Genic Analysis in Rice. IV. Genes for Purple Pericarp and Other Characters

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Two types pericarp coloration, red and purple, are found in rice, *Oryza sativa* L. The red pericarp was considered by NAGAI (1921) as well as by NAGAO (1951) to be due to protocyan pigment, but later was found to be due to catechin, catechol tannin and phlobaphene, produced by the interaction of *Rc* and *Rd* (NAGAO, TAKAHASHI and MIYAMOTO 1957). The purple pericarp was found by RAMIAH *et al.* (1931) to be controlled by a gene *P* which expresses the character if other pigmentation genes *A* and *N* are present. On this basis, NAGAO (1951) considered that this character might be due to the complementary effect of anthocyanic pigmentation genes *C* and *A*, and another gene *Pp* which spreads pigment into the pericarp. Later, NAGAO and TAKAHASHI (1962) found that a gene *Pl* is concerned with the coloration of the leaf blade, leaf sheath, auricle, ligule, node and internode, and further with that of the pericarp exposed to direct sunlight.

The present experiment was conducted with the view of reexamining NAGAO and TAKAHASHI's conclusions and finding linkage relationships between the genes controlling purple pericarp and other characters.

Table 1. List of strains used as cross parents

Strain No.	Genetic characters	Putative genic constitution	Note
7041	Purple apiculus, long empty glume	<i>C^B A lng</i>	JODON's marker
7101	Purple apiculus, stigma, hull and leaf blade	<i>Pl Hp (Rp)</i>	"
7102	Purple apiculus, stigma, leaf blade and hull	<i>Pl Hp (Rp) Pp Pb</i>	"
7107	Purple apiculus, stigma and hull	<i>Hp (Rp)</i>	"
7227	Apiculus ripening tawny, glutinous endosperm, grabrous hull	<i>ap wx lk pp pb</i>	"
7252	Apiculus, stigma, pericarp and leaf purple, minute grain	<i>Pp Pb Mi Pl</i>	"
A-5	Red apiculus, ripening purple hull	<i>C^{Br} A Rp</i>	NAGAO's marker (Akamuro)
D-8-5	Apiculus colorless, dwarf (50 cm in height)	<i>c a d lro pp pb</i>	Mutant from Chianan No.8 (Taiwan)
D-8-9	Apiculus colorless, dwarf (55 cm in height)	<i>c a d pp pb</i>	"
M-8-7	Apiculus colorless, dwarf (50 cm in height) grassy leaf	<i>c a d pp pb</i>	"
La-8-9	Apiculus colorless, lazy	<i>c a la pp pb</i>	"
D-155-5	Apiculus brown, grassy dwarf (30 cm in height), much tiller number	<i>C a d pp pb</i>	Mutant from Taichung No. 155 (Taiwan)
P-167	Brown apiculus, liguleless	<i>C a lg</i>	Pai-kan-tao (Taiwan)
J-308	Red apiculus, liguleless	<i>C^{Br} A lg</i>	Muzetsuto (Japan)
M-514	Purple apiculus, purple pericarp	<i>C^B A Pp Pb</i>	Hun-nou (China mainland)

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Table 2. Segregation of purple pericarp and its relation to apiculus coloration in F_2

(a) When four genes are concerned

Crosses	Apicular color	Pericarp color						Cal. No. of ap. color (9 : 7)	χ^2	P
		Purple		Brown		Colorless				
		<i>Pp</i>	<i>Pb</i>	<i>pb</i>	<i>Pb</i>	<i>Pp</i> <i>pb</i>	<i>Pb</i> <i>pb</i>			
		Total								
D-8-5(<i>c a pb</i>) × 7102 (<i>C^B A Pp Pb</i>)	Ap. purple	109		17		36		162	0.0736	0.7-0.8
	Ap. colorless	40		54		36		130		
	Total (9:3:4)	149	164.7	71	54.7	72	73	292 292	6.2956	0.02-0.05
D-8-9(<i>c a pb</i>) × 7252(<i>C^B A Pp Pb</i>)	Ap. purple	156		10		47		213	0.038	0.8-0.9
	Ap. colorless	55		65		49		169		
	Total (9:3:4)	211	214.9	75	71.6	96	95.5	382 382	0.235	0.8-0.9
M-8-7(<i>c a pb</i>) × 7102(<i>C^B A Pp Pb</i>)	Ap. purple	118		3		40		161	0.058	0.8-0.9
	Ap. colorless	46		49		34		129		
	Total (9:3:4)	164	163.125	52	54.375	74	72.50	290 290	0.139	0.3-0.5
M-514(<i>C^B A Pp Pb</i>) × La-8-9(<i>c a pb</i>)	Ap. purple	121		6		51		178	3.377	0.05-0.10
	Ap. colorless	32		42		37		111		
	Total (9:3:4)	153	162.5	48	54.2	88	72.3	289 289	4.673	0.05-0.10

(b) When three genes are concerned

Crosses	Apicular color	Pericarp color				Cal. No. of ap. color (3 : 1)	χ^2	P
		<i>Pp Pb</i>	<i>pp Pb</i>	<i>Pp pb</i> <i>pp pb</i>	Total			
7227(<i>C^B a pp pb</i>) × 7102(<i>C^B A Pp Pb</i>)	Ap. purple	96	4	34	134	132	0.125	0.7-0.8
	Ap. colorless	8	25	9	42	44		
	Total (9:3:4)	104	29	43	176	176	0.758	0.5-0.7
D-155-5(<i>C^B a pp pb</i>) × 7102(<i>C^B A Pp Pb</i>)	Ap. purple	157	2	50	209	216.8	1.124	0.2-0.3
	Ap. colorless	4	59	17	80	72.2		
	Total (9:3:4)	161	61	67	289	289	1.255	0.5-0.7

Materials and Methods

The strains used for this experiment are listed in Table 1. Among them, six are gene markers sent from Dr. N. E. JODON, and one was furnished by Dr. S. NAGAO; the writers are greatly obliged to those two scholars. The rest are strains selected from Taiwanese, Japanese and Chinese native varieties, and radiation-induced mutants of Ponlai (Japonica type) varieties. These strains were raised in the experimental field of Taiwan Agricultural Research Institute, Taipei, and records were taken regarding pigmentations at the apiculus, leaf blade, pericarp, hull, stigma, internode and ligule. The gene symbols recommended by International Rice Commission of FAO (1959) were used. The gene symbol *A-a*, identical to *Sp-sp* formerly used by Dr. S. NAGAO, is also adopted in this paper.

Presentation of Data

1. Inheritance of purple pigmentation of pericarp

Strains 7102, 7252 and M-514 have purple pericarps; the pigment is spread over the surface of the grains. For examining the distribution of pigment in the grain, sections cut at 20 micra were observed. The pigment was found to be limited to the pericarp.

F_2 segregation ratios for purple pericarp and their relation to apiculus coloration are shown in Table 2. As the data in the table show, crosses between plants with purple and colorless pericarps gave a 9 purple : 3 brown : 4 colorless ratio. This is in accord with the results obtained by Ramiah *et al.* (1931). We may assume from this ratio that the purple pericarp is due to a set of complementary genes, *Pp* and *Pb*, and that *Pb* alone brings about brown pericarp. Under this assumption, strains D-8-5, D-8-9, M-8-7, 7227 and D-155-5 must have the recessive genes *pp* and *pb*, while strains 7102, 7252 and M-514 have *Pp* and *Pb*.

In these crosses, the segregation for apiculus coloration was due to $C^B : c$ and $A : a$ (giving 9 : 7 ratios), or to $A : a$ (3 : 1 ratios). In both cases, it was found that apiculus-purple plants mostly had purple pericarps while apiculus-colorless plants mostly had brown pericarps. This indicates that the gene *Pp* might be linked with the apiculus-pigmentation gene *A*.

Dividing the F_2 data into two groups, one (a) showing 3 : 1 ratio and the other (b) showing 9 : 7 ratio for apiculus coloration, as shown in Table 2, a chi-square test of heterogeneity (c. f. SNEDECOR 1950) was made regarding segregation ratios found in various crosses of each group. The results proved that all the observed segregations in each group could be

Table 3. Frequencies of phenotypic classes with four genes concerned

Apiculus	Pericarp	Frequency	Obs. no.	Exp. no.
Purple	Purple	$\frac{9}{64} (3-2p+p^2)$	504	498.5
"	Brown	$\frac{9}{64} (2p-p^2)$	36	30.1
"	Colorless	$\frac{9}{64}$	174	176.2
Colorless	Purple	$\frac{9}{64} (1+2p-p^2)$	173	206.3
"	Brown	$\frac{3}{64} (4-6p+3p^2)$	210	204.9
"	Colorless	$\frac{7}{64}$	156	137.0
		$p=8.39\%$	$\chi^2=9.72$	$P>0.05$

considered as homogeneous. Then the recombination fraction between *A* and *Pb* was computed from the pooled data as follows:

When a 9 : 7 ratio is found for apiculus coloration, the frequencies of F_2 plants falling under six phenotypic classes will be formulated as given in Table 3. By using the maximum-likelihood technique, the recombination value, p , was estimated to be $8.93 \pm 0.46\%$, and the observed numbers fitted well the expected ones. In the same manner, in crosses showing 3 : 1 ratios for apiculus coloration the frequencies of phenotypic classes were computed as given in Table 4. The recombination value was found to be $5.12 \pm 1.21\%$, also giving a good fitness of observed to expected numbers.

Table 4. Frequencies of phenotypic classes with three genes concerned

Apiculus	Pericarp	Frequency	Obs. no.	Exp. no.
Purple	Purple	$\frac{3}{16} (3-2p+p^2)$	253	252.9
"	Brown	$\frac{3}{16} (2p-p^2)$	6	8.7
"	Colorless	$\frac{3}{16}$	84	87.2
Colorless	Purple	$\frac{3}{16} (2p-p^2)$	12	8.7
"	Brown	$\frac{3}{16} (1-2p+p^2)$	84	78.5
"	Colorless	$\frac{1}{16}$	26	29.1
		$p=5.12\%$	$\chi^2=2.07$	$P>0.9$

2. Inheritance of leaf-blade pigmentation

The leaf blade of strains 7102 and 7252 is purple. These strains might have a gene named *Pl* by NAGAO (1951), which produces purple pigment in the leaf blade in cooperation with the apiculus-pigmentation genes *C* and *A*; their genotype may be assumed to be $C^B A Pl$. When they were crossed with colorless strains D-8-5 etc. ($c a pl$) or 7227 etc. ($C^B a pl$), the F_2 showed 9 : 7 or 3:1 ratios for apiculus pigmentation, and 27 : 37 or 9 : 7 ratios for leaf-blade pigmentation, while the plants with purple leaf blade always showed purple apiculus, as shown in Table 5. This is in accord with the conclusion of NAGAO and TAKAHASHI (1962).

The relation between leaf blade and pericarp colorations was further examined. As

Genotype	Apiculus	Leaf blade	Pericarp
$C A - Pb Pb = Pl$	Purple	Purple	Purple
$C A - Pb pb = pl$	Purple	Colorless	Colorless
$C A - pp Pb = Pl$	Purple	Purple	Brown
$C A - pp pb = pl$	Purple	Colorless	Colorless
$\left. \begin{matrix} c A \\ C a \\ c a \end{matrix} \right\} - Pb Pb = Pl$	Colorless	Colorless	Purple
$\left. \begin{matrix} c A \\ C a \\ c a \end{matrix} \right\} - Pb pb = pl$	Colorless	Colorless	Colorless
$\left. \begin{matrix} c A \\ C a \\ c a \end{matrix} \right\} - pp Pb = Pl$	Colorless	Colorless	Brown
$\left. \begin{matrix} c A \\ C a \\ c a \end{matrix} \right\} - pp pb = pl$	Colorless	Colorless	Colorless

shown in Table 5, no plants with purple leaf blade and colorless pericarp appeared. This suggests that *Pl* and *Pb* are very closely linked, or that the pigmentation of pericarp and that of leaf blade are due to pleiotropic effects of the same gene. Summarizing the above statements, the phenotypes of various gene combinations may be expected to be as given on the left: (=shows linkage.)

The recombination fraction be-

Table 5. Relation between purple pericarp and purple leaf blade
(a) When five genes are concerned

Crosses	Leaf blade color	Pericarp color					Cal. no. of leaf blade color (27:37)	χ^2	P	
		Purple		Brown		Colorless				
		<i>Pp</i>	<i>Pb</i>	<i>pp</i>	<i>pb</i>	<i>Pp</i>				<i>Pb</i>
D-8-5(<i>c a pp pb pl</i>) × 7102(<i>C^B A Pp Pb Pl</i>)	Purple leaf blade Colorless leaf blade Total (9:3:4)	103 46		14 56		73		117 175	0.5397	0.3-0.5
D-8-9(<i>c a pp pb pl</i>) × 7252(<i>C^B A Pp Pb Pl</i>)	Purple leaf blade Colorless leaf blade Total (9:3:4)	146 164.3		70 54.7		73 73		292 292	5.7042	0.05-0.10
M-8-7(<i>c a pp pb pl</i>) × 7102(<i>C^B A Pp Pb Pl</i>)	Purple leaf blade Colorless leaf blade Total (9:3:4)	117 47		3 49		74		120 170	0.078	0.7-0.8
		164 163.125		52 54.375		74 72.50		290 290	1.139	0.9-0.95

(b) When four genes are concerned

Crosses	Leaf blade color	Pericarp color				Cal. no. of leaf blade color (9:7)	χ^2	P
		Purple	Brown		Colorless			
		<i>Pp pb</i>	<i>pp Pb</i>	<i>Pp pb</i>	<i>Pb pb</i>	Total		
7227 (<i>C^B a pp pb pl</i>) × 7102 (<i>C^B A Pp Pb Pl</i>)	Purple leaf blade	95	2			97	0.009	0.99
	Colorless leaf blade	9	27		43	79		
D-155-5 (<i>C^B a pp pb pl</i>) × 7102 (<i>C^B A Pp Pb Pl</i>)	Total (9:3:4)	104	29		43	176	0.758	0.5-0.7
		99	33		44	176		
7102 (<i>C^B A Pp Pb Pl</i>)	Purple leaf blade	149	2			151	1.707	0.2-0.3
	Colorless leaf blade	11	59		67	137		
7102 (<i>C^B A Pp Pb Pl</i>)	Total (9:3:4)	160	61		67	288	1.278	0.5-0.7
		162	54		72	288		

tween *A* and *Pp* was estimated again from the data of Table 5; it was found to be $9.48 \pm 2.23\%$ (from crosses in which five genes are concerned) or $6.78 \pm 0.78\%$ (four genes).

It may then be concluded that the purple coloration of the pericarp is due to two genes *Pp* and *Pb*, and that *Pp* is linked with *A*, while *Pb* is synonymous with *Pl*, which produces the purple pigmentation of leaf blade when *C* and *A* are present.

3. Colorations of hulls

The hulls of 7102 and 7252 are blackish. The gene determining this character was called *Hp* by JODON (1948, 1955, 1956) and *Rp* (*=Pr*) by NAGAO (1951). It was found that *Rp* was linked with *Pl* (*=Pb*) as shown in Table 6. The average recombination fraction was estimated to be $20.26 \pm 1.73\%$.

4. Ligulelessness and other characters

Strains P-167 and J-308 have no ligules. This character showed a monogenic segregation. The gene symbol *lg* was given by JODON (1948). The gene *lg* was found to be linked with *Rp*. The average recombination value was estimated to be $29.24 \pm 2.34\%$ as shown in Table 7. This value is in close agreement with the value found by NAGAO and TAKAHASHI (1952), 28.2 %.

Induced mutant strains D-8-5, D-8-9 and M-8-7 are dwarfs, the height at maturity being about 50 cm; the strain D-155-5 is a "grassy" dwarf with profuse tillers, the height being about 30 cm. These dwarf strains were found to carry a recessive gene, as reported by the writer before (HSIEH 1962). These dwarf genes showed no linkage relations with *Pp* and *Pb*.

Discussion

The main interest in the present study was to analyse the system of genes controlling the pigmentation of the pericarp and other organs and to find out linkage relationships between those and other genes.

It is known that the genes controlling apiculus pigmentation, *C* and *A*, may be regarded as basic factors for the pigmentation of other organs. For instance, regarding stigma pigmentation, the writer (1960) formerly reported that plants with colored stigmas always had colored apiculus, but the coloration of the apiculus is not always correlated with that of stigmas. For leaf-blade coloration, the gene *Pl* seems to cause the distribution of pigment produced by *C* and *A* (*=Sp*) in the leaf blade (NAGAO 1951).

It was found that in certain cases a gene controlling pigmentation of a particular organ becomes effective when *C* and *A* are present, while in other cases a gene produces pigment without the cooperation of *C* and *A*. Different systems of coloration genes seem to make up a complex. It is interesting to find that two genes express the purple coloration of pericarp in apiculus-colorless plants, but one of them simultaneously determines the leaf-blade coloration with the aid of the apiculus-pigmentation genes. This differs from NAGAO and TAKAHASHI's (1962) conclusion that the gene *Pl* is responsible for the distribution of anthocyanin produced by *C* and *A* into the leaf, internode, node and pericarp.

Regarding the linkage relationships of the purple pericarp gene with other genes,

Table 6. Recombination value between purple leaf-blade *Pp* (or *Pb*) and purple lemma and palea *Rp*

Genes in linkage	Crosses	P ₁ genotype	Phase	Combined character				Total	Recombination value (%)	χ^2	P
				AB	Ab	aB	ab				
<i>Pb-Rp</i> (3:1)(9:7)	7227×7102	$\begin{smallmatrix} C^B & a & pb-rp \\ C^B & A & Pb-Rp \end{smallmatrix}$	C	89 (84.6)	44 (47.6)	16 (14.4)	27 (29.6)	176	26.01±8.66	0.879	0.8-0.9
<i>Pb-Rp</i> (3:1)(9:7)	D-8-5×7102	$\begin{smallmatrix} c & a & pb-rp \\ C^B & A & Pb-Rp \end{smallmatrix}$	C	148 (138.1)	70 (79.3)	28 (24.9)	44 (47.7)	290	26.42±4.77	2.050	0.5-0.7
<i>Pb-Rp</i> (3:1)(9:7)	D-8-9×7252	$\begin{smallmatrix} c & a & pb-rp \\ C^B & A & Pb-Rp \end{smallmatrix}$	C	194 (202.4)	90 (99.1)	29 (25.3)	89 (76.8)	402	17.21±2.78	3.663	0.3-0.5
<i>Pb-Rp</i> (3:1)(9:7)	M-8-7×7102	$\begin{smallmatrix} c & a & Pb-rp \\ C^B & A & Pb-Rp \end{smallmatrix}$	C	131 (145.2)	83 (70.8)	14 (16.8)	60 (55.2)	288	16.96±2.26	4.375	0.5-0.7
Total				562 (571.3)	287 (295.7)	87 (78.9)	220 (210.1)	1,156	20.26±1.726	1.7042	0.2-0.3

**Pp=Pl*Table 7. Recombination value between purple lemma and palea *Rp* and ligulelessness *lg*

Genes in linkage	Crosses	F ₁ genotype	Phase	Combined character				Total	Recombination value (%)	χ^2	P
				AB	Ab	aB	ab				
<i>Rp-lg</i> (3:1)(3:1)	P 167×7101	$\begin{smallmatrix} C & a & rp-lg \\ C^B & A & Rp-Lg \end{smallmatrix}$	C	185 (188.5)	30 (36.0)	44 (36.0)	40 (38.7)	299	28.00±0.45	2.761	0.3-0.5
<i>Rp-lg</i> (3:1)(3:1)	J 308×7107	$\begin{smallmatrix} C^{Br} & A & rp-lg \\ C^B & A & Rp-Lg \end{smallmatrix}$	C	142 (146.5)	34 (29)	26 (29)	32 (29.6)	234	28.99±2.22	1.505	0.5-0.7
<i>Rp-lg</i> (3:1)(3:1)	J 308×7041	$\begin{smallmatrix} C^{Br} & A & rp-Lg \\ C^B & A & Rp-Lg \end{smallmatrix}$	C	189 (187.4)	40 (36.1)	30 (36.1)	39 (38.4)	298	28.1 ±2.90	1.753	0.7-0.8
<i>Rp-lg</i> (3:1)(3:1)	J 308×A-5	$\begin{smallmatrix} C^{Br} & A & rp-lg \\ C^B & A & Rp-Lg \end{smallmatrix}$	C	138 (140.8)	33 (31.7)	32 (31.7)	27 (25.8)	230	33.0 ±3.51	0.146	0.98
Total				654 (660.2)	137 (131.8)	132 (131.8)	138 (132.2)	1,061	29.24±2.339	0.6501	0.8-0.9

JODON (1948) found that the purple pericarp gene *Prp* was linked with the purple junctura (*Jpb*), purple glume (*Gpb*), purple hull (*Hpb*) and purple internode (*Ntp*) genes, all belonging to his linkage group III. Later, this group was revised as group II (JODON 1955). This may correspond to NAGAO and TAKAHASHI's (1959) *Pl* group or group II, in which seven genes, *Pl*, *d*₂, *d*₃, *lg*, *Ph*, *Rp* (= *Pr*) and *P* (formerly symbolized as *A*) are involved.

In the present study, it was found that *Pp* was linked with *A* which belongs to NAGAO's group III. Further linkages were found between *Pb* (= *Pl*) and *Rp*, and between *lg* and *Rp*, which belong to NAGAO's group II. The dwarf gene *d*₁ was formerly found to be linked with *lg* (HSIEH 1962). Further, the phenol reaction gene *Ph* was found to be linked with the stigma coloration gene *Ps*₁ (HSIEH unpublished). All these genes seem to belong to the same group. Their order has to be studied in the future.

Summary

In order to analyse the genic system for purple coloration of the pericarp and its linkage relations, the *F*₂ ratios for the purple coloration of pericarp were investigated with particular attention to its linkage relations to the anthocyanic pigmentation of various other organs. When strains with colored and colorless pericarps are crossed, 9 purple : 3 brown : 4 colorless ratios were found in the *F*₂. It was assumed that two genes *Pp* and *Pb* are concerned with the purple coloration of the pericarp; *Pp* is epistatic to *Pb*, and *Pp* was found to be closely linked with *A*, one of apiculus-coloration genes, with a recombination fraction of 5.1-9.4 %. They belong to the linkage group III of NAGAO and TAKAHASHI.

The purple coloration of leaf blade is controlled by a modifier *Pl* which distributes anthocyanic pigment produced by *C*^B and *A*. It is completely linked with, or synonymous with *Pb*. Linkage relations were found further between the purple pericarp gene *Pb* (= *Pl*), the purple lemma and palea gene *Rp*, and the ligulelessness gene *lg*. All of these genes appeared to belong to group II of NAGAO and TAKAHASHI.

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稲の遺伝子分析 第4報

果皮の紫色着色に関与する遺伝子

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稲の果皮部にみられる紫色系着色につき、その関与遺伝子を他部位、着色の遺伝子との関連の下にしらべてみた。得られた知見の概要は次の如くである。

(1) 果皮色には *Pb* 及び *Pp* の2遺伝子が関与し、両者共存してはじめて紫色となる。但し *Pb* は単独でも果皮を褐色ならしめる作用をもつ。

(2) *Pp* は *A* (稈先の花青素着色遺伝子: Activator) と 5.1% 乃至 9.4% の組換え価で連鎖し、これらは長尾・高橋の第Ⅲ連鎖群に所属する。

(3) 葉身の紫色着色は *A* と *C* (稈先の花青素着色遺伝子: Chromogen) の存在の下に *Pl* (葉身色分布遺伝子) が加わつて発現されるものとみなしてよいが、本実験では *Pb* が常に *Pl* と相伴つて行動した。このことは *Pb* が *Pl* と極めて強度に連鎖するか、あるいはまた、*Pb* なるものは *Pl* の多発作用に外ならないかの何れかである

ることを意味する。

(4) 既に知られた如く、*Pl* や *Rp* (穎色分布遺伝子。*Pr* と記す) は長尾・高橋の第Ⅱ連鎖群に所属するが、上記の *Pb* は *Rp* との間に組換え価 20.3% の連鎖を示した。

(5) *lg* (無葉舌) について連鎖分析を行ったところ、*Rp* との間に 29.2% なる組換え価を得た。これは *lg* が第Ⅱ群に所属するとの従来報告に一つの支持資料を加えたことになる。

(6) *C*・*A* 両遺伝子の存在が稲体各部の花青素着色の発現に重要な前提条件であることは事実としても、絶対不可欠か否かについてはなお多くの実験の集積が望ましい。この点に関し、*Pb* 及び *Pp* の今後の詳細なる分析は、若しそれらが花青素系着色であるならば、興味ある資料を提供するものと考えられる。