new flower forms, new leaf and spike



Plate I. Fig. 1, Commercial Variety, "Giant White." Fig. 2, *Freesia Armstrongii*. Fig. 3, *Freesia Howlingii*. Fig. 4, white hybrid with yellow spots on three lower segments. Fig. 5, bright yellow hybrid with deep crimson spots. Fig. 6, hybrid showing lines, venation and spotting.

arrangement, new corm shape, etc., etc. Whether these features will have commercial value is a question that cannot be answered under present conditions.

Hybrid freesias exist in pure white and colors ranging from ivory and light yellow to orange, pale pink to deep, dull red and bright crimson, brown and bronze, pale lilac to deep bluish violet, with and without colored lines and with varying amounts of yellow on the three lower segments. Descriptions are based primarily on the color of the inner part of the corolla. With few exceptions dingy white with yellow splotches and various shades of yellow were the only colorings listed until the addition of the species *Armstrongii* resulted in hybrids far different from its pinkish hue. The color of this species has been given as "pinkish-mauve," "bright rosy pink," or "pink." However, flowers produced in the greenhouse were "phlox pink to pale amaranth pink, striped phlox purple" according to Ridgway color chart. No other pink species has been described. With flowers of *Armstrongii* available, analysis of its contribution was made by numerous crosses with plants that had been progeny tested or were of known parentage.

The results of crosses with *Armstrongii*, especially during 1933 and in subsequent seasons, served as a basis for interpreting the results of crosses among lavender and pink hybrids which had been gathered in previous years. F_1 from crosses with the variety Giant White were

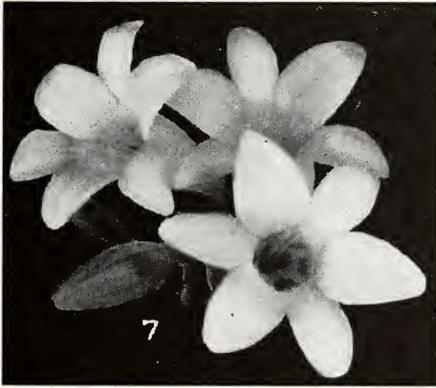


Fig. 7, *Freesia Andersoniae*.

These results confirmed the findings from crosses among the hybrids in which the bluish lavenders were recessive to the pinks. From the results of Scott-Moncrieff, Smith, Onslow, and others on the chemistry of the anthocyanin color was gained from crossing *Armstrongii* with the species *Hurlingii* whose upper segments are dingy green overlaid with "dull bluish purple." F_1 from this cross were all bright pink (Fig. 8). all pale pink with red stripes. Crosses with seedling No. 519, a medium bluish-lavender, produced progeny that were all light pink with darker stripes. Further evidence of the dominance of the pink (reddish) phase

of flower pigments, and simple tests on freesia flowers as a part of this study, it was concluded that this condition was controlled by a single pair of genes. The dominant gene *M* produced a lowering of the pH of the cell sap giving shades of red while the recessive *m* raised the pH changing the anthocyanin to blue.

Since the species crosses produced few seeds for tabulating F_2 results, the interpretation of the genes controlling anthocyanin formation was based on crosses among white and colored hybrids where larger numbers could be easily produced. For this Giant White (Fig. 1) and the white seedlings No. 105, No. 102, No. 117, No. 832, and the varieties Purity and imported *Refracta alba* (*F.lactea*?) were used. Although more crosses were made with lavenders and blues than the pinks and reds the distribution of color intensities were the same. The results could be classed as white, light, medium, deep and dark. This was interpreted as being due to two pairs of cumulative genes, *A* and *A*₁, which controlled the production of anthocyanin. Various crosses indicated the production of this pigment was independent of the yellow pigments and the effects of genes *A* and *A*₁ were limited to certain areas of the corolla. The "blotches" on the three lower segments, usually yellow, were found to be produced by separate genes (Fig. 4). To some extent the flower size, or more specifically, cell size, is correlated with color intensities, the small flowers being darker than the larger of same gene combination. Plants having defective roots or stems produced darker, smaller blossoms that had to be carefully checked in the tabulations.

A dominant gene *L* produced lines in the center of the flower segments in the presence of pigment. The data on this is incomplete and other genes are certainly involved since each of the six segments may have as many as three lines, only one, or more often, none on the upper segments.



Fig. 8, All-pink hybrid from *F. Armstrongi* x *F. Hurlingii*.
 Fig. 9, White hybrid with deep "purple" spots.

In the use of the white species *Andersoniae* in crosses with red and blue freesias some unexpected results were obtained. Crossed with medium blues and reds the results were white in the fully expanded blossoms instead of being light blue or light pink. When crossed with dark blues and reds the results were light blues and pinks but not the expected medium blues and reds. A reduced number of the expected intense colors were regained in F_2 indicating the presence of the normal number of A genes. This was interpreted as being due to the incompletely dominant gene, I , whose effect was limited to the areas covered by A and A_1 but not on L . Figure 10 shows three blossoms of *Andersoniae*. The last two are aging and are becoming mottled with deep purple, however this is not the pathological mottling as seen in "broken" tulips. Apparently the I genes lose their effect as the blossoms age.

Both the effects of gene I on the anthocyanin colors and the effects of two more genes controlling the production red or blue "splotches" on the three lower petals is shown in the progeny of *Andersoniae* crossed with seedling No. 856. Blossoms of this plant are deep pinkish-red with deep red spots on the three lower "petals." The F_1 of this cross had white in areas controlled by A and A_1 but with red or blue splotches on the three lower segments, a new color arrangement for hybrid freesias. This is shown in Figure 9. This was due to No. 856 having the genetic formula of $AAA_1a_1 Mm$ with the cumulative "pansy" genes P and P_1 . This was verified by further crosses. Figure 5 shows these "pansy" spots of deep crimson in a flower that is otherwise a deep yellow. The area covered by the last genes is identical with that covered by cumulative genes S and S_1 controlling the formation of yellow "blotches" (Fig. 4). These are independent of the P genes and varying amount of yellow pigment with either blue or red may be found in the same flower.

Yellow plastid pigment is found in most of the freesia hybrids either alone or in combination with anthocyanin. These crosses of yellow hybrids, especially with the white hybrids listed above, gave color intensities at first somewhat confusing due to the fact that the presence of a single Y gene produced ivory which would usually be classed as "white." The presence of the usual yellow spots on the three lower segments of true whites contributed to the confusion. By separating

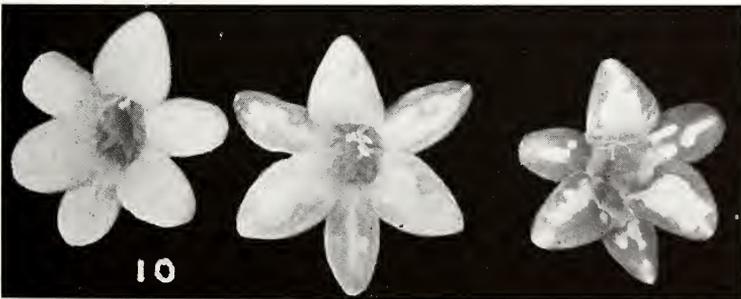


Fig. 10, Flowers of *F. Andersoniae* showing purple mottling that develops as blossoms age.

these two groups it became easy to separate the gradations thus: white, ivory, light yellow or lemon, deep yellow and orange yellow. This being interpreted as being due to two pairs of cumulative genes Y and Y_1 . One hybrid, Giant White, was especially valuable in the crosses used to make the above color analysis (Fig. 1). This variety (clone) lacks any of the dominant genes mentioned above. Since the genes for general flower color are independent, many color variations result from the A and Y genes in the presence of M or m . For instance: with M the range may extend to crimson when homozygous for both A and A_1 and heterozygous for Y . When the combinations are reversed with more Y than A genes, orange color results. However, an orange yellow results in the absence of A but homozygous for both yellow genes (Y and Y_1). In the presence of the gene m , increasing the pH, various shades of bronze to brown result.

The above summary of data has not included the inheritance of color in stamens or their filaments, throat markings (which are conspicuously different in *Andersoniae*), external parts of the corolla, colored venation, "picotee" distribution, length and reduction in number of colored lines (structurally three mid-lines are present in each segment, regardless of color (Fig. 6)). Although the above genes account for all basic coloration in intensities, shades, and distributions, it is recognized that there must be genes that modify the expected results. These exceptions appear mainly as extremes, intermediates, or modification of color boundaries. In part may be due to genes modifying the formation of these complex flower pigments or their precursors. Chromosomal irregularity has been demonstrated in these hybrids and this may account for some of the exceptions.

The above interpretations seem to answer the question concerning origin of certain of the genes which gave rise to so many color combinations. Apparently the m gene was present in early white and yellow hybrids. That one pair of A genes was present is certain since one pale lavender variety was shown before the species *Armstrongi* made its appearance. Since *Armstrongi* is homozygous for a single pair of A genes, it is assumed that the second pair of A genes present in the hybrids had a different origin. It is quite possible that the first source of anthocyanin came from the species here referred to as *Hurlingii*. Specimens of this species were collected at Bonnievale, Cape Province, and are identical with those figured by Jacquin in 1786 and named *Gladiolus refractus* while the same species was figured in the Botanical Register of 1816 and named *Tritonia refracta*. The same species became Foster's *Freesia refracta* in the Gardeners' Chronicle of 1888 and *Freesia Hurlingii* as figured by L. Bolus in South African Gardening in 1933. The fact that the name *refracta* has been used to refer to freesias in general resulted in the name *Hurlingii* being chosen as the most useful in the designation of the plant used in this study. Since this inconspicuous species with flowers "dingy greenish, suffused violaceous or purple" loses its color identity in F_1 , it is quite certain the early hybridizers would avoid retaining any reappearance of its general flower characteristics. In spite of this it may have been the source of the one pair of A

genes and it certainly is homozygous for *m* although the *I* gene referred to above is also present. These facts are not readily seen in F_1 progeny but F_2 produced flowers with anthocyanin intensities which would be difficult to explain otherwise. The source of the yellow colors in the hybrids would be difficult to explain since the early hybridizers probably had access to corms of more than one yellow flowered species.

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