Distribution of Flower Pigments in Perianth of Cattleya and Allied Genera : (II) Hybrids

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Distribution of Flower Pigments in Perianth of *Cattleya* and Allied Genera

II Hybrids

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SUMMARY

Distribution of flower pigments and shapes and sizes of epidermal cells in about 210 hybrids of *Cattleya* and allied genera were examined in relation to their parental species with a microscope and a chromaticity apparatus.

1. The hybrids presented more distribution patterns of carotenoids and anthocyanins in perianth than the species. Most lavender flowers of *Cattleya, Brassocattleya, Brassolaeliocattleya* and *Laeliocattleya* had the same pattern as their parent species. Descendants of *C. intermedia* var. *aquinii* and of *L. pumila* and *C. trianae* included plants containing anthocyanins in epidermis (P3). The "sophro red" flowers of the descendants of *S. coccinea* were P3, when they contained no carotenoids.

Red flowers contained both carotenoids and anthocyanins, and in most *Sophronitis* hybrids the anthocyanins were contained in epidermis and parenchymatous tissues with some exceptions (no anthocyanins in epidermis).

2. *Brassavola* hybrids were distributed in the area showing yellow, white and lavender in the chromaticity diagram, and there were few red and orange ones. The "sophro red" flowers were the most reddish, followed by the "splashed" ones, while the lavenders were less reddish. *S. coccinea* hybrids were distributed in a wide area according to the *Laelia* species used as parents.

3. Shapes and sizes of epidermal cells in perianth of hybrids were markedly affected by the nature of parents ; the regression coefficients of shapes, height of epidermal cells in petals and height of those in lips were 0.32-0.56, 0.40-0.50 and 0.36-0.49, respectively. Also, species and the groups of related species had different effects. Hybrids of *C. aurantiaca* were easily affected by the genotype of their parents, whereas the *C. labiata* group were not so greatly affected.

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Introduction

Laeliinae orchids, *Cattleya* and allied genera include many species which have different types of habits, flowering times and flower colors. In these previously reported genera many species produce white, yellow, orange, red and purple flowers with high chromas. Flowers with the so-called "sophro red" were distinguished by the hue and the epidermal presence of anthocyanins from the lavender ones of *Cattleya* species. Serial changes in the shape of epidermal cells in petals and lips of the same genera were also found, indicating the evolutional direction[1].

At present, many species and hybrids are crossed within not only the same species but also different species and genera with different characteristics related to growth habits, flowers and so on[2,3]. Thus, cross combinations have increased so markedly that much effort has been made to produce new excellent orchids. Now effective countermeasures based on scientific evidence are required.

In order to clarify the genetic behavior of flower characteristics of species and genera in Laeliinae orchids and to establish effective breeding methods, herewith reported are color of perianth, pigment distributions in its tissues and shapes of epodermal cells in 214 intergeneric as well as interspecific hybrids.

MATERIALS AND METHODS

Examined intergeneric and interspecific hybrids are listed in Table 1.

Flowers were collected from the greenhouses of the Experimental Farm of Gifu University, Nagata Engei Co., Ltd. in Aichi Prefecture, Ohgaki Engei in Gifu Prefecture, Kokusai Nursery Co. Ltd. in Tokyo and Ohba Orchids Co. Ltd. in Tokyo.

The procedure for observation of the epidermal cells and the pigment distribution in perianth tissues and for measurement of color chromaticity were the same as in the previous paper[4].

Note : Interspecific and intergeneric hybrids should be written as *C.*×Dinah and× *Sl.* Valda, respectively. However, in this paper the symbol× was omitted.

RESULTS

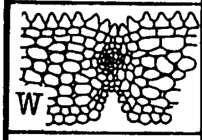
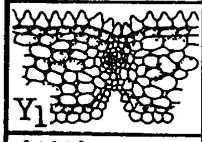
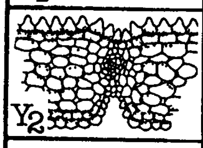
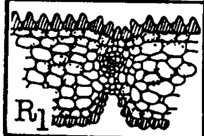
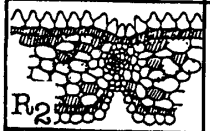
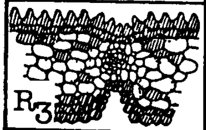
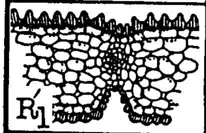
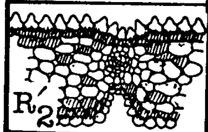
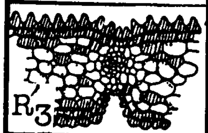
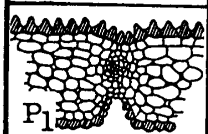
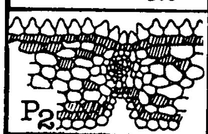
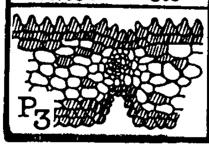
1. *Distribution of flower pigments in perianth tissues*

Species of Laeliinae orchids presented 10 types of pigment distribution in perianth tissues on the basis of the presence and / or absence of carotenoids and anthocyanins in epidermal cells and palisade and spongy tissues (Table 2, Fig. 1). Hybrids showed two more types than the species which have 10 types ; that is, R1 and R2 types showing red color were not observed in species, and the former type included a descendant of *S. coccinea* in which anthocyanins were contained only in epidermis of the petal, while carotenoids were in both epidermis and palisade tissue cells. In the R2 type, anthocyanins were not contained in the epidermis. Therefore, *Lc.* Waianae Sunset showed the normal anthocyanin

Table 1. Examined genera and interspecific hybrids.

Genera	Abbriviation	Number of hybrids used
Brassavola	*B.*	0
Brassocattleya	*Bc.*	15
Brassolaeliocattleya	*Blc.*	36
Cattleya	*C.*	20
Cattletonia	*Ctn. (C. × Broughtonia)*	6
Dialaelia	*Dial. (Diacrinum × L.)*	2
Epicattleya	*Epc. (Epidendrum × C.)*	3
Epilaelia	*Epl. (Epidendrum × L.)*	1
Epiphronitis	*Eps. (Epidendrum × S.)*	3
Laelia	*L.*	2
Laeliocattleya	*Lc.*	60
Potinara	*Pot. (B. ×C. ×L. ×S.)*	9
Sophronitis	*S.*	1
Sophrocattleya	*Sc.*	6
Sophrolaelia	*Sl.*	8
Sophrolaeliocattleya	*Slc.*	42
	Total	214

Table 2. Distribution patterns of flower pigments in perianth and their variations in hybrids.

Classification[z]	Species[z]	Hybrids
 W	*B digbyana* *C intermedia* *C mossiae* *L purpurata*	*Bc*. Alabaster, *Bc* Deese, *Bc* Mon, *Bc* Mrs J Leeman, *B nodosa* × *C* Ohkami *Bc* Sonia alba, *C* Bob Betts, *C* Christina Wagley, *C*. Bow Bells, *C* Picasso, *C* Tiffin Bells, *Lc* Aconcagua, *Lc* Alubra, *Lc* Blanckette, *Lc* Blue Ribon, *Lc* Ray McMillan, *Lc* Seshin, *Lc* Twilight Song, *Diac* Colmaniae, *Dial* Alice Hart, *Dial* Snow Flake.
 Y_1	*C aurantiaca* *C dowiana* *L flava* *En. mariae*	*Bc* Binosa × *C*. Landate, *Epc*. Vienna Wood, *Lc* Amelia, *Lc* Golden Digger, *Lc* Hazel Angel, *Lc*. Leaf Wood Lane, *Lc* Little Sunbeam
 Y_2	*C forbesii* *L cinnabarina* *L xanthina* *En vitellina*	*B digbyana* × *C guttata*, *Blc* Brigitte, *Blc* Dear Me *Blc* Golden Concolor, *Blc* Golden Ember, *Blc*. Harlequin, *Blc* Ojai, *C* Lutiaca, *Lc* Amelia *L cinnabarina*, *Lc* American Heritage, *Lc*. El Cerrito, *Lc* Eva, *Lc* Glodskes Gold, *Lc* Golden Sparkle, *Lc*. G S Ball, *Lc* Palolo Gold, *Lc* September Moon, *Lc* Washington Slope, *Pot* Lemon Tree, *Sl* Valda, *S coccinea* × *L*. Coronet
 R_1		*Slc* Vermilion Cherub
 R_2		*Lc* Waianae Sunset, *Slc* Eastmona, *Pot* Bunty
 R_3	*Br. sanguinea*	*C guttata* × *Ctn*. Jamaica Red, *Ctn* Keith Roth, *Sl* Orpetii, *C*. *shillerana* × *Slc* Jewel Box, *Slc* Jewel Box, *Slc* Extace, *Slc* Paprica
 R'_1	*L milleri* *S cernua* *S coccinea*	*S* Alizona, *Sl* Mariotiana, *Slc*. Canzac, *Slc* Miura, *Sc* Bewitched
 R'_2	*C bicolor* *En. cordigera* *L tenebrosa*	*Blc* George King, *Blc* Orange Empress, *C guatemalensis*, *C luteola* × *En cordigera* *Lc* Amelia, *Lc* Janice Mathews, *Lc* Sun Mist, *Lc*. Trick or Treat, *Slc* George Hauserman, *Slc*. Stacy Miyamoto
 R'_3	*C velutina**	*Ctn*. Jamaica Red, *Ctn* Keith Roth, *Epi prismatocarpa* × *L milleri*, *Pot* Naokazu, *Eps* Veitchii, *Eps*. Radians *Sc*. Doris, *C* Batalini × *Lc* Edgard Van Belle, *Lc*. Rojo *Sl* Psyche, *Slc*. Falcon, *Slc* Petit Rouge, *Slc* Rocket Burst, *Slc* Dexie Jewel, *Slc* Madge Fordyce, *Slc* Morning Glory, *Slc* Tropic Dawn
 P_1	*S coccinea rosea* *Sn violacea*	*Sl* Atreus, *Slc* Meuzac, Slc Anzac,
 P_2	*C amethystoglossa* *C labiata* *L pumila* *L purpurata*	*B*. *nodosa* × *C* Dinah, *C* Sedlescombe, *Ctn* Rosy Jewel, *L pumila* × *L*. *rupestris*, *Lc* Don de Michaelis, *Lc* Dr Peng, *Lc*. Gila, *Lc*. Helen Wilmer, *Lc*. Olga, *Lc*. Ramo Prada, *Lc* Windermere, *Pot*. Gordon Siu, *Pot* Mem. H Gauda, *Sc* Batemaniana, *Sc*. Rose Pixie, *Slc* Anzac, *Slc* Estella Jewel, *Slc* Jewel Box, *Slc* Lindoress, *Slc* Phena, *Slc* Trizac, *Slc*. Vallepatra, *Slc* Vallezac
 P_3	*C intermedia aquinii* *L. pumila* *L purpurata sanguinea* *L rupestris*	*Bc* Admiral, *Bc* Mount Hood, Bc Mount Anderson *Bc* Princess Patricia, *Blc*. Amy Wakasugi, *Blc*. Helons Ghyll, *Blc* Normans Bay, *Blc*. Pamela Farell, *C* Adalio, *C* Fabingiana, *C* J. A Carbone *C* Portia, *C*. Remy Chollet, *Lc* Alcidar, *Lc* Cecile Simons, *Lc* Bonanza, *Lc* Consul, *Lc* Governer Gore *Lc*. Hyperion, *Lc* Medon, *Lc* Momus, *Lc* Supervia, *Lc* Victoria, *Epc* Rosita, *Pot* Medea, *Slc* Cibola

z The same as the previous paper(1)

* Spots on the ground

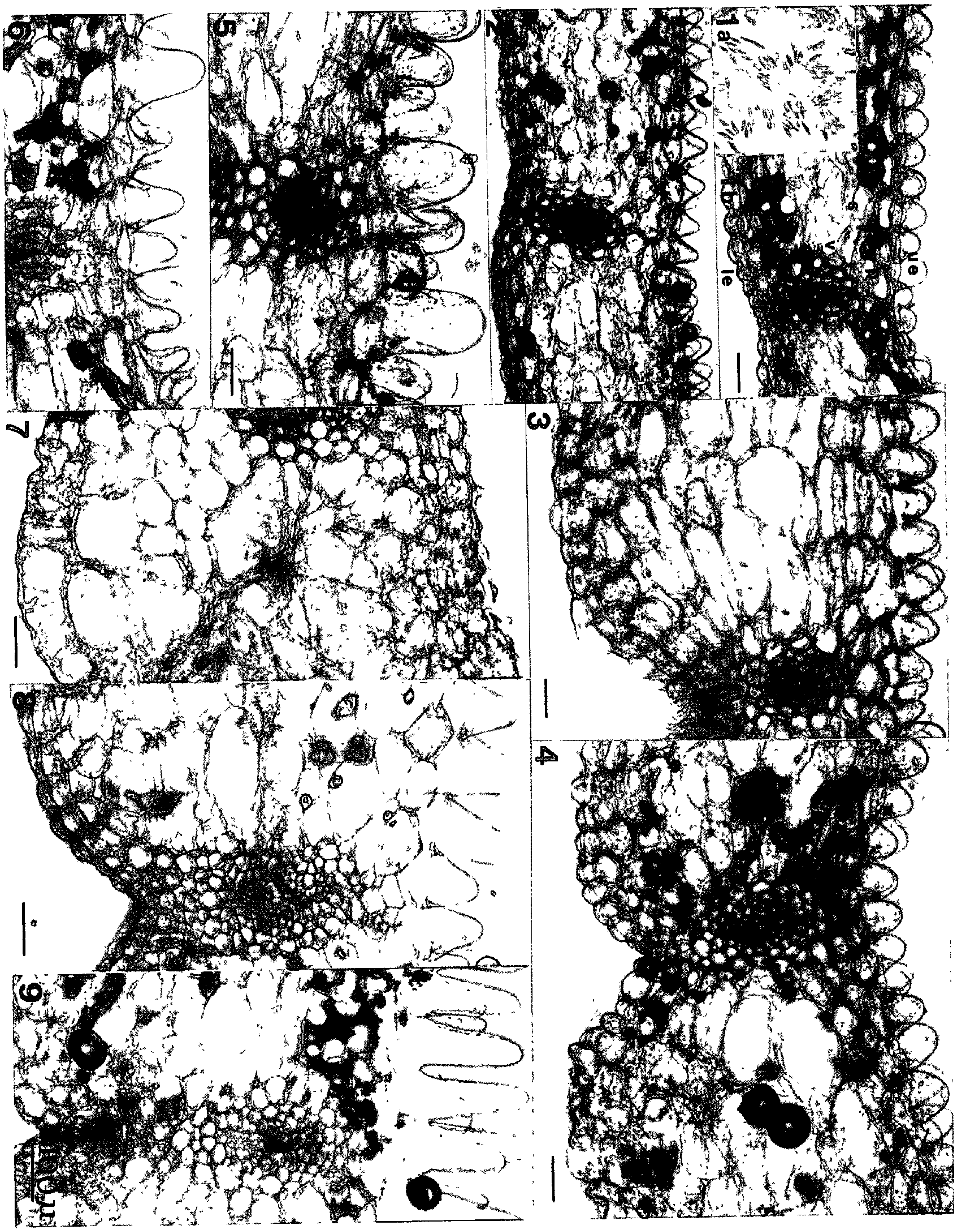


Fig. 1 Distribution of flower pigments in petals and lips.
1, *Sl.* Valda, chromoplasts in the bottom of epidermal cells (a), Y2,
2, *S.* Alizona, R'1, 3. *Slc.* Madge Fordyce, R'3, 4, *Slc.* George Hauserman, R'2,
5, *Slc.* Anzac, P3, 6, *Lc.* Helen Wilmer, P3, 7, *B. nodosa* × *C.* Dinah, P3,
8, *Lc.* Irene Finney, P2, 1-8, petal, 9, *Lc.* Windermere, Lip.
Details : le, lower epidermis; p, palisade tissue; s, spongy tissue; ue, upper epidermis; v, vascular bundle.

distribution. In spite of the descendants (Fig. 1—2 and 3) of *S. coccinea*, *Slc.* George Hauserman (Fig. 1—4) lost the anthocyanin distribution in epidermis. The R′3 type was found in many hybrids (Fig. 1—3), although among the species only *C. velutina* (not ground but spots of the petal) was included in this type[1]. In conclusion, the hybridization resulted in the increased patterns of pigment distribution. Besides, patterns unexpected from that of the used parent appeared. For example, *B. nodosa* blooms a white flower and *C.* Dinah blooms P2 type flowers which show no anthocyanin pigmentation in epidermis but in palisade and spongy tissues. Their hybrid blooms purple flowers, but the epidermis of the petal was P3 of which anthocyanins were contained in both epidermis and parenchymatous tissues (Fig. 1—7).

Although the Y1 type (no carotenoids in epidermis) is expected to be main in yellow petals of hybrids because of no pigmentation of the epidermis of leaves, the homologous organ of perianth, it included a few plant descendants of *L. flava* and *En. mariae*. However, the Y2 types were found in many hybrids (e. g., *Sl.* Valda in Fig. 1—1).

Descendants of *S. coccinea*, which is a species blooming a true red flower and showing the R′ 1 pattern (Fig. 1—2), expressed many patterns. However, in terms of anthocyanin pigmentation, a great part of them (Fig. 1—3 and 5) yielded anthocyanins in epidermis in the same way as the parent. *Cattleya* and their intergeneric hybrids such as *Brassocattleya*, *Brassolaeliocattleya* and *Laeliocattleya* bloom lavender flowers. They contained anthocyanins in the same way as both petals and lips of their parents (Fig. 1—8 and 9). However, descendants of *C. intermedia* var. *aquinii* and *Lc.* Helen Wilmer (Fig. 1—6), a descendant of *C. trianae* and *L. pumila*, contained anthocyanins in the epidermis of perianth.

2. *Distribution of flower color of hybrids according to Hunter's color chromaticity*

Brassavola hybrids were distributed in the area of yellow green (e. g., *Blc.* Mem. Helen Brown) to white (*Bc.* Deese), then purple (*Blc.* Helons Ghyll) in the chromaticity diagram (Fig. 2, straight line bounds). Those of *Sophronitis* were located around the red area, especially when it was crossed with *Laelia* species : hues (expressed by b / a value) changed markedly according to the nature of the parent *Laelia*s. Thus, sometimes carotenoids and anthocyanins coexisting in *S. coccinea* were separated as shown by yellow petals in *Sl.* Valda and purple ones in *Sl.* Orpetii. *Laelia*s and their intergeneric hybrids (pink dots in Fig. 2) presented the greatest diversity of hues and the distribution patterns in the perianth tissues of Laeliinae orchids as shown in the species[1].

In *Cattleya* hybrids, the *C. labiata* group was distributed in an area presenting purplish red (Fig. 2—8) which are called the "lavender" *Cattleya*s, but hybrids of *C. intermedia* var. *aquinii* with "splashed" petals (Fig. 2—7) were distributed in the relatively narrow area showing more reddish than the *C. labiata* group (Fig. 2, two dot chain bounds). The hue of *Lc.* Victoria coerulea, usually named the "blue" *Cattleya*, was −1.1, presenting not real blue but purple.

The part for the chromaticity measurement was one third of the way from the perianth-tips, because on the same perianth, it is usual for the perianth colors to change in the part measured, especially in red flowers. One of them was *Slc.* Paprica "Sunset Hill" (Fig. 2—5) of which both petal and sepal changed orange red at the base to red at the tip (Fig. 3). High chromas presented by b/a decreased in brightness (L value). *Broughtonia* hybrids were located in a narrow red area with low brightness (Fig. 2, dot chain bounds).

3. *Shape and size of upper epidermal cells of perianth*

The shapes of the upper epidermal cells in petals and lips of hybrids were classified into 5 types according to the characteristics of parental species[5] and shown numerically in Table 3. For example, a hybrid of an a—type species and a 1—type one might be expected to be 5.0 because the a—type and

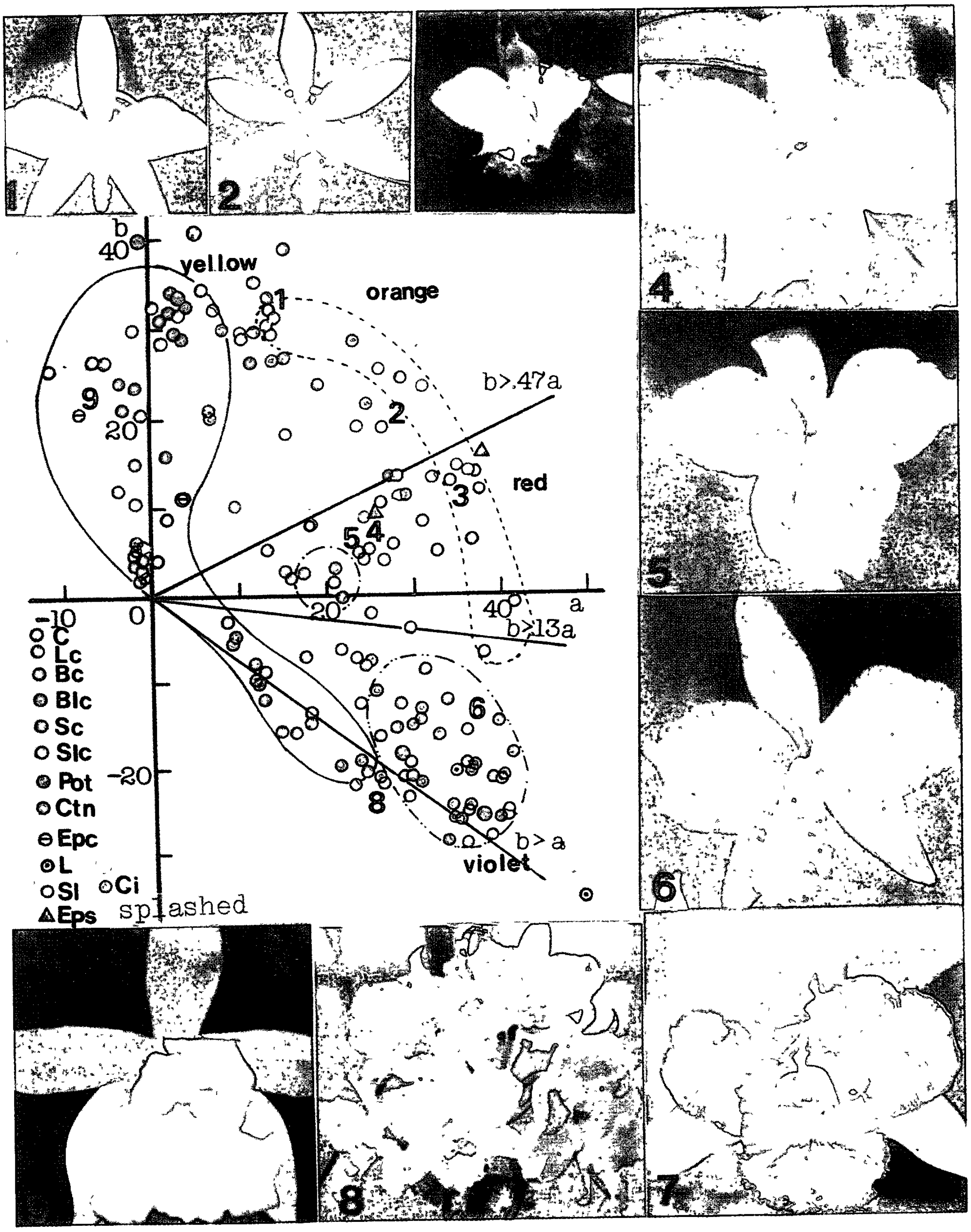


Fig. 2. A chromaticity diagram of hybrids and some flower colors.
1, *Sl*. Valda, 2, *Lc*. Eva, 3, *Sl* Psyche, 4, *Slc*. Falcon, 5, *Slc*. Paprica, 6, *Slc*. Anzac, 7, *Sc*. Batemaniana, 8, *C*. Fabingiana, 9, *Epc*. Vienna Wood.
$b \geqq .47a$: carotenoids only.
$-.13a \leqq b < .47a$: carotenoids and anthocyanins.
$b < -.13a$: anthocyanins only.

the l—type are 1.0 and 9.0, respectively, and the crossing is (1.0+9.0) / 2. This may indicate the f—type (5.0). However, the actual value was 7.7, which was near the value of the p-type, indicating a likely shape of *L. purpurata*. The ratios of height to width of epidermal cells in both petals and lips increased according to the crossing of a×a to l×l. The ratios also affected brightness (data omitted).

Regression equations of the epidermal cell sizes in 67 hybrids to those of parents were calculated as follows :

Shape $y=1.082+.320x1+.568x2^{***}$
$R^2=.861$

Petal height $y=.874+.500x1+.406x2^{***}$
$R^2=.819$

width $y=-1.041-.057x1+1.276x2^{*}$
$R^2=.242$

h/w $y=33.006+.350x1+.329x2^{**}$
$R^2=.515$

Lip height $y=2.798+.494x1+.366x2^{***}$
$R^2=.732$

width $y=3.242+.228x1+.371x2^{**}$
$R^2=.602$

h/w $y=35.695+.283x1+.448x2^{***}$
$R^2=.668$

R^2 of the shape types was high, indicating that the characteristics of hybrids were significantly inherited from the parents and their shape types were able to be estimated from the parent types. The shape types were mainly dependent on the height of epidermal cells in petals and lips. The characteristics of some genera and species, *C. aurantiaca* (a—type), *L. flava*, *L. pumila*, *L. cinnabarina* and *L. milleri* (f—type), *S. coccinea* (f—type) and the *C. labiata* group (l—type) were genetically examined (Fig. 4). The remaining genera except the *C. labiata* group showed a significant correlation of the shape type, in which *C. aur-*

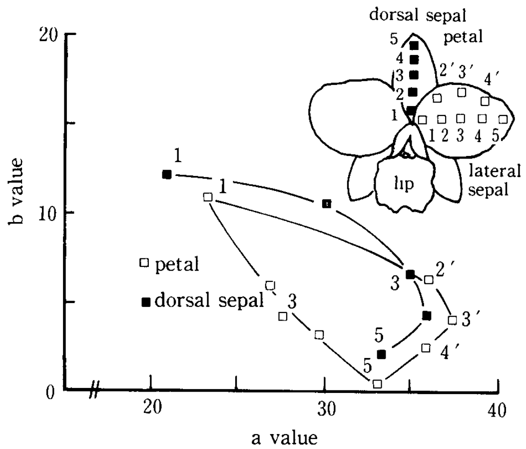


Fig. 3 Difference of hue (b/a value) in petal and sepal parts of a hybrid, *Slc.* Paprica 'Sunset Hill' (see Fig. 2—5).

Table 3. Characteristics of epidermal cell shape in petals and lips of hybrids produced by the crossings of parents with different types of the epidermal cell shape in flowers

Classification of parental type of plants used		a	h	f	p	l
a	Classification of hybrids[z]	1.0	3.0	4.0	3.0	7.7
	H/W for petal[y]	0.54	0.78	0.79	0.60	1.14
	H/W for lip[y]	0.75	0.80	0.91	1.00	2.39
h	Classification of hybrids		3.0	4.3		6.3
	H/W for petal		0.60	0.87		0.98
	H/W for lip		0.75	1.03		1.16
f	Classification of hybrids			6.1	5.7	7.7
	H/W for petal			1.07	0.90	1.14
	H/W for lip			1.18	1.17	1.63
p	Classification of hybrids				7.0	7.5
	H/W for petal				1.10	0.97
	H/W for lip				1.45	1.67
l	Classification of hybrids					9.0
	H/W for petal					1.46
	H/W for lip					2.03

z Values are calculated from the values given to the cell shapes (a-, h-, f-, p- and l-types are 1, 3, 5, 7, and 9, respectively).

y Ratios of hight to width of the epidermal cells in petals and lips, respectively.

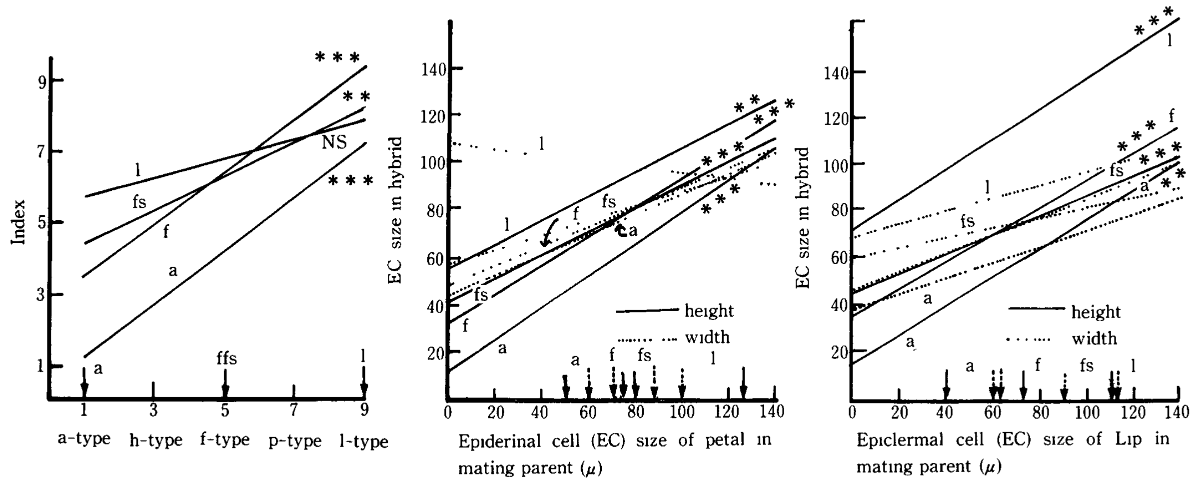


Fig. 4. Parental ability of *C. aurantiaca* (a) (a-type), *L. flava* type *Laelias* (f) (f-type), *S. coccinea* (fs) (f-type) and the *C. Labiata* group (l) (l-type) to affect the cell shape and size of epidermis.
N. S. : Not significant; ** and ***, significant at the 1% and 0.1% levels, respectively.

antiaca was most dependent on genotype of another parent, and *S. coccinea* tended to persist in expressing its own nature. Data also show that the correlation between those of hybrids and parents were mainly attributable to the inheritance of height of epidermal cells in both petals and lips.

DISCUSSION

In *Cattleya* and allied genera, excellent hybrids blooming large white and lavender flowers with heavy texture were obtained relatively early in this century. However, it takes a long time to remedy defects of flowers in *C. dowiana* and yellow *Laelia*s and to produce a nearly complete shape and good yellow color, though we can see good yellow varieties at present. The same red flowers as those of *S. coccinea*, which has a defect of small flower size, have been acquired through further breeding. In addition to these attempts hybrids revealing the attractive nature of a species, such as green, blue and "splashed" flowers, also tend to increase.

The genetics in relation to flower color is not sufficiently clarified. As to white and lavender, Woodward stated Hurst's theory of the complementary genes in which the genotype C—R— produces lavender flowers but C—rr and ccR— white[5]. Thus, *Bc.* Mount Hood with lavender flowers is result of the crossing of *C.* Bow Bells (ccRR) and *Bc.* Deese (CCrr). The distribution patterns of anthocyanins in most hybrids were P2. This included *Cattleya*, *Bc.*, *Lc.*, and *Blc.* hybrids. The epidermal presence of anthocyanins (P3) in hybrids of *S. coccinea* and *C. intermedia* var. *aquinii* indicates that this distribution is dominant. Assuming that the pigmentation in epidermis is controlled by one gene, a famous tetraploid hybrid, *Slc.* Anzac, is considered to be produced as follows : *S. coccinea* (AA) × *L. cinnabarina* (——) ⟶*Sl.* Psyche (A—) × *C.* Empress Frederick (aa)⟶*Slc.* Marathon (Aa) × *Lc.* Dominiana (aa)⟶*Slc.* Anzac (AAaa). Thus, it is explained to be a good parent producing the "sophro red" flowers.

Another species, *C. intermedia* var. *aquinii*, forms a group of so-called "splashed" flowers. Its color was more reddish than the lavender flowers but less than the "sophro red", implying that it is available to breed red flowers. This may come from petals transformed into lips (splashed)[1] and the anthocyanin constituents revealed by Yokoi[6], indicating that petals of species and hybrids contain only cyanidin, whereas the lips contain both cyanidin and peonidin.

An unexpected hybrid from its parents was observed as in the case of *Vanda* hybrids[4]. The reason is not clear but it is useful to produce new types of flower colors.

As to the reason that there were no hybrids with large, yellow and well-shaped flowers, Karasawa provided the following explanation : *C. dowiana* producing large yellow flowers with a well-shaped lip is not dominant in relation to lavender flowers, and species such as *L. cinnabarina, L. xanthina* and *L. tenebrosa* are dominant but produce small flowers or those with narrow and twisted petals[3]. The effort to produce good hybrids from these imperfect species has been continued.

Variations of flower colors in color chromaticity show the release of genetic potentialities included in the species or genera concerned. *Brassavola* hybrids were spread in yellow, white and lavender areas, that is, in symmetrical areas centered on the origin and in the area with no "sophro".

The attempt to produce large flowers with the same red color as *S. coccinea* was almost completed in *Slc.* Vallezac, both by gross observation and with apparatus as well. Thus, not only in species but also in hybrids the coexistence of carotenoids and antocyanins is necessary to express true red. Orange flowers in species contained no anthocyanins. However, "sunset" color flowers are found in hybrids (e. g., *Slc.* George Hauserman) and contained the anthocyanins in the parenchymatous cells in low color density.

Inheritance of epidermal cell shapes and sizes was partially clarified in relation to genera and species. As shown in the tables and the regression equations, on the average F1 shows intermediate characteristics of both parents. The *C. labiata* group insisted on the appearance of characteristics. Thus, it was one of good parents blooming large white and lavender flowers with heavy texture. On the other hand, shapes and sizes of epidermal cells in *C. aurantiaca*, the group of *L. flava* and their hybrids were relatively dependent on mating parents, suggesting that these can be useful to produce hybrids containing carotenoids.

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Cattleya およびその近縁属における花被組織内の色素分布

II 交　配　種

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農　　　　　場

（1988年8月1日受理）

要　　　約

Cattleya および近縁属の交配種約210について原種と同様に花色素の花被内分布，花被色および表皮細胞の形状について調査し，原種との相関について検討した。

1　花被内のカロチノイドとアントシアニンの分布様式は原種より多く，12のパターンに分類した。ラベンダー系の *Cattleya, Brassocattleya, Brassolaeliocattleya* や *Laeliocattleya* は親と同じ分布様式 P_2 を示したが，*C. intermedia* var. *aquinii* や *C. trianae* と *L. pumila* の子孫で表皮にアントシアニンを含む（P_3）交配種があった。また，*Sophronitis* の子孫でもカロチノイドを欠く“ソフロレッド”のものは P_3 であった。

赤色花はカロチノイドとアントシアニンを共に含んでいた。アントシアニン色素を表皮に含む *Sophronitis* の子孫が多かった。しかし，表皮にアントシアニンを含まない赤色の *Sophronitis* の子孫も少数あった。

2　*Brassavola* の子孫は黄緑，白，ラベンダー色と色度図上原点を通って分布し、赤色の交配種はなかった。色度図上から，ラベンダー系の交配種より，楔花，楔花より“ソフロレッド”の花の方がより赤味が強かった。*S. coccinea* は *Laelia* と交配したとき，その親となる種によって広く分布した。

3　交配種の表皮細胞の形や大きさは両親の性質を強く受けた（回帰係数で，形，0.32～0.56，花弁・高さ，0.40～0.50，唇弁・高さ，0.37～49）。また，種や種を構成するグループによって影響の表われ方は異なった。*C. aurantiaca* は交配相手の影響が出やすく，*C. labiata* グループはグループの形質の影響が強く出た。