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THE INHERITANCE OF ALBINISM IN DENDROBIUM ORCHIDS

MONTAKAN VAJRABHAYA AND THAVORN VAJRABHAYA
Department of Botany, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand.

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ABSTRACT

Seven grexes of dendrobium orchid species and hybrids in the section Phalaenanthe *were bred to determine the inheritance of flower color. It was found that the genes controlling alba and semi-alba phenotypes were similar to those reported earlier in cattleya orchids. The genetic ratios of some of the crosses, however, were unexpected. The adjustment of genotypes was made by designating the kk genes to the white keels of the purple flowers. The same genes, in the homozygous state, suppress the rest of the purple color in the lip of a hypothetical semi-alba, the flower becoming alba. The designation of the K and k genes is reported here for the first time. The results of distribution of the purple, semi-alba, and alba phenotypes obtained from the crosses, fit the hypothetical genotypes.*

INTRODUCTION

Information on the inheritance of flower color in orchids is trailing far behind that of all other important ornamental plants. There are four reasons for this. Their long life cycles require three years or more for each generation. Open pollination, even among genera, allows complex heterozygosity to accumulate both in nature and in cultivation. The prevalence of polyploidy can either cause sterility or change patterns of inheritance. The cost of maintaining specific lines of little or no commercial value is high.

The first scientific report on the inheritance of albinism in orchids was published soon after the beginning of the modern period of genetics.[1] In papers published in 1912 and 1913,[2,3] Hurst listed a number of white cattleyas and proposed that both C and R genes were required for the production of purple flowers in *Cattleya* and *Paphiopedilum*, while the absence of either gene resulted in white flowers (ccR-, C-rr, ccrr). The lists, with additions and revisions by other authors, have proved to be very valuable information for both geneticists and breeders until the present day.[1,4,5]

Any seedling obtained from selfing and crossing among members within the same group is expected to bear white flowers. In contrast, the seedlings of the parents belonging to different groups would generally produce purple flowers. The genetic compositions of the latter would include the hypothetical C gene, producing a colorless chromogen, and an R gene producing enzymes which convert the colorless chromogen into colored pigments. This type of inheritance is referred to as complementary gene action or duplicate recessive epistasis.[6]

The genetics of the semi-alba (white with colored lip) is more complex than that of the alba. Mehlquist[4] proposed that the p gene in cattleyas, when homozygous, suppresses purple color in sepals and two lateral petals but not in the lip which is a modified petal. This condition would arise only in the presence of both C and R genes.

Storey and Kamemoto,[7] after studying the unnamed offspring derived from self pollination of a complex hybrid between C. Rubio (dark lavender) × *C. warscewiczii* 'Firmin Lambeau' (alba), stated that their findings fit Mehlquist's hypothesis.

The alba forms were found in several species of *Dendrobium* both in the soft and hard cane groups.[1,6] Semi-alba was reported to occur in the section *Phalaenanthe*.[6] Both C and R genes are required for coloration of the flowers like those in *Cattleya*, but only a dominant P gene, and not the pp, is required to produce semi-alba in the dendrobium orchid populations studied.[6]

This work is an attempt to verify previous hypotheses by making crosses of plants with similar and diverse flower colors. It is also hoped that the results of these studies will contribute information to Orchidology and will be of value to breeders.

MATERIALS AND METHODS

The plants used in this study were obtained from the following sources.

Table 1 Stud Plant

Name	Source
Den. bigibbum[1] No. 17 (2n = 38, purple, white keels)	Mr. Allan Burrows, Queensland, Australia
Den. bigibbum[1] No. 82 (2n = 38, alba)	William Kirch Orchids, Hawaii, U.S.A.
Den. bigibbum[1] No. 16 (2n = 38, alba)	Our own cross between two alba forms
Den. × Merritt Island[2] No. 21 (2n = 38, semi-alba)	T. Orchids, Bangkok
Den. Somsak 'Six Stars'[3] No. 47 (semi-alba)	-ditto-

[1] *Dendrobium bigibbum* L. (syn. *Den. phalaenopsis* Fitz.; *syn. Den. schroederanum* Gentil.)

[2] Primary interspecific hybrid

[3] Advanced hybrid with a trace of *Ceratobium* in the background; judging from fertility and breeding behavior, it could be a diploid.

Three clones of *Dendrobium bigibbum* L. one primary hybrid, and one advanced hybrid belonging to the section *Phalaenanthe* and *Ceratobium* were used as stud plants. Crossing and selfing among these clones and their descendants were made between 1988 and 1993. Their offspring were used for genetic studies.

Due to difficulties in recognizing similar groups of orchids, the authors choose to use the name *Dendrobium bigibbum* L. instead of their synonyms: *Den. phalaenopsis* Fitz. or *Den. schroederanum* Gentil. The R.H.S. Color Chart, produced in Association with the Flower Council of Holland, was used as a standard reference for flower color. Chi-square tests were made to determine the ratios reliability.

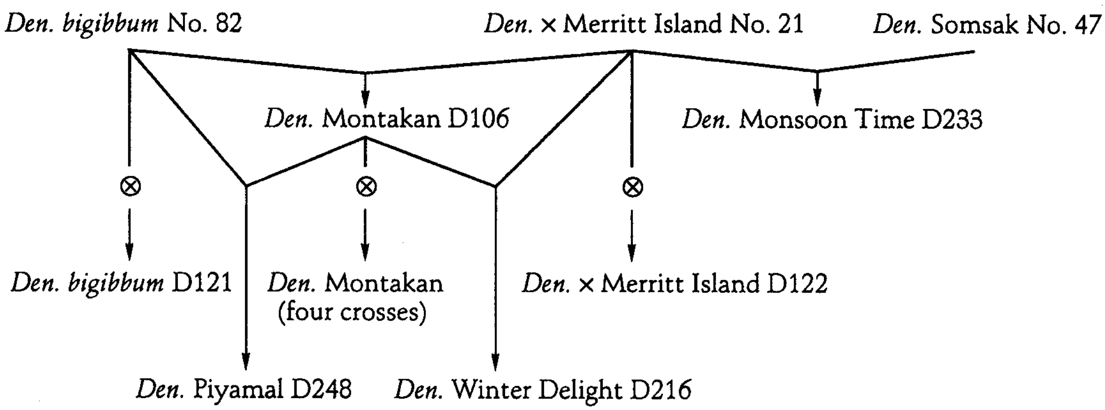


Fig. 1 Hybridizing Scheme ; No. = clone number ; D = grex number

RESULTS AND DISCUSSION

A. The ⊗ Alba (No. 1, Table 2, Fig. 2A)

All 28 plants resulting from selfing the diploid *Den. bigibbum* No. 16 produced white flowers without tinged sepals, memtums, or columns. The leaf sheaths had no purple veins. Such plants may be classified either as C-class (C-rr) or R-class (ccR-, ccrr).[1,8] This designation is widely accepted in *Cattleya* and also in *Dendrobium*,[6,7] but no one has assigned any specific genotype to a dendrobium orchid. Therefore, we propose CCrr to be the genotype of this particular plant based on the results obtained in the grexes Nos. 1 and 7 (Table 2).

B. The Semi-alba Crosses (Nos. 2 and 3, Table 2, Fig. 2B-2D)

Plants obtained from selfing of the diploid *Den.* × Merritt Island No.21 (*Den. bigibbum* var. *compactum* 'Redlip' × *Den. dicuphum*) produced interesting results. The offspring can be classified into three distinct groups according to their flower color and the coloration of the veins on the leaf sheaths. The plants with green leaf sheaths produced white flowers with varying traces of green on the sepals and mentums. Those with purple veins had either white flowers with colored lips (semi-alba), or white flowers with tinged sepals, mentums and sometimes anther cap (alba). The genotypes of the offspring are expected to vary more than the phenotypes due to the presence of more than two pairs of genes controlling color expression.[4,6,7] Mehlquist proposed that the presence of a recessive p gene, when homozygous, suppresses color in sepals, lateral petals and outer parts of the lip, a modified petal.[4] A plant with both C and R genes (genetically purple) produces semi-alba flowers. With such assumption, all offspring from selfing a semi-alba plant would produce only semi-alba. Infact, out of 84 offspring, 48 were semi-alba, 19 were tinged white (alba) and 17 were white (alba). The ratios are close to a dihybrid ratio of 9:7 (semi-alba:alba) or 9:3:4 (semi-alba : tinged : white). An additional assumption is that the k gene, when homozygous, suppresses the color in the keels and central part of the lip, thus making the flower an alba type. The K gene must be heterozygous in the stud plant, otherwise the offspring would produce only semi-alba flowers in the presence of KK. Selfing of a plant with Kk genes would produce a semi-alba:alba ratio of 3:1 (Table 2). Finally, the C-R system, proposed by Hurst, was considered to control the other type of alba. Therefore, the Rr genotype was assigned to be another determining factor for producing alba flowers. The genotype given in Table 2 shows that the results obtained in this particular case fit the ratio. Other crosses made from this clone or its descendants produced offspring having characteristics as predicted.

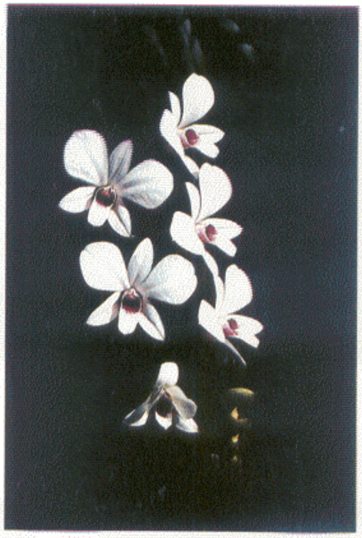
The genetics of semi-alba has long been a problem for orchid breeders especially concerning crosses between semi-alba and alba of *Cattleya* and *Dendrobium*. Mehlquist proposed that semi-alba would occur only in the presence of pp, C- and R- in cattleyas.[4] He predicted that selfing of a plant with CCRrPp genotype would result in a ratio of 9 colored to 3 semi-alba to 4 white. Storey and Kamemoto made a study of the offspring of self-pollination of a colored cattleya hybrid having such a genotype and obtained the predicted results.[7] They also predicted that the offspring results of selfing or crossing of the semi-alba individuals would be all semi-alba. In 1990, Kamemoto and Amore found that the genes controlling semi-alba in *Dendrobium* were P- instead of pp.[6] Their observations were made on the all semi-alba offspring derived from crossing between a semi-alba *Den. dicuphum* and an alba *Den. affine*. The F_2 ratio was 3 semi-alba to 1 alba, and the backcrossing of F_1 to *Den. affine* produced a 1:1 ratio. Therefore, they believed that the semi-alba and alba characteristics in *Cattleya* and *Dendrobium* were likely to be controlled by different mechanisms. Our results, however, are similar to those originally found in cattleya hybrids. The difference may be due to our designation of the suppressor gene "k". When this gene is homozygous, a genetically semi-alba plant has ppKK genotype, an alba plant has ppkk genotype, and all members of the F_1 have ppKk genotype. Selfing of F_1 would produce offspring having a ratio of 3 semi-alba to 1 alba, backcrossing of F_1 to the alba (ppKk × ppkk) would produce a ratio of 1 semi-alba to 1 alba. This means that the hypothetical genotypes of the semi-alba and alba could be different even the ratios of the phenotype appear to be the same. *Den.* Monsoon Time (No. 3, Table 2) produced semi-alba flowers or white with tinged sepals, but not pure white. The genotype of the male parent is expected to be similar to *Den.* × Merritt Island except that the C gene is likely to be homozygous because the ratio of the semi-alba to alba is 3 to 1 as a result of segregation of Kk genes on both sides. Neither C- nor R- white is expected from this grex.

Table 2 Inheritance of Flower Color and Their Genotypes

Parent		Offspring							
No.	Name and Genotype	Grex No.	No. of plant	Flower Color: purple	Flower Color: semi-alba	Flower Color: alba, tinged	Flower Color: alba, white	Keel Color: purple	Keel Color: white
1	⊗ *Den. bigibbum* No. 16 (alba) CCrrPPKk	D121	28	0	0	0	28	0	28
2	⊗ *Den.* × Merritt Island No. 21 (semi-alba) CcRRppKk	D122	84	0	48	19	17	48	19
			(0:9:3:4), P=0.30 - 0.50					(3:1)[1], P=0.50 - 0.70	
3	*Den.* Monsoon Time *Den.* × Merritt Island No. 21 × *Den.* Somsak No. 47 Semi-alba × semi-alba CcRRppKk × CCRRppKk	D233	14	0	10	4	0	10	4
			(0:3:1:0), P=0.70 - 0.80					(3:1), P=0.70 - 0.80	
4	*Den.* Montakan *Den. bigibbum* No. 82 × *Den.* × Merritt Island No. 21 alba × semi-alba CCrrPPKk × CcRRppKk	D106	75	75	0	0	0	56	19
								(3:1), P=0.99 - 1.00	
5	*Den.* Winter Delight *Den.* Montakan D106/17 × *Den.* × Merritt Island No. 21 purple × semi-alba CCRrPpkk × CcRRppKk	D216	18	10	4	4	0	10[2]	8[2]
			(2:1:1:0), P=0.80 - 0.90					(1:1), P=0.50 - 0.70	
6	*Den.* Piyamal *Den.* Montakan D106/19 × *Den. bigibbum* No. 17 purple × purple CCRrPpkk × C-RRPPkk or C-RrPpkk × CCRRPPkk	D248	51	51	0	0	0	0	51
7	*Den.* Piyamal *Den.* Montakan D106/17 × *Den. bigibbum* No. 16 purple × alba CCRrPpkk × CCrrPPKk	D208	19	12	0	4	3	8[3]	8[3]
			(2:0:1:1), P=0.3 - 0.5					(1:1)[1]	

( ) = expected ratio; P = results of chi-square test; [1] when only the ratio of semi-alba (ppK-) to tinged (ppkk) is determined; [2] purple keel group = 6 from purple fls. + 4 from semi-alba, white keel group = 4 from purple fls. + 4 tinged fls.; [3] purple keel group = 8 from purple fls., white keel group = 4 from purple fls. + 4 tinged fls.

A



B

C

D

Fig. 2 Stud plants and their ⊗ offspring.

A. Infraspecific variation in the section *Phalaenanthe*. Top row, *Den. dicuphum* (tinged), *Den. bigibbum* No. 82 (alba), *Den. bigibbum* No. 16 (alba); Bottom row, *Den. bigibbum* var. *compactum* No. 42, *Den. bigibbum* var. *compactum* No. 51, *Den. bigibbum* D206.

B. *Den.* × Merritt Island No. 21 (semi-alba).

C. Variation in the offspring of ⊗ *Den.* × Merritt Island No. 21. Front view: semi-alba, tinged, alba.

D. Offspring of ⊗ *Den.* × Merritt Island No. 21. Rear view: Top, semi-alba; Bottom left, alba; Bottom right, tinged.

Fig. 3 Variation in the offspring

A. Top left, *Den. bigibbum* No. 82; Top right, *Den.* × Merritt Island No. 21. Bottom row, their offspring (*Den.* Montakan) showing slight variation in the floral parts except the keel colors (see Table 2).

B. Variation in the offspring of ⊗ *Den.* Montakan. Note: the appearance of alba but not semi-alba.

C. Extreme variation. Top left, *Den.* Montakan D106/17 (white keels); Top right, *Den. bigibbum* No. 16 (alba); Bottom row, their offspring (*Den.* Piyamal) showing extreme variation in color and size of floral parts. Note: There are both purple and white keels.

D. Uniform offspring (purple with white keels). Top left, *Den.* Montakan D106/19 (white keels); Top right, *Den. bigibbum* No. 17 (white keels). Bottom row, their offspring (*Den.* Piyamal) showing fairly uniform offspring.

C. The Alba × Semi-alba (No. 4, Table 2, Fig. 3A)

This grex has fairly uniform plants and flower characteristics. All seventy five plants from the same cross produced purple flowers. Eventhough all had purple flowers, their keel colors could easily be distinguished. The color could be divided into two groups with an approximate ratio of 3 purple to 1 white. This grex is interesting and informative because none of the member had color similar to either parent. The genotypes of *Den. bigibbum* No. 82 (C-white) must have genotype of CCrrPP and *Den.* × Merritt Island No. 21 with CcRRpp (Nos. 2-5, Table 2) in order to produce flower with all purple color. The K genes must be in a heterozygous state on both sides to produce the purple to white keels at a ratio of 3 to 1. It should be noted that the kk suppress only the keel color in purple flowers but they suppress the color of both keels and the central area of the lip.

Another "semi-alba", *Den. dicuphum* was crossed to *Den. phalaenopsis* var. *compactum* 'Mauna Kea' (alba) by Kamemoto and Amore.[6] All of the offspring produced purple flowers, but they had already assigned the P gene for the semi-alba to a similar cross which produced all semi-alba character. It is hard to imagine that any cross could produce all purple flowers in the presence of the P gene unless there is a gene in the alba form that alters the action of the P gene.

D. The Backcrosses (Nos. 5-7, Table 2, Fig. 3C, 3D)

Backcrossing of the F_1 to their parents were made in order to obtain more information about the genetic compositions of the stud plants and their descendants.

Unfortunately, backcrossing of *Den.* Montakan to the original clone of *Den. bigibbum* No. 82 was not made. However, two crosses were made on two different clones of *Den. bigibbum.* All 51 plants of *Den.* Piyamal (*Den.* Montakan D106/19, purple, white keels × *Den. bigibbum* No. 17, purple, white keels) produced purple flowers (violet group, 88D) similar to the color of their parents.

Although the genotype of the *Den. bigibbum* No. 17 has not been studied before, its white keel character in the offspring indicates the possesion of kk in both parents. Any individual of the same grex of *Den.* Montakan D106 has been proven to carry RrPp gene combinations. Therefore, its mate must carry RRPP in order to produce all purple offspring. Only the states of CC or Cc are not known in *Den. bigibbum* No. 17, because any *Den.* Montakan plant has an equal chance of having CC or Cc genotypes (see No. 6, Table 2). This needs to be verified further. Therefore, the genotypes of *Den. bigibbum* No. 17 should be either CCRRPPkk or CcRRPPkk.

Assuming the genotypes of *Den. bigibbum* No. 82 are the same (see Nos. 1, 4 and 7, Table 2), the results of backcrossing the same clone of *Den.* Montakan D106/17 (violet group, 88D) to either parent had shed some light on the inheritance of this group of Dendrobiums. This particular clone could possess either CCRrPpkk or CcRrPpkk genotypes (Nos. 4, 5 and 7, Table 2). When it was backcrossed to *Den.* × Merritt Island No. 21 (CcRRppKk), its genetic ratio of flower color of purple to semi-alba to tinged was 2:1:1; and purple to white keels was 1:1. The results favor the CCRrPpkk genotype. Therefore, their alba offspring of *Den.* Winter Delight would not be either C-white (C-rr) or R-white (ccR-), but could arise through ppkk gene combination as a result of Ppkk × ppKk. **This is assumming that the genotype P-K- produces purple flowers with purple keels; P-kk produces purple flowers with white keels; ppK- produces semi-alba; ppkk produces tinged white.**

On the contrary, *Den.* piyamal No. 208 from backcrossing the particular clone of *Den.* Montakan mentioned above onto *Den. bigibbum* No. 16 (CCrrPPKk) showed no semi-alba in the offspring. This is due to the presence of PP genes in the latter (Nos. 1 and 7, Table 2), therefore the alba form could arise only through the C-R combination according to Hurst's hypothesis.[8] The ratio of flower color, purple to tinged to white was 2:1:1; and purple to white keels was 1:1. Eventhough the number of plants studied is small, all four phenotypes appear accordingly.

E. The Selfcrosses of F_1 (Fig. 3B)

Three selfcrosses and one sibcross of *Den.* Montakan D106 were made. A total of 35 seedlings just came to flower at this writing. Due to heterozygosity at different gene loci of the parents, the outcome was expected to be highly variable. However, the pooled data of flower color showed 18 purple, 8 tinged, and 9 alba. It is surprising that the semi-alba did not appear in the populations. The inheritance of semi-alba has always presented problems to growers and scientists alike, because several genes are involved in the synthesis of the pigments. Other lesser known genes may either intensify or inhibit the expression of other genes in varying degrees, causing changes in color or even inhibition of the synthesis of the expected colors.

CONCLUSIONS

1. Seven grexes of dendrobium orchids were bred from three stud plants of alba and semi-alba phenotypes for determination of color inheritance.

2. The occurrences of alba and semi-alba are complex, requiring four different pairs of genes. When each of these genes becomes homozygous recessive, they either suppress color production completely or partially on different flower parts.

3. The presence of either cc or rr supresses color production of the whole flower and probably of the leaf sheaths, regardless of other genes. The pp supresses the color of sepals and lateral petals in the presence of both C and K genes, but it suppresses only the outer part of the lip, a modified petal, leaving purple color on the keels and area around them. With the combination of both pp and kk in the presence of C and R, the flowers become tinged white. However, the pure white and tinged white are sometimes difficult to differentiate in loosely controlled growing conditions.

4. Probable genotypes of seven different clones have been constructed from the results obtained from the crossing of these plants. Genetic ratios of all phenotypes appeared in these crosses were subjected to the chi-square test. All the results fit the tests in Table 2.

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