Distribution of Flower Pigments in Perianth of *Cattleya* and Allied Genera I. Species

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Summary

Distribution patterns of flower pigments and the shape of epidermal cells in perianth tissues in 11 genera of Laeliinae orchids were investigated in relation to flower colors.

1. The 68 species examined were classified into nine groups on the basis of differences in distribution patterns of the carotenoids and anthocyanins contained in epidermal and/or parenchymatous cells in petal tissues. Yellow and orange flowers in such species as *Laelia harpophylla* and *L. cinnabarina* contained carotenoids in both epidermal and parenchymatous cells but those of *Cattleya dowiana* and *L. flava* contained them only in parenchymatous cells. Red flowers were ascribed to the coexistence of carotenoids and anthocyanins. In *Sophranitis coccinea* and *L. milleri* carotenoids were contained in both the epidermal and parenchymatous cells but anthocyanins only in the epidermis, while *L. tenebrosa* contained anthocyanins only in the parenchymatous cells.

Purple flowers were classified into three groups according to the presence or absence of anthocyanins in the epidermal and parenchymatous cells. The purplish red flowers of most *Cattleya* species contained anthocyanins in the parenchymatous cells. Some exceptional *Cattleyas*, *C. intermedia* var. *aquinii* and *C. leopoldii*, contained anthocyanins in the epidermis of splashed or spotted petals. *Laelia* species blooming in deep purple flowers contained anthocyanins in the epidermis but those of pale flowers did not.

2. A Hunter's diagram of the color chromaticity of petals was divided into three sections according to hue: in the first, the b/a value of yellow to orange petals was more than .47, due to carotenoid pigmentation only; in the second, the value lay between .47 and —.13 and the flowers were red due to both carotenoid and anthocyanin pigments with one exception (*S. coccinea* var. *rosea*); in the third, with values between —.13 and —1.0, purplish-red, so-called 'orchid tone', prevailed.

In petals containing carotenoids, increased chromas corresponded to greater brightness, but increased chromas caused by intensive anthocyanin coloration in petals and lips corresponded to less brightness, as exemplified in the velvety texture of the lips in *Cattleyas*.

3. The size and shape of the upper epidermal cells in petals and lips varied by species, but within the same genus the variations were serial; small cells were square and appeared in glossy flowers, while large ones were triangular and caused the velvety appearance. The augmented size and the change from square to triangular shape might manifest the direction of evolution. Plants with large showy flowers in such species as *C. labiata*, *L. purpurata* and *Brassavola digbyana* had the largest and longest epidermal cells in each genus.

Introduction

Numerous interspecific, intergeneric hybrids of *Cattleya* and allied genera (Subtribe

Laeliinae) have been produced in order to improve flower characteristics, i.e., the size, shape and color of flowers and desired flowering time. Cross combinations have increased so markedly that much effort has been made

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to breed new varieties yielding bright red or yellow flowers with excellent shape(4, 5). Basic information about flower color and perianth substance is necessary for effective

breeding and for taxonomy. The taxonomic significance of orchid anthocyanins has already been proved in various genera and species(2, 3, 9). Carotenoids, chlorophylls

Table 1. Distribution patterns of flower pigments in perianth and their variations in species.

Classification*	y	Species
W		<i>B. cuculata</i> (W, 1) ^z , <i>B. digbyana</i> (W, 2), <i>B. glauca</i> (W, 3), <i>B. nodosa</i> (W, 4), <i>B. perrinii</i> (W, 5), <i>C. intermedia alba</i> (W, 15), <i>C. intermedia coerulea</i> (P3, 17), <i>C. mendelii</i> (P3, 21), <i>C. mossiae semialba</i> (P3, 23), <i>C. percivaliana alba</i> (R' 3, 24), <i>C. skinneri alba</i> (W, 26), <i>En. cochleata</i> (W, 2), <i>En. radiata</i> (W, 6), <i>L. purpurata alba</i> (P3, 15), <i>L. purpurata carnea</i> (P3, 16), <i>L. rubescens</i> (W, 21), <i>Lpt. bicolor</i> (P3, 1)
Y ₁	Cp	<i>C. aurantiaca</i> (Y 1, 3), <i>C. dowiana</i> (P3, 9), <i>L. flava</i> (Y 1, 5), <i>L. mixtra</i> (Y 1, 13), <i>En. mariae</i> (W, 4)
Y ₂	Ce Cp	<i>C. aurantiaca</i> 'yellow' (Y 2, 4), <i>C. forbesii</i> (Y 2, 10), <i>C. granulosa</i> (P3, 12), <i>C. leopoldii</i> (P3, 14), <i>C. velutina</i> (P3, 28), <i>L. cinnabarina</i> (Y 2, 3), <i>L. harpophylla</i> (Y 2, 6), <i>L. milleri</i> 'yellow' (Y 2, 12), <i>L. xanthina</i> (W, 20), <i>En. aromatica</i> (1), <i>En. prismatocarpa</i> (5), <i>En. vitellina</i> (Y 2, 7), <i>Epi. cinnabarinum</i> (Y 2, 8), <i>Epi. falcatum</i> (Y 2, 9)
R ₃	Cp Ae Ap	<i>Bro. sanguinea</i> (R 3, 1)
R ₁	Ce Cp Ae	<i>L. miller</i> (R' 1, 11), <i>S. cernua</i> (R' 1, 1), <i>S. coccinea</i> (R' 1, 2)
R ₂	Ce Cp Ap	<i>C. bicolor</i> (P2, 5), <i>C. dormaniana</i> (P3, 8), <i>C. granulosa</i> *, <i>En. cordigera</i> (P2, 3), <i>L. tenebrosa</i> (P2, 3), <i>Schom. thomsoniana</i> (Y2, 1)
R ₃ '	Ce Cp Ae Ap	<i>C. velutina</i> *
P ₁	Ae	<i>S. coccinea rosea</i> (P1, 3), <i>Spn. violacea</i> (P1, 1)
P ₃	Ae Ap	<i>C. leopoldii</i> *, <i>C. intermedia aquinii</i> (P3, 16), <i>En. prismatocarpa</i> *, <i>L. gouldiana</i> (P3, 7), <i>L. pumilia</i> (P3, 14), <i>L. purpurata sanguinea</i> (P3, 17), <i>L. rupestris</i> (P3, 18)
P ₂	Ap	<i>Bark. spectabilis</i> (P2, 1), <i>C. amethystoglossa</i> (P3, 1), <i>C. amethystoglossa coerulea</i> (P3, 13), <i>C. bowringiana</i> (P3, 6), <i>C. guatemalensis</i> (P3, 13), <i>C. labiata autumnalis</i> (P3, 18), <i>C. lueddemanniana</i> (P3, 19), <i>C. maxima</i> (P2, 20), <i>C. mendelii</i> (P3, 21), <i>C. mossiae</i> (R 2, 22), <i>C. skinneri</i> (P3, 25), <i>C. trianae</i> (R 3, 27), <i>C. walkeriana</i> (P2, 29), <i>L. anceps</i> (P1, 1), <i>L. perrinii</i> (P3, 22), <i>L. pumila</i> (P2, 14), <i>L. purpurata</i> (P3, 15)

* Alphabet letters and arabic numerals in parenthesis indicate the distribution pattern in lips and species number appearing in the following figures.

^z Ce and Cp indicate the presence of carotenoids in epidermal and parenchymatous cells, respectively. Ae and Ap indicate the presence of anthocyanins in epidermal and parenchymatous cells, respectively.

* Dots indicate carotenoids and striped cells contain anthocyanins.

* Distribution in spots and barred patterns in petals.

and anthocyanins are the main components affecting flower color in orchids. However, variations in flower color are well-known to be affected not only by the chemical nature and amount of pigment but also by the distribution of pigment in tissues and the shapes of the epidermal cells(11,12). The shape and size of epidermal cells also affect flower texture such as a velvety and glossy appearance. Black roses(11) and *Renanthera* orchid flowers(7), which have a velvety appearance, have ovate epidermal cells.

Laeliinae orchids, that is, *Cattleya* and allied genera, bear flowers with very different colors and substances. However, specific information on species is scanty at present. The aims in this study were clarify difference among species and genera in pigment distribution and epidermal cell characteristics, and to examine the relationship between these factors and flower color, from the point of view of their efficacy for taxonomic classification and new crossings.

Materials and Methods

Flowers of Laeliinae orchids including *Barleria* (abbreviation, *Bark.*), *Brassavola*(*B.*), *Broughtonia*(*Bro.*), *Cattleya*(*C.*), *Encyclia*(*En.*), *Epidendrum*(*Epi.*), *Laelia*(*L.*), *Lep-totes*(*Lpt.*), *Schomburgkia*(*Schom.*), *Sophronitella*(*Spn.*) and *Sophronitis*(*S.*) were collected from the greenhouse of the Experimental Farm of Gifu University, Nagata Engei Co. in Aichi Prefecture, Ohgaki Engei in Gifu Pref., Kokusai Nursery Co. in Tokyo and Ohba Orchids Co. in Tokyo. First, the colors of the dorsal and lateral sepals, petals and lip (labellum) were separately measured with a color chromaticity apparatus (Nihon Denko Model 503-DE). Flower color was expressed in Hunter's color notation. For microscopic observation the petals and lips were hand-sectioned one third of the way from the tips, in the same area as used for the chromaticity measurement. With a micrometer-equipped microscope(Olympus BHS) the size of the epidermal cells of the petals and lips were measured and their shape and the distribution of anthocyanins and carotenoids in the tissues observed. Anthocyanins

were identifiable by the red to purple color in cell sap and carotenoids by yellow- to orange-colored plastids in the cells(7,12).

Results

1. Distribution of flower pigments in perianth tissues

Distribution patterns of flower pigments in the petals of the 68 species examined were classified into nine groups on the basis of the presence or absence of carotenoids and anthocyanins in upper epidermal and/or parenchymatous (palisade and spongy) cells (Table 1). Yellow petals contained carotenoids either only in parenchymatous cells (Y 1) or in both parenchymatous and epidermal cells (Y 2). In the parenchymatous tissues palisade cells contained granulated yellow or orange plastids, while in the epidermal cells most colored plastids were deposited at the cell bottom (Fig.1 a and b). Group Y 1 included *C. dowiana*, *C. aurantiaca* and *L. flava* and also the leaves belonging to this group, whereas Y 2 included *L. harpophylla*, *L. cin-nabarina*, *L. xanthina* and *En. vitellina*. Carotenoids were contained in yellow lips in the same way as in yellow petals.

Red color was ascribed to the coexistence of carotenoids and anthocyanins. In petals of *L. milleri*, *S. coccinea* and *Bro. sanguinea* anthocyanins were distributed in the epidermal cells, while carotenoids were found in the epidermal cells and parenchymatous tissues in the former two species (R' 1, Fig. 1 c) and in the parenchymatous ones in the latter (R 3). However, the brown petals of *L. tenebrosa*, *C. bicolor* and *En. cordigera* contained anthocyanins in the parenchymatous rather than the epidermal cells, along with carotenoids and chlorophylls (R'2). Purplish-red flowers were classified into group P 1, P 2 and P 3, according to whether anthocyanins were found in the epidermis only (P 1), in the parenchymatous tissues (P 2), or in both tissues (P 3). No *Cattleya* examined contained anthocyanins in the epidermal cells (P 2) (Fig.1 f) except for the spots on petals of *C. leopoldii* and the splashed petals of *C. intermedia* var. *aquinii* (Fig. 1 d), which were P 3. The anthocyanin-

Fig. 1. Flower colors and distribution of pigments in perianth tissues of Laeliinae orchids.

a : Flower color and carotenoids in peeled epidermis of *L. cinnabarina* petal, b : carotenoids in *L. harpophylla* petal, c : anthocyanins in epidermis with carotenoids in *L. milleri* petal and its flower color, d : splashed petals of *C. intermedia* var. *aquinii*, e : Flower color of *S. coccinea* var. *rosea*, f : anthocyanins in parenchymatous cells in *C. trianae* and its flower color, g : anthocyanin distribution in *C. mossii* lip.
 Note: e : epidermis, le : lower epidermis, p : parenchymatous cell, v : vascular bundle

colored lips of most *Cattleyas* belonged to P 3 as well (Fig. 1g), even when the petals belonged to P 2.

Three species bearing flowers close to blue, *C. amethystoglossa* var. *coerulea*, *C. intermedia* var. *coerulea* and *L. rubescens*, were examined. In the lip of the first species, anthocyanins existed in granules in the vacuole of cells and in the second in soluble state in it, whereas in the third species the anthocyanins lay in the colored vacuoles but in granular form in some cells.

Sophronitella is a species close to *Sophronitis*, and the distribution of anthocyanins was the same (P 1) as that in *S. coccinea* var. *rosea* (Fig. 1e), which is a variety of *S. coccinea* producing mauve flowers due to the absence of carotenoids. *Laelia* species such as *L. pumila*, *L. purpurata* and *L. gouldiana* blooming in intensely colored flowers were classified as P 3, although *L. pumila* and *L. purpurata* plants with pale pink flowers and *L. anceps*, morphologically close to *L. gouldiana*, were P 2.

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

In Hunter's color notation, L indicates brightness (value), and a and b coordinates give hue (b/a) and chroma ($\sqrt{a^2+b^2}$). The hues and chromas of Laeliinae orchids examined are shown in Fig. 2. It can be useful to divide the diagram into three sections on the basis of hues and the presence or absence of carotenoid and anthocyanin pigments. The same procedure has been used as in a survey of miscellaneous orchids by Yokoi (13). The section in which $b/a \geq .47$ included greenish-yellow to yellow flower species such as *C. dowiana*, and *L. xanthina*, the well-known parents of yellow hybrids. *L. cinnabarina* (Fig. 1a), *Epi. cinnabarinum*, *En. vitellina* and *C. aurantiaca* bear similar orange flowers; therefore, their hues were close to each other. This section was characterized by the carotenoid origin of the colors. However, *L. tenebrosa*, a parent of yellow hybrids, *En. aromatica*, *En. cordigera*, *C. bicolor* and *Schom. thompsoniana*, all of which have brown flowers due to the presence of carotenoids, chlorophylls and anthocyanins,

Fig. 2. Distribution of petal colors in Laeliinae orchids on a Hunter's color chromaticity diagram. Numbers are of species shown in Table 1.

were located close to the origin, presenting no hue with low brightness.

The species in the section bounded by $-.13 \leq b/a < .47$ display red flowers and contained coexisting carotenoids and anthocyanins with one exception (Fig. 1c). This section corresponded to the R and R' distribution patterns in the Table 1. One representative species was *S. coccinea*, which is the most fascinating and the most valued because it bears a true red flower itself and hands down its ability to descendants. *S. coccinea* var. *rosea* was located in the red color section in spite of the absence of carotenoids.

Most 'orchid tone' colored petals were located in the range between $-.13$ and -1.0 and characterized by the presence of anthocyanins only (Fig. 1f). In some species varietal plants called 'coerulea' having more purplish flowers than usual are found. The two 'coerulea' varieties of *C. amethystoglossa* and

Fig. 3. Relationship between brightness and b values of petals containing carotenoids or both carotenoids and anthocyanins. Numbers are of species shown in Table 1.

C. intermedia had almost the same b/a values for petals which were more than -1.0 like those of *C. labiata* and *L. pumila*, and the hues their lips were similar to those of the latter species. However, distinct difference are observable by the naked eye.

High chroma is considered indicative of high carotenoid and anthocyanin contents and it is expected to correlate with brightness. A regression equation relating brightness (L values) and b values (yellowness) of petals in species containing carotenoids alone and those containing both carotenoids and anthocyanins was as follows: $y = .864x + 32.0$, $r = .620^{**}$ (Fig. 3). Brightness is positively related to the amount of carotenoid expressed by the b values. In the species containing only anthocyanins in their petals and lips, regression correlating brightness and chroma were $y = .940x + 68.8$, $r = -.930^{**}$ for petals and $y = -.596x + 51.2$, $r = -.498^{**}$ for lips (Fig. 4). Obviously, high levels of anthocyanins decreased brightness. Data on sepals is omitted because of the similarity of their hue to petals.

3. Shape and size of upper epidermal

Fig. 4. Relationship between brightness and chromas of petals (above) and of lips (bottom) containing anthocyanins. Numbers are of species shown in Table 1.

cells

Floral organs are referred to as floral leaves. The original shape and size of their epidermal cells might be noticed in cells of leaves which are small and square. Changes in shape from square to deltate suggest the direction of evolution in the genera. In Laeliinae orchids, serial variations in the shape and size of the upper epidermal cells of petals and lips were found. Five typical shapes appeared: *C. aurantiaca*, with square cells in both petals and lips (a-type); *L. harpophylla*, square cells in petals and deltate ones in lips (h-type); *L. flava*, deltate cells in both petals and lips (f-type); *L. purpurata*, deltate cells in petals and long deltate or triangular ones in lips (p-type); *C. labiata*, long deltate cells in both petals and lips (l-type). As shown in Fig. 5, the *Cattleya* genera showed the most varietal

Fig. 5. Changes in size and shape of epidermal cells in perianth of Lealiinae orchids.
^a 16/10 and 25/12 indicate height and width of cells in petal and lip, respectively ($\times 10 \mu$)
a: *C. aurantiaca* type, h: *L. harpophylla* type, f: *L. flava* type
p: *L. purpurata* type, l: *C. labiata* type.

difference in shapes and sizes of epidermal cells in perianth.

It is noticeable that the greater the size of the epidermal cells and the more deltate their shape, the more showy and larger the flowers were. These species were *C. labiata*, *L. purpurata*. *En. mariae* and *B. digbyana*, all of which have produced so many excellent progeny by interspecific and intergeneric crossings as to prove their significant parentage.

The shape and size of epidermal cells, especially the ratio of height to width, affect flower texture. *C. aurantiaca* produces glossy flowers, and the height/width ratio of its epidermal cells, each shaped like a brick, was less than 1.0. On the other hand, unifoliate *Cattleyas* have heavy substances and velvety appearance, and the ratios were high. In addition, when the ratios were large, the color brightness was generally low. A multiple regression equation expressing the L

value(y) as a function of chroma (x1) and the ratio of height to width (x2) was calculated as follows: $y = -1.268x_1 - 1.00x_2 + 82.9$. The regression coefficient R^2 was 898** and the single regression coefficients for x1 and x2 were $-.782^{**}$ and $-.582^{**}$, respectively. This shows that high ratios as well as high chroma correlate with low brightness.

Discussion

It is said that flower pigments are usually contained in the epidermis(12), and indeed, a microphotograph of a petal section of a *Papiyopedilum* hybrid shows anthocyanins in the epidermis(4). However, the petals of *Cattleya* orchids examined first showed no pigment, although the lips contained it as was expected. This finding led to further investigation in other genera and species.

Leaves, especially the lower surface, of

species such as *B. digbyana*, *C. labiata*, *L. cinnabarina*, *Lpt. bicolor* and *S. coccinea*, exhibit the anthocyanin pigmentation. In all of them the pigmentation was observed in the parenchymatous tissue, not in the epidermis (P2). Thus, considering that perianths are floral leaves, species classified into P2 could be manifesting the original distribution pattern of anthocyanins. P3 species might have originated from those of P2. This was evidenced by the P3 anthocyanin pigmentation observed in unusual barred patterns and spots on petals in some *Cattleya* and *Encyclia* species, and also by some *Laelia* species which have the P2 pattern in pale colored petals but P3 in deep colored ones. Most species examined, furthermore, exhibited P3 pigmentation in the lips, which are highly modified and thus more advanced organ than other two petals. The same observation was made of Vandae orchids(7). Therefore, anthocyanin pigmentation of barred patterns in petals and of lips might be related to evolutionary direction. At the same time, it has taxonomic significance; *Cattleya* is regarded as the genus containing no anthocyanin in the epidermis of the petals, whereas *Sophronitis*, *Sophronitella* and *Broughtonia* have it. These genera could be intermediated by *Laelia* because *Laelia* showed both P2 and P3 distributions.

The P2 distribution is also related to the so-called 'orchid tone' or lavender color (Fig. 1f). The distribution in *Cattleya* species was measured as a narrow hue in the chromaticity diagram, showing no presence of true blue flowers. This might be due to the likely presence of only one anthocyanidin in the flowers; Robinson and Robinson(8), Lawrence *et al.*(6) and Yokoi(13) found the same anthocyanin, cyanidin, in *C. labiata*, *C. skinneri* and *C. boweringiana*, respectively.

Another interesting point concerns the so-called 'sophro' red presented by *Sophronitis* and its progeny. The flower color of *S. coccinea* var. *rosea* (Fig. 1e) is so clear and reddish with a velvety appearance as to be clearly distinguishable from 'orchid tone' color and exemplifies the meaning of 'sophro' red. The difference in these colors was

observable under the microscope; the epidermis of the perianth in *S. coccinea rosea* had more reddish vacuoles than that of the latter. This might be thought to be related to the consistent data of Robinson and Robinson(8) that *S. coccinea* species contains pelargonidin and *Cattleya* species cyanidin in their petals. However, according to Yokoi(13), cyanidin is found in the former species, so that another explanation is needed.

The true red coloration of *S. coccinea* flowers, as indicated in the literary meaning of 'coccinea', was revealed under microscopical observation to be expressed by virtue of the coexistence of anthocyanins and carotenoids rather than that of anthocyanins and flavones as stated in Die Orchideen(10). This observation corresponds with the result of the chemical analysis by Yokoi(13), who refers to the coloration as a background effect of carotenoids on the cyanin color expression, and with a phenomenon found in *Renanthera* orchids(7). This finding can also explain why *S. coccinea rosea* and the yellow plant of *L. milleri* produce mauve and yellow flowers, respectively; their species lack either carotenoids or anthocyanins. This knowledge can also be used to obtain new hybrids yielding yellow, red and purple flowers, as exemplified by *Sophrolaeliocattleya* Eastmona, which blooms in yellow flowers that were produced by crossing *Slc. Ramona* with its sunset toned flowers and *Laeliocattleya* Goerge Eastman with its white flowers.

Although the epidermis of leaves and yellow petals contain no chloroplasts, some species in different genera such as *En. vitellina*, *Epi. cinnabarinum* and *L. cinnabarina* with orange blooms do contain carotenoids in the epidermis. This difference may be due to the components of carotenoids, that is, decreasing b/a values and changes in color from yellow to orange indicate an increase in hydrocarbon carotenoids such as carotenes in the epidermis.

Serial changes in the shapes and sizes of epidermal cells in each genus, as shown in Fig. 5, might manifest the evolutionary direction. These changes also provided the taxonomical significance: all 1-type, an f-type,

most of h- or a-type *Cattleya* species belong respectively to *Cattleya*, *Skinneri* and *Diphyllae* subgenera as classified by Schlechter (10). Also, p-type *Laelias* except *L. rubescens* belong to the same section (Crispa section). On the other hand, that *En. mariae* is separated from *Epidendrum*(3) and that *B. digbyana* is classified as *Rhyncolaelia*(10) are understandable on the basis of the shape of their cells. The similarity in shape and size of epidermal cells among *L. pumila*, *L. milleri*, *S. coccinea*, *Bro. sanguinea* and *Sophonitella* suggests that they are closely related. In addition, they contained anthocyanins in their epidermal cells, and three species, *L. milleri*, *S. coccinea* and *Bro. sanguinea*, also contained carotenoids, as mentioned above.

A velvety and substantial texture is one of the desirable flower characteristics. A velvety texture is usually seen in lips, and the data in this study concerning lips show that velvety is defined by high ratios of height to width for epidermal cells and by the presence of anthocyanins. However, these characteristics entail a decrease in petal brightness as shown by the regression equations and by the case of black roses(11). High chromas due to anthocyanin pigmentation also decreased brightness, because the intensively colored vacuoles absorb more light, while the carotenoids increased it, because the granules in the cells easily reflect incident light.

In conclusion, this study has confirmed the well-known facts that desirable characteristics found in *C. labiata*, *L. purpurata*, *S. coccinea* and other significant species are concentrated in present hybrids with large purple flowers, whereas the delayed improvement in the breeding of yellow varieties is attributable to scanty stock species, except *C. dowiana* and *L. tenebrosa*, which will yield satisfactory progeny. Understanding pigmentation and its inheritance patterns may contribute to the breeding of yellow varieties.

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Cattleya およびその近縁属における花被組織の色素分布 I. 原種

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摘 要

Cattleya とその近縁のラン科 11 属の種の花被組織における色素分布および花被表皮細胞の形状を調査し、花被の表色との関係を考察した。

1. 供試した 68 種は、花卉の表皮と柵状および海綿状組織におけるカロチノイドとアントシアニンの分布の違いから 9 群に分類できた。黄色花は花卉にカロチノイドがあるが、*Cattleya* (C.) *dowiana* や *Laelia* (L.) *flava* などでは柵状・海綿状組織にのみあり、*L. harpophylla* や *L. cinnabarina* などでは表皮細胞にも含まれていた。

赤色花には、カロチノイドおよびアントシアニン両者ともにあり、*Sophronitis coccinea* や *L. milleri* ではカロチノイドが表皮および柵状・海綿状組織に、アントシアニンは表皮にのみあった。*L. tenebrosa* の褐色の花弁ではアントシアニンは柵状海綿状組織にあった。

赤紫色花はアントシアニンが表皮にのみあるか、柵状海綿状組織にあるか、その両者にあるかによって 3 群に分けられた。*Cattleya* はこの花色の代表的な属であるが、多くの種ではアントシアニンは柵状・海綿状組織にあった。*C. intermedia* var. *aquinii* や *C. leopoldii* の花卉着色部分やスポットには表皮細胞にもあった。

Laelia の濃紫赤色花は表皮および柵状・海綿状組織ともにアントシアニンを含み、淡紫赤色のものでは表皮にはなかった。

2. 供試した種は Hunter 表色法によって 3 群に分けられた。花卉にカロチノイドのみを含む、黄色ないし橙色花は色相 (b/a) が 0.47 以上に、カロチノイドとアントシアニンが共にある赤色花は $0.47 \geq b/a > -0.13$ に、アントシアニンのみを含むいわゆるカトレア色の紫赤色花は $-0.13 \geq b/a > -1.0$ にあった。

カロチノイドを含む花卉では、カロチノイドが多いと明度が高くなった。アントシアニンのみを含む花卉や唇弁では、アントシアニンが多いと明度が低くなった。

3. 花卉と唇弁の上面表皮細胞は種によって大きさおよび形に変異がみられた。属を同じくする種ごとにみると変異は連続的であり、小さいものは四角で、光沢のある花にみられ、大きいものはビロード状を示す花にみられて長三角形であった。表皮細胞の大型化と四角形から長三角形への変化は進化の方向を示すものと思われ、*C. labiata*, *L. purpurata* や *Brassavola digbyana* などのように鑑賞価値が高く、花径の大きな花の表皮細胞は、それぞれの属内では最大で長三角形であった。