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Genetic Studies on the Dominant White Flower in *Pharbitis Nil*

By

Tokio Hagiwara.

Most white flowers in various plants behave, as a rule, to coloured flowers as a Mendelian recessive, but sometime there occurs so called dominant whites being dominant to the coloured flower, as those in *Primula* studied by KEEBLE and PELLEW.[1] The author met with the occurrence of such dominant whites in Japanese Morning Glories (*Pharbitis Nil*) that he has been studying. The normal recessive white in this plant has been already studied in detail by these Japanese investigator, but not the dominant white flower, since So[2] has descrived briefly on this white, indicating what is due to the suppression of the colours of a inhibiting factor as well as the case in *Primula*. Moreover, the problem remained unkown whether the inhibiting factor acts to anyone of two factors at least being indispensable to the production of the colour, or acts to both.

Then, the author wants to determine not only this question, but to conclude that the dominant white flower is due to the existence of one or two of the inhibiting factors.

Experiments and Considerations

The crossing experiment between two white strains designated respectively as 420.27, 242.31, worked out. Both white parents are colour in tube, but not in stem though they are different each other in other characters. All the six F_1 plants obtained from the crossing, grew up

1) KEEBLE, F., and PELLEW, C., J. Genet., Vol. I Cambridge 1910.
2) So, M., "Ikushugaku Kōgi" (Lectures of Plant-breeding) Tôkyô 1923.

to the white coloured tubes and green stems, exhibiting the same character with both parents.

These F_1 plants gave respectively the segregation indicated in the following table, in the subsequent generation.

Table I

Crossing			Segregation in F_2 White	Colour	Total
242.31 × 420.27		I	61	2	63
〃	〃	II	6	0	6
〃	〃	III	7	0	7
〃	〃	IV	42	1	43
〃	〃	V	11	0	11
〃	〃	VI	12	0	12
			139	**3**	**142**
			135.40	6.60	142.00
			±3.60		

In looking over this table, some F_1 plant segregated into many whites and a few colour, but some the white alone. Here the author presumed that coloured plants unexpectedly appeared may be a mutant. But the data from the further raising of the present crossing, and from the other crossing in connection with it, made the cause of the appearance of such a ruffian bring to light, indicating that it is only the factor segregation, against the previous superficial presumption.

With 61 plants in F_2 of one of the crossing (242.31 × 420.27—I) the F_3 rearing was made. The full data are shown in Table II.

About 30.5% of these F_2 white plants segregated the coloured plant to the proportion from 1.8% to 24%, in spite of its segregating proportion in F_2 was law. And two coloured plants in F_2 gave the white plant according to recessive ratio.

Table II

Character shown in F_2	Pedigree no.	Segregation in F_3 White	Colour	Total
White	1	48	2	50
	3	39	2	41
	6	22	5	27
	7	54	1	55
	8	14	1	15
	11	41	13	54
	13	25	4	29
	16	4	1	5
	23	53	1	54
	24	12	2	14

Character shown in F_2	Pedigree no.	Segregation in F_3 White	Segregation in F_3 Colour	Total
	26	22	7	29
	31	17	4	21
	32	45	2	47
	36	31	1	32
	40	27	2	29
	46	15	4	19
	63	13	1	14
	65	24	1	25
White	4	35	0	35
	5	7	0	7
	9	19	0	19
	12	10	0	10
	15	32	0	32
	18	18	0	18
	19	37	0	37
	20	20	0	20
	21	17	0	17
	22	62	0	62
	25	8	0	8
	27	3	0	3
	28	38	0	38
	29	21	0	21
	30	5	0	5
	33	16	0	16
	34	13	0	13
	35	7	0	7
	37	14	0	14
	38	13	0	13
	39	10	0	10
	41	32	0	32
	42	15	0	15
	43	53	0	53
	44	11	0	11
	45	7	0	7
	47	20	0	20
	48	59	0	59
	49	42	0	42
	50	40	0	40
	51	18	0	18
	52	13	0	13
	53	20	0	20
	54	38	0	38
	55	25	0	25
	57	9	0	9
	58	41	0	41
	59	18	0	18
	61	13	0	13
	62	47	0	47
	64	9	0	9
Colour	56	25	45	70
	60	17	63	80

With only the evidence thus obtained, it may be difficult to determine that the inhibiting factor concerns this prsent crossing in what manner, though it may be said that the appearence of such a coloured plant owes to the factor segregation.

Especially the obtained data may be not enough to determine the number of factor concerning this but for any accessory experiment, For the wanting actual numbers treated to explain this results. But the data of the crossing performed between the coloured flower plant designated as 401.4 and the white flower plant designated as 242.114 which belongs to same pedigree with one parent of the previous crossing, made the author decide easily this point.

Unexpectedly, the F_1 plant of this crossing grew up to a white flower having the resemblance in corolla and stem with one of parents, and segregated numerically into 65 white plants with coloured tube and 7 coloured pants, just in accordance with the 15:1 ratio of dihybrid in F_2.

The further raising was not treated, but from the data given by F_1 and F_2 of this crossing, it may be deduced the fact that the white flowered plant adopted to present crossing isa dominant white carrying two inhibiting factors, and that these inhibiting factors may act independently to the factor for the colour-production, resulting in self-coloured plants. Consequently, from the result of this crossing, it may be said that one of parents of proceeding crossing, or 241.31 which belongs to the same pedigree with 242.114 being one parent of the present crossing manifested to have two inhibiting factors, should be also a dominant white carrying these factors. Thus, the genetic constitution of 241.31, one parent of the crossing being subjects was manifested. Next, we shall manifest of the genetic constitution of its partner, 420.27. The complementary factors **C** and **R** have been already given to this plant as the factor being essential to produce the colour of several organs. And three recessive white plants having respectively the genetic constitution **Cr, cR** and **cr** in regard to these factors have been already found. Only **Cr** type among these recessive white plants have been considered possible to be coloured in tube. Of course, this white transmits to the coloured as a simple Mendelian recessive.

Here, we are able to conclude what the parent 420.27 is identical to the **Cr** type, owing to the evidence that it behaved to the normal coloured plant as a simple Mendelian recessive on the crossing between it and a coloured plant.

Then, if two inhibiting factors above mentioned are designated respectively as $\mathbf{H^1}, \mathbf{H^2}$, the genetic composition of 242.31 may be considered to be $\mathbf{CRH^1H^2}$, and its partner 420.27 may be regarded as $\mathbf{Crh^1h^2}$. Hence, in F_2 of the crossing 242.31×420.27 namely $\mathbf{CRH^1H^2} \times \mathbf{Crh^1h^2}$, the white and the coloured should be expected to segregate at the ratio 61:3, in the trihybride fasion in regard to the factor **R** and two inhibiting factors $\mathbf{H^1}$, $\mathbf{H^2}$. The numbers observed in F_2 quite satisfies the expected ratio of 61:3 as indicated in the bottom of Table I.

Taking further consideration on the data of F_3 on such a basis, about 39.3% of the white in F_2 should segregate the colour with the several proportion as follows 3:1, 13:3, 15:1 and 61:3 in subsequent generation. In other word, the segregating percentage of a recessive plant in the offspring of these whites should be from 4.7% to 25%. However, the proportion calculated from the F_3 data was from 1.8% to 24%, indicating a somewhat discrepancy in the proportion.

The summerized data of F_3 families is shown in Table III indicating the comprision of the actual pedigree numbers with the expected ones.

Table III

Character of F_2	Genotype	Ratio	Total	Segregation of F_3		Total	Its expected numbers	Experi. numbers
				White	Colour			
	$\mathbf{CCRRH^1H^1H^2H^2}$	1						
	$\mathbf{CCRRH^1H^1H^2h^2}$	2						
	$\mathbf{CCRRH^1h^1H^2H^2}$	2						
	$\mathbf{CCRRH^1H^1h^2h^2}$	1						
	$\mathbf{CCRRh^1h^1H^2H^2}$	1						
	$\mathbf{CCRrH^1H^1H^2H^2}$	2	37	breed true		37	35.26	**41**
	$\mathbf{CCRrH^1H^1H^2h^2}$	4						
	$\mathbf{CCRrH^1h^1H^2H^2}$	4						
White flower	$\mathbf{CCRrH^1H^1h^2h^2}$	2						
	$\mathbf{CCRrh^1h^1H^2H^2}$	2						
	$\mathbf{CCrrH^1(h^1)H^2(h^2)}$	16						
	$\mathbf{CCRRH^1h^1h^2h^2}$	2	4	3	1	12	11.44	**8**
	$\mathbf{CCRRh^1H^1H^2H^2}$	2						
	$\mathbf{CCRrH^1h^1h^2h^2}$	4	8	13	3			
	$\mathbf{CCRrh^1h^1H^2h^2}$	4						
	$\mathbf{CCRrH^1h^1H^2H^2}$	4	4	15	1	12	11.44	**10**
	$\mathbf{CCRrH^1h^1H^2h^2}$	8	8	61	3			
Coloured flower	$\mathbf{CCRRh^1h^1h^2h^2}$	1	1		breed true	1	0.95	**0**
	$\mathbf{CCRrh^1h^1h^2h^2}$	2	2	1	3	2	1.91	**2**
		64	64			64	61.00	**61**

$X^2 = 3.19$ $P = 0.529$

The goodness of fit is so high that one case takes place in every three trials.

Inhibiting factors for the factor R

By above experiment, it was comfirmed that the dominant described in this paper is the genetic composition **CRH^{1}H^2**, **CRH^{1}h^2** and **CRh^{1}H^2**. This white flower is diffcult to distinguish appearently from the recessive white of **Cr** type bearing the coloured tube and the green stem, but it is possible by cross breeding tests.

Here, we must make clear whether inhibiting factors act the factor **C** or the factor **R**.

The author[1] has studied through the method of the genetico-physiological study on the white flower as to how the factor **C**, **R** which are essential to produce the pigment in corolla affects to the pigmentation of the tube, stem and seed in this plant.

And it was obtained the fact that the factor **C** may concern the substances essential to formation of chromogens, and that factor **R** may concern an enzyume having function to turn the chromogen to anthocyanin pigment, moreover, that the factor **C** may be also essential as chromogen for the pigment in tube, that the factor **R** may play the important rôle to the colour-production in stem.

Considering the white in question from the evidence described above, the conclution that the inhibiting factor acts to **R**, resulting in a dominant white, may be introduced.

However, it may be not impossible to think that if the factor **C** is inhibited only in the corolla, a dominant white may be resulted, though the colour is produced in tube. Hence, the detection either the factor **C** present or not in the corolla must be taken for the purpose to confirm this point.

The chemical method examing the corolla of the dominant white by the ammonia vapour and the method reducing its alcohol extracts by ClH and Mg powders, was taken. The results being identical to the case observed in **Cr** type white, that is, there exsists the chromogen in corolla of this white, was given by this treating.

So, the white appearance of the dominant white is responsible for the suppression of the function of **R** by inhibiting factor **H^1** or **H^2**. The factor to inhibit the function of **R** is two in number. And these each inhibiting factors act independently to **R** through the plant body. Hence, the dominant white of this plant is green in stem.

According to the genetic study by KEEBLE and PELLEW, one of the dominant white in *Primula* being due to the inhibiting factors is

1) HAGIWARA, T., Bot. Mag. Tôkyô Vol. XLII, 1928.
2) KEEBLE, F., and PELLEW, C., J. Genet. Vol. I, Cambridge 1910.

colour in stem as well as a recessive white in the same plant and also Japanese Morning Glory. They reported that the dominant white give no peroxidase reaction, applying a microchemical method invented by them, but after treatment with certain reagents, the inhibitor removed and the peroxidase reaction appeared in the petals.

Considering this fact, it may be considered that the inhibiting factor in the dominant white of *Primula* may act upon either the factor **R** only in flower but not in stem, or the factor **C**. But it is not impossible to think that the factor concerning the colouration in stem may be the other factor, in stead of **R**.

There is another factor to inhibit partially the function of **R** in the Japanese Morning Glory. It may be considered that such a factor is identical to the factor to produce the white-margined flower. In this case, the inhibiting factor acts to **R** only on the margin of corolla, resulting in a white-margin flower which is familiar in our garden.

Since TAKEZAKI[1] had reported the fact that this character transmits to the self-coloured flower as a simple Mendelian dominant, its comfirmation and further study have been elaborated repeatedly by MIYAZAWA,[2] IMAI[3][4] and HAGIWARA.[5] IMAI[4] has reported recently the fact that the complete production of the white pattern is effected by two factors. One of these factors is the factor which have been already identified as one for the white margin, but another is one acting complementary with the former factor, accordiug to him.

The presence of an inhibiting factor to suppress the manifestation of the complemental factors, resulting in a self-coloured flower, has been comfirmed by the studies of TAKEZAKI[1] and HAGIWARA.[5] Another partial inhibitor which inhibits the formation of white-margin, resulting in a indistinct white-margin flower has been found by IMAI.[4]

Hence we may have each both two factors to inhibit entirely the function of **R** and two factors to do partially. And the former acts respectively to **R**, giving white flower, but the latter does cooperatively, giving the white-margined flowers.

Moreover, we may recongnize the occurrence of the factor to inhibit the complemental factor concerning the white margin, namely inhibiting factors for inhibiting factors of **R**.

1) TAKEZAKI, K., J. Japanese Breeders Assoc. (Japanese) Vol. I. 1916.
2) MIYAZAWA, B., J. Genet Vol. 8 Cambridge 1919.
3) IMAI, Y., Bot. Mag. Tôkyô (Japanese) Vol. XXXIII. 1919.
4) 〃 Genetics Vol. 12. 1927.
5) HAGIWARA, T., Bot. Mag. Tôkyô (Japanese) Vol. XXXVI. 1922 a.
〃 J. Sci. Agri. Soc. (Japanese) No. 236. 1922 b.
〃 Bot. Mag. Tôkyô (Japanese) Vol. XL. 1926.

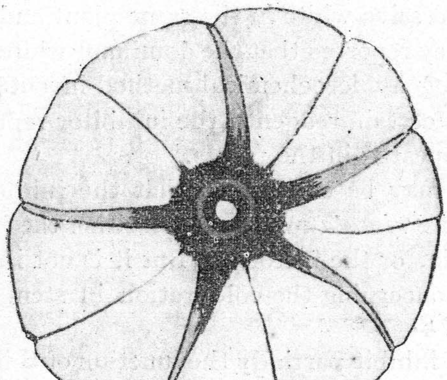


Fig. I
Dominant white flower

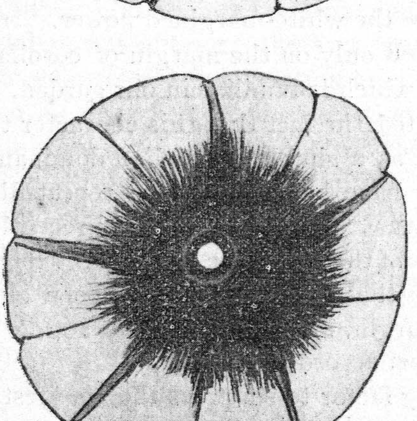


Fig. II shaded off flower

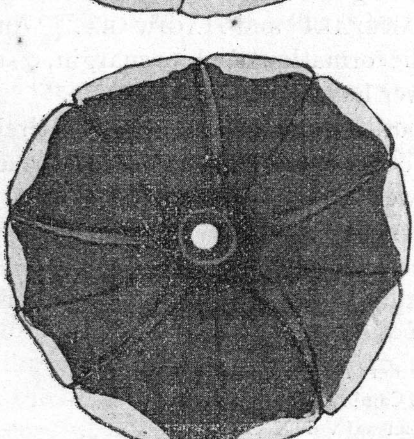


Fig. III.
White-margined flower.

The matter above mentioned concerns especially the inhibiting factor for **R.** Furtheremore, something about the inhibiting factors of other factors to act cooperatively with **R** as a supporter may be given in follwing lines.

As a strain of this plant, we have one blooming a pattern-coloured flower shading off to almost white towards the margin from zone round the tube. This flower is distinctly different from the white-margined flower, but its genetic behaviour[1] is something like the latter, that is as either a Mendelian dominant or recessive to the normal, self-coloured flower.

Two crossings were made between two white strains, one designed as 5 and A, white flower having green stem and coloured tube, the other designed as 106, white flower having coloured stem.

The F_1 plants grew up to the coloured flower having the said pattern different from both parents, and given the segregation throwing the coloured and the white flower to the ratio 9:7 in F_2 and some pedigree of F_3.

On account of that two white parents used in this crossing is respectively **Cr** type and **cR** type, it is reasonable that the F_1 plant is the coloured, and that the coloured and the white segregates in accordance to the ratio 9:7 in the further generation.

Table IV

Crossing	Shaded off flower	Self-coloured flower	White	Total
5×106	27	7	12	46
106×A	26	8	38	72
Observed	53	15	50	118
Expected (13:3)	55.25	12.75		

Since no linkage case between the factors concerning the present character and the factors **c**, **r** for the white flower was found, the white flower segregants will be omitted in the further deseription of this crossing data. Then the segregation of both coloured flowers in this table, indicates the better agreement to the ratio 13:3.

The results of the raising of F_3 of the crossing 5×106 was obtained as follows :—

Table V

Pedigree no.	Shaded off flower	Self-coloured flower	Total
1	24	6	30
7	31	7	38
11	60	14	74
13	13	3	16
16	51	11	62
34	69	17	86
46	15	2	17
Observed	**263**	**60**	**323**
Expected (13:3)	262.34	60.54	323.00

1) HAGIWARA, T., Bot. Mag. Tôkyô (Japanese) Vol. XL. 1926.

Table VI

Pedigree no.	Shaded off flower	Self-coloured flower	Total
2	11	5	16
4	13	8	21
10	19	5	24
14	22	7	29
18	11	9	20
20	11	3	14
26	34	13	47
30	28	9	37
32	22	7	29
39	12	4	16
44	34	14	48
Observed	**217**	**84**	**301**
Expected (3 : 1)	225.75	75.25	301.00

Table VII

Pedigree no.	Shaded off flowers	Self-coloured flowers	Total
8	6	18	24
40	4	10	14
45	7	10	17
Observed	**17**	**38**	**55**
Expected (1 : 3)	13.50	40.5	55.0

Seven of families exhibited the shaded off flowers segregated the shaded off flower and the self-coloured flower in the ratio 13 : 3 in their offspring, and eleven, in the ratio 3 : 1, but eight bred true.

Three families exhibited the self-coloured flowers segregated the self-color flower and the shaded-off flower in the ratio 3 : 1 in these offspring, and four bred true.

From the F_2 and F_3 results above mentioned, the following conclusion should be introduced.

Two factors involve in this crossing, one the factor $\mathbf{S}_f$ to support the function of the factor **R** in the zone outside near the tube, the other the factor $\mathbf{H}_f$ to inhibit the factor $\mathbf{S}_f$.

Then the genetical formula of these crossings is indicated as $\mathbf{CrS_fh_f} \times \mathbf{cRs_fH_f}$ or $\mathbf{cRs_fH_f} \times \mathbf{CrS_fh_f}$. Basing upon this genetical formula, the results of F_3 was summerrized as Table VIII.

Table VIII

Genotypic constitution	Ratio	Segregation ratio: Shaded off flower	Segregation ratio: Self-coloured flower	Pedigree: Observed number	Pedigree: Expected number
$\mathbf{S_fS_fh_fh_f}$	1	—	constant	**4**	2.06
$\mathbf{S_fs_fh_fh_f}$	2	1	3	**3**	4.13
$\mathbf{S_fs_fH_fh_f}$	4	13	3	**7**	8.25
$\mathbf{S_fS_fH_fh_f}$	2	3	1	**11**	4.13
$\mathbf{S_fS_fH_fH}$, $\mathbf{S_fs_fH_fH_f}$, $\mathbf{s_fs_fH_fh_f}$, $\mathbf{s_fs_fH_fH_f}$, $\mathbf{s_fs_fh_fh_f}$	7	constant	—	**8**	14.44
	16			**33**	33.01

As above description, some patterns of the colouration in corolla refer to the factors acting either totally or partially to the function of **R** being a partner of **C** to be indispensable to the production of the colour, in manner of the modification or suppression which is complicated by their inhibitor or modifier.

In consequence, the inhibitor with regards to **R**, so far studied, may be seven pairs in numbers, that is :—

H^1, H^2, Factors to inhibit totally the function of **R**, resulting in the white flowers.

F^a, F^b, Factors to inhibit partially the function of **R** only in the margin of corolla, resulting in the white-margin flower.

F_h, Factor to inhibit totally the inhibiting factors **F^a, F^b**, resulting in the self-coloured flower.

F^f, Factor to inhibit partially the inhibiting factors **F^a, F^b**, resulting in the slight or dotted margin flower.

H^f, Factor to inhibit totally the function of the factor **S_f** to support the function of **R** in the zone beside the near part round the tube, resulting in the pattern coloured flower shading off the almost white towards the margin from the zone round the tube.

When a diagram to indicate the part where **R** is acted by these inhibitors and the activator is taken in convenience, these factors are summarized as following table. (Fig. IV)

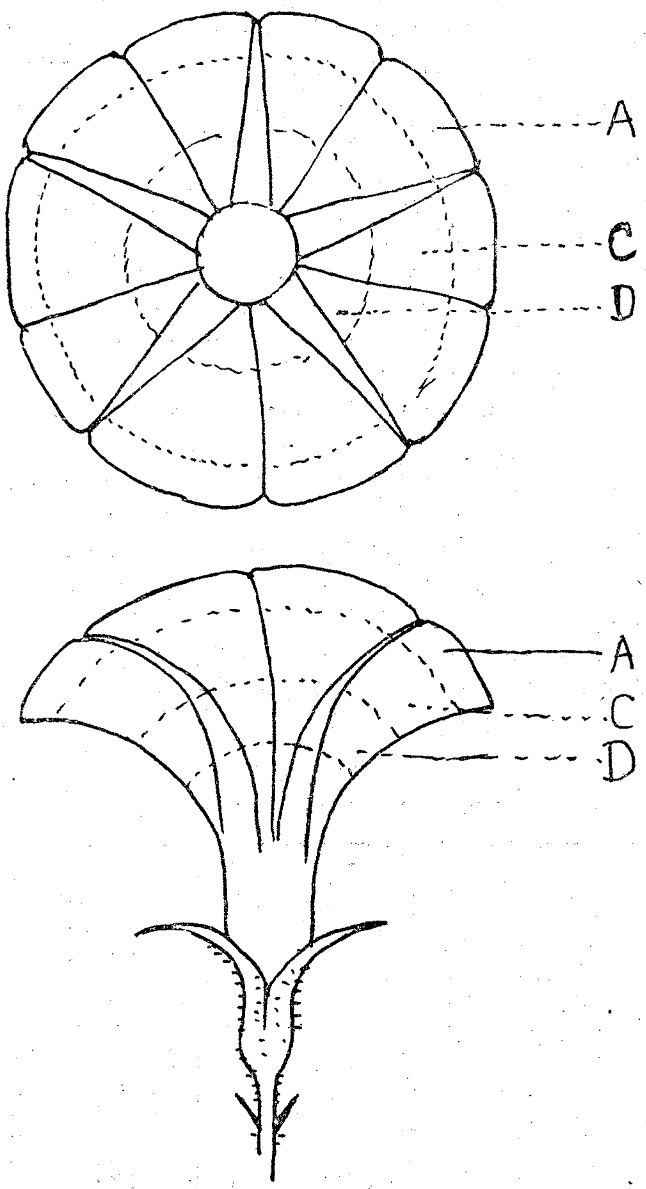
Table IX

Inhibitor and Activator of **R** in Corolla

Factor \ Part		R: A	R: C	R: D	Pattern resulted by the factor
Inhibitor		**F^a, F^b**			White-margined flower
Its inhibitor	Totally	**F^h**			Self-coloured flower
	Partially	**F^f**			White-dotted margined flower
Activator		S_f			Self-coloured flower
Its inhibitor		**H^f**			Shaded off flower
Inhibitor		**H^1, H^2**			White flower

The fact that the inhibiting factor for the factor **R** considered as an enzyme was thus found, but no factors for the **C** concerning the chromogen-production was found, may be of interest from the physiological point of views.

Fig. IV. Diagram to show the part where inhibito s act to R.



The author must express his hearty thanks to Mr. Hikoichi Motoyama and Mr. Tetugoro Hara who kindly gave him the grant for this study, and also to Marquis Saigo who allowed him to use the experimental farm.

Summary

1. Some white flower in Japanese Morning Glories (*Pharbitis Nil*) behaves to a coloured flower as a Mendelian dominant, giving the segregating ratio being in accordance with the ratio 15:1 or 3:1.

This dominant white is due to the suppression of the colour, caused by inhibiting factors.

2. The dominant white is coloured in tube and green in stem as well as the recessive white with coloured tube. The ratio of white and coloured flowers in F_2 of some crossing between these whites was 61:3.

3. The inhibiting factor concerning the formation of the dominant white is two, each of which acts independently to the factor **R**, the partner of the factor **C** being essential to produce the colour in corolla.

4. The factor for the white margined flower is considered as an inhibiting factor by which the factor **R** in margin-zone of corolla is inhibited its function. Moreover, there occurs the factor to inhibit the factor for the white margin flower, therefore it may be considered as inhibiting factors for inhibiting factors of **R**.

5. A flower having a pattern shaded off almost white towards the margin from center zone round the tube, is due to the absence of a factor $\mathbf{S_r}$ by which the function of **R** may be supported. The factor $\mathbf{S_r}$ is inhibited its function by an inhibiting factor $\mathbf{H_r}$.

6. Hence, some patterns are considered as being due to the absence or presence of the factor which acts only to **R** in some part of corolla as its sapportor or modifier. So far studied, inhibitors to inhibit totally or partially the factor **R** may be at least seven pairs.

April, 1928. Botanical Institute, Agricultural College,
Tokyo Imperiai University.

Bibliographie von Aspergillus.

1729 bis 1928.

von

Hiroshi Tamiya und Shinkichi Morita.

(FORTSETZUNG I.)

1870

127. 1. BARY, A. DE. Eurotium, Erysiphe, Cicinnobolus, nebst Bemerkungen über die Geschlechtsorgane der Ascomyceten.