TRIAL CONSTRUCTION OF TWELVE LINKAGE GROUPS IN JAPANESE RICE

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I. Introduction

Notwithstanding the fact that rice is the world's most important food crop and consequently the rice plant has been studied to practical and fundamental genetic studies, some important phases of this field are still unexplored. Especially, in a phase of linkage studies, only a fraction of the possible paired combinations between recognized characters has been tested, and no comprehensive search has been undertaken.

The first instance of linkage, that between blackhull and colored internode, was reported by PARNELL et al in 1917. The best known linkage, however, is that between the apiculus color and the waxy viz. glutinous enosperm. This was first found out by YAMAGUCHI (1921, 1926) and was confirmed by many workers (CHAO 1928, RAMIAH et al 1931, TAKAHASHI 1935, JODON 1940, BREAUX 1940, NAGAO and TAKAHASHI 1942, COMEAUX 1946 etc.). Based on this linkage, so called "waxy" linkage group has been set up. The next known linkage group of Japanese rice, that is termed as "purple leaf" group is based upon linkages among purple leaf, liguleless and phenol staining characters. The first reporters of this linkage relationship are MORINAGA and his co-workers (1942).

Though the linkage analysis on rice plant have usually been incidental to studies for a different purpose, and thus have seldom found their way into the literature—in a word, linkages in this plant have not been the subject of a systematic search, attempts have been made for summarizing data and for advocating provisional linkage groups, by such workers as MATSUURA (1933), NAGAO (1936, 1951), RAMIAH and RAO (1953), and JODON (1948, 1956). RAMIAH (1953) has summarized the results of linkage groups, and JODON (1948) suggested the possibility of exsistence of eight groups, based on data reported principally in India and the United States. In 1951, NAGAO, in Japan, added some new data on linkage and comment on JODON's conclusion. JODON (1956), again, made report and has revised the linkage grouping advocated by him earlier in 1948 (eight groups) and in 1955 (six groups) to seven groups to

accomodate the linkage relationships reported up to that time.

Thus at present, it may be said that seven of the expected twelve groups have been supplied. However, as pointed out by JODON (1948, 1956) and NAGAO (1951), there may still be some question and uncertainty regarding grouping and identification of genes concerned, and therefore, present data are far from sufficient to fully establish twelve linkage groups corresponding to the haploid number of chromosomes.

During the past several years the writers have been engaged in studies of genic analysis in Jasanese rice varieties. In the process, strains that were segregating simultaneously for two or more monogenically inherited characters became available and some multiple-gene-markers were built up. Through these segregations, supplemented with hybrids made specifically for the study of linkage, some indications of twelve linkage groups in Japanese rice varieties were obtained. This paper summarizes these experimental results and presents a linkage map of Japanese rice on a trial basis as the first step of systematic studies on linkage relationships in this valuable crop plant[1].

Without adequate knowledge or information on gene systems of characters concerned, experimental results on linkage would be difficult and would not furnish enough data for mapping linkage groups. For example, the expression of anthocyanin color in the apiculus of Japanese varieties depends on the complementary effect of three genes, *C* (chromogen), *A* (activator) and *P* (spreading the chromogen of *C* throughout the apiculus). Therefore, if the available information merely indicates that a certain character is linked with apiculus coloration, it is actually impossible to determine with which apiculus coloration genes, *C*, *A*, *P*, or possibly another gene, is the causal gene of the said character linked.

Thus, before going into the presentation of linkage data, a brief resume of character expression of genes, which are worth special mention in the present paper, will be made.

Linkage intensities were computed using IMMER's table, except when indicated otherwise. In the present paper the writers will use the gene symbols recommended by the Meeting of the FAO international Rice Commision Working Party on Rice Production and Protection (1955 and 1959). A list of standard gene symbols and nomenclature adopted at the said meeting is being submitted through R. C. ADAIR and N. E. JODON to the USDA-ARS, for "Crop Research" of the Agricultural Research Service, U. S. Department of Agriculture. In order to avoid confusion, the writers have inserted their pre-

1) A preliminary report has already been made public by the writers (NAGAO and TAKAHASHI 1960).

viously used symbols in parentheses in the descriptive notes of the genes referred to, whenever it is applicable.

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II. Character Expression of Genes Included in Linkage Studies

A. Genes for anthocyanin and its related color expression, the so-called "Tawny".

Coloration due to the presence of anthocyanin and its related pigments occurs quite commonly in several parts of the rice plant. The anthocyanin color shows a wide scope of variation, from pink to purplish black, and its related color expression, the so-called "tawny", ranges from light to dark brown. Among causal genes of these colorations, the following seven genes were examined for their loci in linkage groups:

C……Chromogen for anthocyanin color
A……Anthocyanin activator (*Sp*)
P……Completely colored apiculus (*A*)
Ps……Purple stigma
Pr……Purple hull (*Rp*)
Pl……Purple leaf
Pn……Purple node

According to the writers' genic scheme, the occurrence of the anthocyanin color depends on the complementary action of genes *C* and *A*; *C* is the basic gene for the production of chromogen, and *A* exerts its activation effect on *C* and turns the chromogen into anthocyanin.

C and *A* both comprise multiple allelic series of genes: six alleles have been found at the *C* locus and four at the *A* locus (NAGAO 1951; TAKAHASHI 1957; NAGAO, TAKAHASHI, & KINOSHITA 1962). They are arranged in the rank of dominancy as $C^{B}>C^{Bp}>C^{Bt}>C^{Br}>C^{Bm}>C^{+}$ and $A^{E}>A>A^{d}>A^{+}$.

Biochemically, *C* is considered to be responsible for the production of

such substances as flavon or catechin, or is considered to be the common precursor. *A* is connected with the conversion into anthocyanin pigment, or is related with the prevention of changing of substances into other substances (TAKAHASHI 1957).

The expression of anthocyanin color of the apiculus is generally attributed to the complementary effect of *C* and *A*, which are essentially considered to be color-producing genes. However, with these genes alone, coloration is so limited and appears so thinly scattered at the very tip of the apiculus that plant of this genotype usually is considered to be colorless in ordinary outdoor observation. For distinct coloration in the apiculus, it is necessary, in the presence of *C* and *A*, for another gene *P* to be present. *P* is concerned with the spreading of chromogenic substances over the entirety of the apiculus. The majority of the Japanese varieties or strains, examined by the writers, possess *P* in common, and it follows that the principal color types of the apiculus studied so far are mainly a result of combinations of any alleles of the *C* and *A* loci (NAGAO 1951, NAGAO & TAKAHASHI 1956; TAKAHASHI 1957, 1958). (Fig. 1).

The rank of dominancy of each allele at the *C* and *A* loci is in direct proportion to the potency of chromogen production and also to the assimilative ability of chromogenic substances in the production of anthocyanin pigment, respectively.

In the absence of *C* or *A* the anthocyanin color does not appear and the plant is uncolored at the time of flowering. Upon ripening and when *C* is present alone or with A^d, that is when it is without A^E or *A*, *C* makes the apiculus brown or "tawny" in several intensities of color shade, depending on which allele of *C* is present. In this phenomenon, it is assumed that, when *A* is absent, the chromogenic substances producee by *C* change to brown pigment. A^d is less potent than A^E and *A*, that is, only a fraction of the chromogenic substances produced can be utilized in the formation of anthocyanin pigment. Therefore, when *C* co-exists with A^d the remaining quantity of unchanged chromogenic substances is turned into brown pigment. This is the reason why certain plants with the genotype C^B A^d and C^{Bl} A^d show a particular mode of coloration in which the anthocyanin and the tawny colors overlap each other.

In these genic schemes of the anthocyanin color, it should be pointed out that there is no need of proposing a modifying gene or genes, which are responsible to convert color hue or shade, in explaining the existence of several color types in rice plant.

Every allele at the *C*-locus, in cooperation with any allele at the *A*-locus,

give rise to respective color shades in awnes and empty glumes as well as in apiculus. And further, when a high ranking allele at the *C*-locus is involved, some other parts are also colored as a result of a pleiotropic effect of the said allele. The expanse of coloring parts by any allele of the *C*-locus is proportional to the rank of dominancy of the allele concerned, showing that, for example, C^{B}, one of the higher allele, exerts its effect on internode, while C^{Br}, one of the lower allele, has no effect in this part (Table. 1).

TABLE 1. Color distribution caused by *C*-allele in combination with *A*-allele

		Apiculus	Awn	Empty glume	Stigma	Inner surface of leaf sheath	Outer surface of leaf sheath	Outer surface of inter node
C^{B}	A	+	+	+	+	+	+	+
	A^{a}	+	+	+	+	+	+	+
C^{Bp}	A	+	+	+	+	±		
	A^{a}	+	+	+				
C^{Bt}	A	+	+	+				
	A^{a}	+	+	+				
C^{Br}	A	+	+	+				
	A^{a}	±	±					
C^{Bm}	A	±						
	A^{a}							
C^{+}	A							
	A^{a}							

(*P* presents in common)

With regard to the action of genes, *Ps*, *Pr*, *Pl* and *Pn* are considered functional in distributing the anthocyanin color into respective parts, and thus coloration occurs in these parts when these genes co-exist with two basic genes at the *C* and *A* loci (NAGAO & TAKAHASHI 1951). The hue and shade of the colored parts is connected with the combination of *C* and *A*.

It has been revealed that in most Japanese varieties stigma coloration occurs by the dual effect of *P*. But in addition to this, there is another gene, *Ps*, which localizes the pigment in the stigma (TAKAHASHI 1958). Here it should be noted that in a case where an allele at the *C* locus is less potent than C^{Bt}, no color develops in the stigma in spite of the presence of *P* and/or

Ps together with *C* and *A*.

Pr is a gene responsible for distributing the color over the entire surface of floral glumes, viz. lemma and palea, and in some cases the rachilla. This also holds true in the tawny color of these parts, since *Pr* exerts its action on *C*, not on *A*. The genic constitution of predominant self-colored floral glumes in Japanese rice has been postulated as: dark purple (C^B *A Pr*), red purple (C^{Bp} *A Pr*), red overlapping with brown (C^B A^d *Pr*), pink overlapping with light brown (C^{Bp} A^d *Pr*), and the tawny (dark brown, C^B A^+ *Pr*; light brown, C^{Bp} A^+ *Pr*). In connection with this, it is worthy to note that in such genotypes as C^{Br} *A Pr* and C^{Br} A^+ *Pr*, there is no sign of coloration in glumes except in apiculus, showing no difference of coloration mode in each two genotypes between C^{Br} *A Pr* and C^{Br} *A* Pr^+, or between C^{Br} A^+ *Pr* and C^{Br} A^+ Pr^+. This is due to the fact that C^{Br} produces too small amount of chromogenic substance to distribute pigment all over the floral glums.

Pl, the purple leaf gene, is comprised of three alleles, *Pl*, Pl^W and Pl^+. The distribution effects of *Pl* and Pl^W are similar to each other, showing coloration in the entire surface of the leaf blade, leaf sheath, collar, auricle, ligule, node and internode. However, they are principally different in the following points, that (i) color by Pl^W almost fades out in the later part of the growing period, whereas color by *Pl* does not show any noticeable change up to maturity, (ii) Pl^W causes purple pericarp regardless of its exposure to direct sunlight during its development, while pericarp color by *Pl* is expressed only when it is exposed to the direct sunlight, and (iii) as to internode coloration a striking expression is observed as the pleiotropic effect of Pl^W, but as to node or collar coloration *Pl* is more effective than Pl^W (NAGAO, TAKAHASHI & KINOSHITA 1962). There remains, however, a possibility that *Pl* and Pl^W are pseudoallelic. The effect of alleles at the *Pl*-locus is diminished by the presence of such inhibitors as *I*–Pl_1, *I*–Pl_2 and *I*–Pl_3 (Fig. 2 & 4 d).

Pn, the so-called purple node gene, is connected with the distribution of color in leaf apex, leaf margin and the entire surface of stem node, collar, auricle and ligule. The most strikingly colored part due to *Pn* is the stem noee (Fig. 3).

These genes for anthocyanin coloration are arranged and classified into the following three groups of causal genes, according to how many other genes are necessary when the proper gene exerts its effect to the eye.

i) Basic group
   C: fundamental gene for apiculus coloration.
   A: ditto
   P: sub-basic; gives some modifying effect on *C*.

ii) Distribution gene group
Ps: exerts its effect under the existence of basic gene.
Pr: ditto
Pl: ditto
Pn: ditto

iii) Inhibitor group
I-Pl$_1$: exerts its influence, only when it coexists with a gene at *Pl*-locus.
I-Pl$_2$: ditto
I-Pl$_3$: ditto

The genic interrelation and the mode of color expression caused by these genes are diagramatically represented as in Fig. 1.

B. Genes for other colors

Among genes for coloration other than the anthocyanin and its related colors, the following were included in the linkage studies:

Rc……Brown pericarp
Rd……Red pericarp
gh……gold hull (*rg*)
I-Bf……Inhibitor for dark (or brown) furrows in lemma and palea (*I-F* or *df*)

Rc is responsible for the production of the pigment in the so-called brown rice, which has dark-brown irregular speckles on a reddish brown background. *Rd*, when *Rc* co-exists, is responsible for spreading the color of *Rc*, giving a dark red pericarp and seed coat, or red rice. *Rd* itself does not produce any pigment. Thus, the genic constitution of red rice is assumed to be *Rc Rd*, that for brown rice *Rc Rd*$^+$, and that for white rice either *Rc*$^+$ *Rd* or *Rc*$^+$ *Rd*$^+$ (NAGAO 1951).

As to the chemical properties of this pigment the writers have arrived at the conclusion that it is a series of catechin, catechol tannin and phlobaphane. A greater amount of "catechin + catechol tannin" was estimated from the red pericarp and the smaller from the brown pericarp. The brown pericarp gene, *Rc*, is regarded to have an effect of accumulating the pigment in the pigment layers, and *Rd* is regarded as causing a greater accumulation of the pigment than in case of the brown pericarp. The dark colored speckles in brown pericarp are probably caused by precipitaion viz. extreme accumulation of the pigments which coagulate the protains of living cells around them (Fig. 4 b, 4 c, 6 & 7), (NAGO, TAKAHASHI & MIYAMOTO 1957).

In connection with the red pericarp character it is worthy of note that,

besides the effects of *Rc* and *Rd*, reddish brown color is expressed by a pleiotropic effect of Pl^w (as mentioned before, Pl^w is a gene for purple leaf) when it co-exists with *C* in the absence of *A* (NAGAO, TAKAHASHI & KINOSHITA 1962).

Some varieties have yellow pigment in the cell wall of the floral glumes and internode (Fig 5 b). There are two types of this coloration; one is self colored and is called "ripening gold or gold hull", and the other "dark or brown furrows", in which only the inter-veins of the floral glumes are colored (Fig. 5 a & 8). The "gold hull" is a single recessive (gene symbol; *gh*) to normal straw color; the "dark furrows" is due to a dominant gene *Bf*; and the co-existence of *Bf* and its inhibitor *I-Bf* or the deficiency of *Bf* cause the normal straw color (NAGAO & TAKAHASHI 1954). According to this scheme the genic formulae are given as:

gold ·····*gh Bf I-Bf*, *gh* + *I-Bf*, *gh Bf* +, *gh* + +
furrows ····· + *Bf* +
normal····· + *Bf I-Bf*, + + *I-Bf*, + + +

C. Genes for presence of floral structures

Among several morphological traits, awning, pubescence of floral glumes and long empty glumes will be briefly mentionned.

An·····Awned
gl·····glabrous glume and leaf
g·····recessive long glume (*lng*)

The only distinct criterion in the grouping of awnedness is awned vs. awnless, and in this respect 3 : 1, 15 : 1 and 63 : 1 are the representative segregation ratios in Japanese varieties. However, and although the scaling of the awness was conducted in a simplified form, five types of this character are roughly explained on the basis of three pairs of multiple genes. The medium awned, the short awned and the tip awned are characterized by the action of the genes An_1, An_2 and An_3 respectively. The fully awned can be produced by the mutual effect of An_1 and An_2. An_3 is considered to be the weakest in its action, no remarkable effect being seen upon the awnedness of An_1 or An_2, even if An_3 co-exists with these genes. Accordingly, the five types can be denoted as follows (NAGAO & TAKAHASHI 1942):

Full awn ·····An_1 An_2 An_3 or An_1 An_2 +
Medium awn·····An_1 + An_3 or An_1 + +
Short awn····· + An_2 An_3 or + An_2 +
Tip-awn ····· + + An_3
Awnless ····· + + +

It has been shown that there exist four kinds of major genes, *Hla*, *Hlb*, *Hg* and *gl*, all of which are responsible for an expression and development of pubescence of floral glume and/or leaf. A gene *gl* is responsible for glabrous leaf and floral glumes, and *Hla* ond *Hlb* are complementary in producing long pubescence on leaves, but when then co-exist with *gl* the hairs are remarkably shortened. The last one, *Hg* is a gene for long pubescence on floral glumes, and *Hg* exerts its pleiotropic effect on pubescence of the leaf margin, auricle and panicle branch (Fig. 10 & 11). As a result of these schemes, the following hair types have been accounted for (NAGAO, TAKAHASHI & KINOSHITA 1960) :

Floral Glumes	Leaf	Genes concerned
pubescent	pubescent	*Hla Hlb Hg*
pubescent	glabrous	*Hg gl*
glabrous	pubescent	*Hla Hlb gl*
glabrous	glabrous	*gl*

In some varieties empty glumes are as long as or longer than the lemma and palea. It is known that these two types are generally governed by the respective single genes, *g* and *Gm*, except in the few cases where duplicate genes are considered to be existent, giving a F_2 ratio of 15 normal (short) vs. 1 long (Fig. 12 & 13).

These are the prevailing types of long empty glumes, however, there is still another type of such glumes in which the length of the empty glumes is uneven, giving a long empty glume on the palea side and a normal short empty glume in the lemma side. It was revealed that this type is given when a suppressor, *Su-g* co-exists with *g*. Thus the relations between phenotypes and their genotypes are: normal short (+ +, *su-g* +) uneven long (*Su-g g*) and even long (+*g*) (NAGAO, TAKAHASHI & KINOSHITA 1960).

D. Genes for modified structures

The following morphologically modified characters will be discussed.

Cl……Clustered spikelets (*Scl*)
d_7……"cleistogamous" dwarf
Dn……Dense (vs. normal) panicle
Ur……Undulate rachis
ri……verticillate arrangement of rachis
nl……neck leaf, bract leaf at the basal node of panicle (*hk*, *nk*)
lg……liguleless
la……lazy

Clustered spikelets are usually controlled by a simple pair of allelomorphs (*Cl*), "clustered" being incompletely dominant (Fig. 14).

A cleisogamous mutant found by NAGAO and TAKAHASHI (1954) has a singular form, with compact panicles, small spikelets and somewhat short plant height. Morphologically, this plant has abnormal glumes in which the lower parts can not be differentiated and the lemma and palea are united. As a result the spikelets are tightly held in at flowering time, while having normal swelled lodiculus (Fig. 18). This mutant behaves as single recessive to the normal, and is designated as d_7 in its gene symbol.

The writers found a variant with a singular panicle type which is characterized by a Japanese barnyard grass-like panicle (Fig. 15 & 19). A single gene, *Dn*, is responsible for this character, showing that dense is incompletely dominant over normal.

In connection with the panicle density, there exists another type of dense panicle of which the causal gene is designated as *Ur* (NAGAO, TAKAHASHI & KINOSHITA 1958). The *Ur* is incompletely dominant over the recessive allelomorph. This panicle type has well-branching rachises, and it is characterized by undulating rachises, showing an open panicle. The cause of undulation seems to be attributable to the growing of branching rachises in the flag leaf sheath, which produces this irregularity by mechanical suppression (Fig. 16).

Verticillate or whorled arrangement of rachis is the name given to the particular arrangement of branches on the panicle stem, when five or even more rachises are borne around the basal node of the panicle (Fig. 20). In the writers' examination, this behaves as a simple recessive (gene symbol ; *ri*) to the normal. The letter "*ri*" is an abbreviation of "rinshi", which means whorled branches in Japanese.

Neckleaf is a bract arising at the basal node or panicle. Usually the large part of the panicle is enclosed in the bract leaf. When this is longer than the panicle, no spikelets appear from the sheath, while the panicle is already mature (Fig. 17). This character is a single recessive (*nl*) to the normal.

It is known that in a liguleless leaf, the auricle and collar are also absent (Fig. 22). In every instance, liguleless behaves as a simple recessive (*lg*) to the normal, the liguled form.

Normally the stem of rice grows upright from the surface of the soil, however, one type of growth habit which is called lazy, spreading or prostrate has been reported by many workers (Fig. 21). This type of growth is characterized by the stem growing obliquely so that the young plant has an extreme spreading form. This is a simple recessive (*la*) to the normal.

A mutant with ageotropic growth habit was isolated by RAMIAH and

PARTHASARATHY (1936), and in their description this type seems to be similar to the lazy. But, as far as the writers are aware, no positive evidence that the ageotropic is identical with the lazy has been made yet. Among rice varieties, though habit does never take such en extreme spreadnig form mentioned above, there are many types of which tillers arise at several angles from the ground. Some genes are proposed for this character, however the genic interrelation between these genes and the gene for the lazy is not yet clear.

E. Genes for dwarfness

Dwarf forms of Japanese rice plants are roughly classified into two main types, one is the "Daikoku" type which is more common, and the other is the "Bonsai" type. In the former, all of them are similar in that plant height is nearly two-thirds to one-third of the original forms, the leaves are upright, short and rigid, having a deep green color. The panicle is short and compact, and in some forms it is erect even when ripened. The grains are small and roundish. The latter, "Bonsai" type, is characterized by many tillers with narrow and slender leaves, and stand panicles with no so round or small floral glumes.

The following genes for the "Daikoku" type dwarf characters were examined as to their loci in linkage groups:

d_1……"Daikoku" dwarf
d_2……"Ebisu" dwarf
d_7……"cleistogamous" dwarf
d_8……"Nohrin 28" dwarf

The "Daikoku" and "Ebisu" dwarfs are simple recessives to the normal, their causal genes being d_1 and d_2 respectively (NAGAO & TAKHASHI 1946). Character expression by d_1 is the typical "Daikoku" type with short and stout stems, short, sinuate but broad leaves, erect and compact panicles, small and round floral glumes (Fig. 23 & 30).

The appearance of d_2 is similar to that of d_1. However, the d_2 plant is relatively taller than the d_1 and the floral glumes are not so reduced in size when they are compared with the original normal form (Fig. 24 & 30).

As mentioned in the preceding paragraph, the "cleistogamous" dwarf is characterized by its closed glumes, but at the same time it shows the "Daikoku" type of dwarf stature, somewhat short and broad leaves, erect and compact panicles, and small and round floral glumes (Fig. 25 & 30).

The "Nohrin 28" dwarf was considered to be a simple recessive (d_8) to the normal. The character expressions by d_1 and d_8 are almost the same, but they definitely belong to different loci (Fig. 26).

Many dwarf forms of the "Bonsai" type have been found. Among them, the so-called "tillering" dwarf of the writers was studied in respect to its causal genes and their linkage relationships (Fig. 27, 28 & 30).

d_3……One of the multiple genes for "tillering" dwarf
d_4……do
d_5……do

In crosses between the "tillering" dwarf and the normal forms, three segregation rations, 3 : 1, 15 : 1 and 63 : 1 were found, indicating that three multiple genes d_3, d_4 and d_5 are responsible for this character (NAGAO & TAKAHASHI 1946, NAGAO 1951).

Besides the Daikoku and Bonsai types, another "lop-leave" dwarf characterized by sinuous panicle neck and leaves with lopped blades and shortened sheaths were examined (Fig. 29 & 30). In all crosses of the lop-leaved dwarf × the normal, the former behaves as single recessive to the latter. The causal gene for the dwarfness is designated as d_6.

The double dwarf plants which are the combined types of two dwarf formes are highly sterile and sometimes cleistogamous fertilization takes place. Triple dwarfs, which involve more than three different dwarf genes in homozygous condition, were produced by the writers, but these dwarfs were hardly meritorious in building up multiple-gene-markers because of the fact that these dwarfs usually set no seed owing to the imperfect development of reproductive organs (Fig. 30, 31, 32 & 33).

F. Genes for modified composition

The following three genes and their character expressions will be mentioned:

wx……waxy (glutinous) endosperm (*m* or *gl*)
sh……shattering or easy threshing, recessive to difficult or intermediate threshing
bc……brittle culm

Though certain varieties are called waxy or glutinous, they contain neither waxy nor real gluten substances. The recessive gene which governs the waxy endosperm is designated as *wx* (Fig. 34). It may be worthy of note that many workers have generally found a deficiency in the number of waxy segregates in F_2 from crosses of waxy × non-waxy. To explain this, various hypothesis below mentioned have been suggested. i) The existence of modifiers which inhibits hydrolysis. ii) The existence of a linkage between the waxy gene and the lethal or the gamete development genes. iii) The selective fertilization or

gamete selection. iv) The lesser vitality or lesser dynamic activity of the waxy pollens. v) The gene mutations from the recessive to the dominant, which occur in the gamete. Among them, which is the most appropriate explanation and thus what factor may act as an important role of disturbing the proper segregation ratio, is not determined yet.

The worst form of shattering is exhibited by the wild rices, but, even in some varieties of cultivated rice, some degree of shattering is inevitable. It is known that in crosses between wild and cultivated forms more than one gene are involved and shattering behaves as a single or double dominant over non-shattering. In crosses among cultivated varieties which show varying degrees of shattering, shattering shows three modes of segregrtion, viz., dominant, intermediate or recessive. A case where non-shattering behaves as a monogenically dominant over shattering was found by the writers (Fig. 35). The causal gene of shattering is designated as *sh*. Anatomically easiness of shattering is chiefly due to the development of a tissue called abscission layer, which lies between the caryopsis and the pedicel attached to the rachis. This tissue consists of one to three layers of lignified thin walled cells. In rices that shatter easily, these cells develop well and dry up early.

The character "brittle culm" behaves as a simple recessive to the normal type without exception and is designated as *bc* (Fig. 36). The brittle culm mutant has a comparatively lower content of α-cellulose in its cell wall. No noticeable differende of water, crude protein, crude fiber, silica and pentosan contents are found out between the brittle culm and the normal (NAGAO, TAKAHASHI & MIYAMOTO unpublished).

G. Genes for chlorophyll deficiency

The linkage relationships of the following genes have been examined:

fs……fine stripes in leaf margin of young plants
gw……green-and -white-striped
v……virescent

The "fine striped" type is characterized by the appearance of minute white flecks or fine white stripes at the tip and margin of leaf blade in young plants (Fig. 38). This is a simple recessive to the normal green. The expression of the causal gene (*fs*) is to a large extent dependent upon the environmental conditions, showing no phenotypic difference between plants with *fs* and fs^+ when they are grown under relatively high temperature conditions (TAKAHASHI 1950).

The green-and-white-striped types mentioned above are some of the most common striped patterns in rice. The variegated portions are in streaks, in-

tersepting the green portion of leaf blade with more or less regular intervals. The white streaks appear not only in leaf blade but also in leaf sheath, stem and even in spikelet through the whole green stage (Fig. 39). This is a simple recessive character and is designated as *gw* in its gene symbol (TAKAGASHI 1950).

Besides these two types of variegations, the virescent type and its causal gene, *v*, should be added here. This is characterized in that there is some delay in the development of chlorophyll in the seedlings so that they sppear first almost white or slightly yellow and then gradually change to green, though sometimes whitish green or whitish yellow portion remains up to the maturity. This was kindly sent to the writers by Mr. JODON, and is being studied (Fig. 40).

H. Genes for other characters

Three genes, *Ph*, *bl* and *wh* are the objects of the description in the present paragraph.

Ph……Phenol staining
bl……Physiological disease showing dark brown or blackish mottled discoloration of leaves (*mt* or *mg*)
wh……White hull (*Hw*)

It has been known that a sidgle dominant gene, designated as *Ph*, is connected with the presence of the substance by which the pericarps and hulls are stained a brownish purple color when those parts are treated with an aqueous solution of phenol (MORINAGA, NAGAMATSU & KAWAHARA 1943, NAGAO & TAKAHASHI 1952, etc), (Fig. 40).

Dark-brown mottled discoloration is a singular color type in which brown spots begin to develop shortly after panicle emergence. The discoloration of the chlorophyll appears first on the leaves as brown spots resembling fungus lesions. In spreads and by maturity extends even into panicles, giving the entire plant a dirty brown appearance. Many crosses indicate that this color type is caused by a single recessive gene, *bl* (NAGAO & TAKAHASHI 1954). JONES's (1952) and JODON's (1957) brown or black spot mutants were crossed with the writers' mottled type, and it was revealed that these were governed by different genes (Fig. 41).

White hull, in contrast to straw color, appears dull chalky white. This was first analyzed by JODON (1957) and was reported to be due to a single dominant gene, *wh*. According to him, *wh* is not allelic to the gold hull gene, *gh*, and this observation was verfied by the writers. The white hull appears in segregants of identical F_2 population both with and without purple

or red apiculus, indicating that it has no relation to the anthocyanin production (Fig. 9).

III. Linkage Relations

A. Linkage data involving the above mentioned genes

Both linked inheritance data and independent inheritance data are essential to demarcate each linkage group. In this paper, emphasis is laid on linkage relationships within each group. For experimental results on indepence between groups, only summarized recombination values will be given.

Linked genes and their segregation modes examined by the writers are shown in Table 2. The summarized data of recombination values are listed in Table 3.

TABLE 2. Linked genes and their segregation modes in Japanese rice

Gene pair	Linkage phase and number of crosses	Segregation mode AB	Ab	aB	ab	Total	Recombination value	χ^{2} [1]	n	p
Group I ("*wx*"-group)										
d_4—wx (3 : 1) (3 : 1) (21.5%)	r	309	122	122	5	558	21.5 ±2.70			
	2	(285.5)	(133.1)	(133.1)	(6.5)			2.94	3	0.5—0.3
wx—C (3 : 1) (3 : 1) (22.8%)	c	1148	167	175	242	1732	22.8 ±0.79			
	2	(1124.1)	(174.9)	(174.9)	(258.1)			1.87	3	0.7—0.5
d_4—C (3 : 1) (3 : 1) (38.2%)	r	295	127	114	21	557	38.2 ±2.41			
	2	(298.8)	(118.9)	(118.9)	(20.3)			0.82	3	0.9—0.8
Pla—wx (3 : 1) (3 : 1) (44.7%)	c	385	123	113	53	674	44.7 ±1.83			
	1	(388.5)	(117.0)	(117.0)	(51.5)			0.52	3	0.95—0.90
Cl—C (3 : 1) (3 : 1) (40.3%)	c	360	114	84	54	612	40.3 ±1.81			
	2	(360.5)	(98.5)	(98.5)	(54.5)			4.58	3	0.3—0.2
Cl—wx (3 : 1) (3 : 1) (41.0%)	c	77	14	26	9	126	41.0 ±4.00			
	1	(73.9)	(20.6)	(20.6)	(10.9)			3.99	3	0.3—0.2

1) χ^{2} for goodness of fit, under respective linkage intensities.

TABLE 2. (continued-1)

Group II ("*Pl*"-group)

d_2—d_3 (3 : 1) (3 : 1) (25.4%)	r	207	86	79	5	377	25.4 ±3.21			
	1	(194.6)	(88.2)	(88.2)	(6.1)			1.99	3	0.7—0.5
d_3—*Pl* (15:1) (3:1) (35.2%)	r	354	125	21	3	503	35.2 ±5.53			
	1	(349.7)	(121.9)	(27.5)	(3.9)			1.89	2	0.5—0.3
Pl—*lg* (3 : 1) (3 : 1) (30.9%)	c	1325	289	267	272	2153	30.9 ±0.84			
	7	(1344.4)	(271.0)	(271.0)	(260.8)			2.02	3	0.7—0.5
lg—*Ph* (3 : 1) (3 : 1) (7.4%)	c	218	13	11	79	321	7.4±1.03			
	1	(229.3)	(11.5)	(11.5)	(68.8)			2.30	3	0.7—0.5
Ph—*Pr* (3 : 1) (3 : 1) (24.2%)	c	333	55	64	86	538	24.2 ±1.47			
	2	(346.3)	(57.2)	(57.2)	(77.3)			2.38	3	0.5—0.3
d_2—*Pl* (3 : 1) (9 : 7) (38.1%)	c	232	157	51	59	499	38.1 ±2.80			
	2	(223.8)	(152.0)	(58.1)	(65.1)			1.91	3	0.7—0.5
d_3—*lg* (15:1) (3:1) (39.7%)	c	146	44	13	7	210	39.7 ±7.13			
	2	(149.1)	(47.7)	(8.4)	(4.8)			3.99	3	0.3—0.2
lg—*Pr* (3 : 1) (3 : 1) (28.2%)	c	486	93	103	109	791	28.2 ±1.31			
	5	(497.4)	(95.8)	(95.8)	(101.9)			1.37	3	0.8—0.7
Pl—*Pr* (3 : 1) (3 : 1) (48.6%)	c	341	99	114	30	584	48.6 ±2.06			
	2	(325.1)	(112.9)	(112.9)	(33.1)			2.79	3	0.5—0.3
d_2—*lg* (3 : 1) (3 : 1) (47.2%)	c	920	297	243	96	1556	47.2 ±1.24			
	5	(886.5)	(280.6)	(280.6)	(108.5)			8.69	3	0.05 —0.02
d_2—*Ph* (3 : 1) (3 : 1) (50.0%)	c	165	65	48	17	295	51.5 ±2.99			
	1	(165.9)	(55.3)	(55.3)	(18.4)			2.78	3	0.5—0.3
d_2—*Pr* (3 : 1) (3 : 1) (50.0%)	c	341	121	90	26	578	52.8 ±2.16			
	2	(325.1)	(108.4)	(108.4)	(36.1)			8.19	3	0.05 —0.02
Pl—*P* (3 : 1) (3 : 1) (2.1%)	c	580	4	13	147	744	2.1±0.36			
	2	(550.3)	(7.7)	(7.7)	(178.3)			11.85	2	0.005 —0.001

Group III ("*A*"-group)

A—*Rd* (3 : 1) (3 : 1) (0.3%)	c	2298	4	10	797	3109	0.3±0.07			
	9	(2326.7)	(5.0)	(5.0)	(772.2)			5.95	2	0.1—0.05

TABLE 2. (continued-2)

Rd—Pn (3 : 1) (3 : 1) (26.8%)	r	241	132	137	13	523	26.8 ±2.70			
	2	(270.9)	(121.4)	(121.4)	(9.4)			7.63	3	0.1—0.05
A—Pn (3 : 1) (3 : 1) (29.9%)	r	333	173	162	19	687	29.9 ±2.13			
	2	(358.9)	(156.4)	(156.4)	(15.4)			4.69	3	0.2—0.1
Group IV ("*g*"-group)										
d_6—*g* (3 : 1) (3 : 1) (14.0%)	r	383	178	156	3	720	14.0 ±2.45			
	3	(363.5)	(176.5)	(176.5)	(3.5)			3.42	2	0.2—0.1
g—Rc (3 : 1) (3 : 1) (28.9%)	c	947	194	181	192	1514	28.9 ±0.97			
	4	(947.8)	(188.0)	(188.0)	(190.2)			0.47	3	0.95 —0.90
d_6—*Rc* (3 : 1) (3 : 1) (29.9%)	c	1557	319	330	321	2527	29.9 ±0.76			
	3	(1573.9)	(321.3)	(321.3)	(310.4)			0.79	3	0.9—0.8
d_6—d_7 (3 : 1) (3 : 1) (39.4%)	r	192	85	87	18	382	39.4 ±2.62			
	1	(206.3)	(80.2)	(80.2)	(15.3)			2.33	3	0.7-0.5
Group V ("*I-Bf*"-group)										
I-Bf—Ps (3 : 1) (3 : 1) (42.1%)	c	114	35	33	18	200	42.1 ±3.25			
	2	(116.8)	(33.2)	(33.2)	(16.8)			0.25	3	0.98 —0.95
Group VI ("d_1"-group)										
gw—d_1 (3 : 1) (3 : 1) (17.8%)	r	745	304	323	9	1381	17.8 ±1.75			
	4	(701.4)	(334.3)	(334.3)	(10.9)			6.12	3	0.2—0.1
d_1—*gh* (3 : 1) (3 : 1) (27.8%)	r	350	138	148	11	647	27.8 ±2.42			
	2	(336.0)	(149.3)	(149.3)	(12.5)			1.62	3	0.7—0.5
gw—gh (3 : 1) (3 : 1) (40.9%)	r	282	101	106	20	509	40.9 ±2.43			
	2	(275.9)	(105.9)	(105.9)	(21.4)			0.45	3	0.95 —0.90
gh—An_3 (3 : 1) (3 : 1) (42.9%)	c	265	70	77	34	446	42.9 ±2.20			
	2	(259.4)	(75.2)	(75.2)	(36.4)			0.67	3	0.9—0.8
Group VII ("*fs*"-group)										
Ur—fs (3 : 1) (3 : 1) (27.5%)	c	414	90	80	103	687	27.5 ±1.39			
	2	(433.8)	(81.5)	(81.5)	(90.3)			3.61	3	0.5—0.3

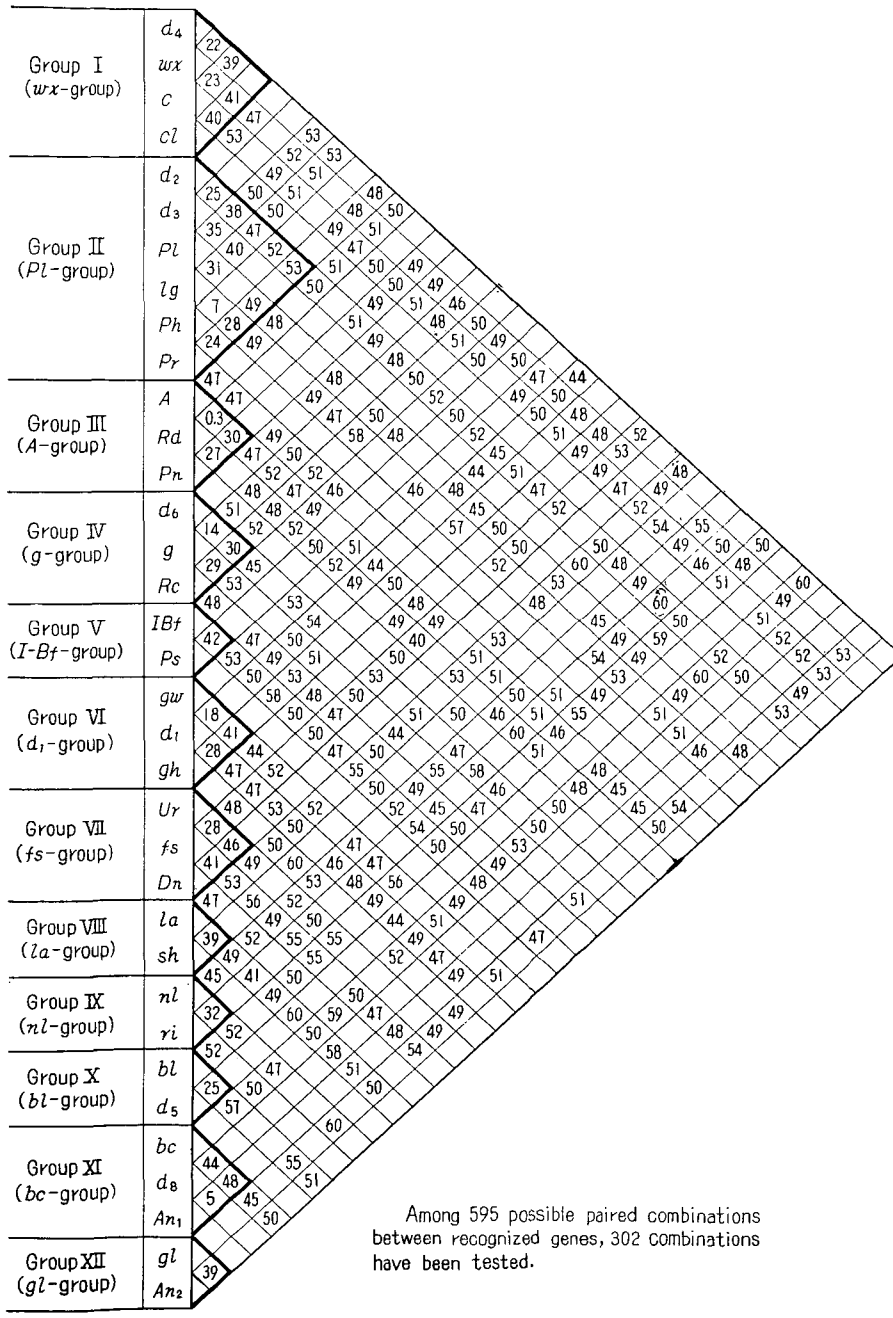
TABLE 2. (continued-3)

fs—Dn (3 : 1) (3 : 1) (41.1%)	c	511	147	160	88	906	41.1 ±1.51			
	2	(531.6)	(147.9)	(147.9)	(78.6)			2.92	3	0.5—0.3

Hence the gene *Dn* is epistatic over the gene *Ur*, the recombination value in *Ur-Dn* was calculated by FISCHER's Maximum Likelihood Method. This is as follows.

Ur—Dn (1:2:1)(3:1) (46.2%)	r	246	27	44	20	337	46.2 ±4.99			
	1	(252.8)	(24.4)	(41.9)	(17.9)			0.79	3	0.9—0.8
Group VIII (*"la"*-group)										
la—sh (3 : 1) (3 : 1) (38.7%)	r	215	98	74	15	402	38.7 ±2.82			
	1	(216.1)	(85.5)	(85.5)	(15.1)			3.38	3	0.5—0.3
Group IX (*"nl"*-group)										
nl—ri (3 : 1) (3 : 1) (32.4%)	r	853	404	391	51	1699	32.4 ±0.67			
	4	(897.5)	(377.4)	(377.4)	(46.7)			4.97	3	0.2—0.1
Group X (*"bl"*-group)										
bl—d$_5$ (3 : 1) (15 : 1) (25.1%)	c	215	6	50	6	277	25.1 ±2.09			
	1	(200.2)	(7.6)	(59.5)	(9.7)			4.84	3	0.3-0.2
Group XI (*"bc"*-group)										
bc—d$_8$ (3 : 1) (3 : 1) (43.5%)	r	178	51	50	9	288	43.5 ±3.19			
	1	(157.6)	(58.4)	(58.4)	(13.6)			6.34	3	0.1—0.05
d$_8$*—An*$_1$ (3 : 1) (3 : 1) (5.4%)	c	840	23	39	247	1149	5.4±0.50			
	3	(831.6)	(30.2)	(30.2)	(257.1)			4.76	3	0.2—0.1
bc—An$_1$ (3 : 1) (3 : 1) (48.4%)	r	170	46	58	14	288	48.4 ±3.00			
	1	(166.0)	(54.0)	(54.0)	(14.0)			2.77	3	0.5-0.3
Group XII (*"gl"*-group)										
gl—An$_2$ (3 : 1) (3 : 1) (39.4%)	c	272	68	76	41	457	39.5 ±2.08			
	1	(271.0)	(71.7)	(71.7)	(42.5)			0.51	3	0.95 —0.90
gl—Hg (3 : 1) (3 : 1) (38.7%)	c	269	70	67	40	446	38.7 ±2.08			
	1	(264.9)	(69.6)	(69.6)	(41.9)			0.25	3	0.98 —0.95

TABLE 3. Recombination values in Japanese rice



B. Trial Construction of linkage maps estimated from the above data

Based on the data mentioned above, twelve linkage groups are postulated and the genes of each group are arranged in the order which will be mentioned below. Each group is provisionally designated with a Roman numeral, but at the same time, it is temporarily named with the symbol of one of the representative gene.

The followings are the process by which the location of genes in each linkage group is estimated.

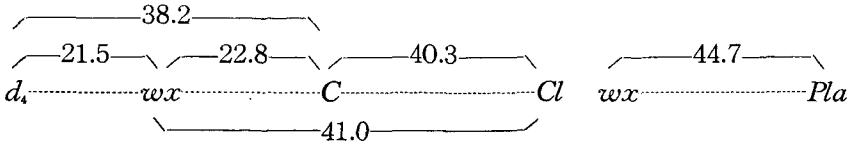
a. "*wx*" linkage group (Group I)

This group corresponds to Group I of JODON's system. The best-established case of linkage in this group is that between the apiculus color gene and the waxy or glutinous endosperm gene. Of the three genes, *C*, *A* and *P* which are responsible for apiculus coloration, *C* is linked with *wx* for waxy character. The recombination value between *C* and *wx* amounts to about 22.8%, though considerable variation from this value are seen in several crosses. Based on this linkage relation it is suggested that *C* is identical with genes described under different names by many workers, for example, *Ap* for purple apiculus (JODON 1948 and others), *S* for reddish apiculus (YAMAGUCHI 1926), Ap_4 for colored apiculus (CHAO 1928), *Ty* for tawny color of ripened apiculus (CHAO 1928), and others..

Besides the *C*, two genes, d_4 for "tillering" dwarf and *Cl* for clustered spikelets are inserted in this group. The percentage of recombination values between d_4 and *wx*, and between d_4 and *C*, are 21.5% and 38.2% respectively. Owing to fluctuations of these values in individual crosses, precise mapping is difficult, however, these data may indicate that d_4 is situated in this group in the order of d_4-*wx*-*C*.

In addition to those mentioned above, linkages between *C* and *Cl*, and between *wx* and *Cl*, that were first reported by JODON (1940), were reexamined, giving recombination values of 40.3 and 41.0% respectively. Further work would be necessary to determine whether *Cl* is located on the same side of *wx*, putting *C* in the center, or not. However, available data suggest the relative gene sequence of *wx*-*C*-*Cl*. A possibility that a gene for colored leaf margin, *Pla*, may be inserted in this group. This is based upon a weak linkage between *wx* and *Pla*, with an intensity of 44.7% recombination value.

On the whole therefore the gene order of this group may be arranged as;



b. "*Pl*" linkage group (Group II)

This goup is based upon linkages among *Pl* (purple leaf), *lg* (liguleless) and *Ph* (phenol stanining). MORINAGA et al (1942, 1943) first reported linkages between *Pl* and *lg*, and between *Pl* and *Ph*, giving recombination values of 21% and 7% respectively.

This was confirmed by the writers, who further added four genes to this group. These are d_2 ("Ebisu" dwarf), d_3 ("tillering" dwarf), *Pr* (purple hull) and *P* (completely colored apiculus). Recombination value between *Pl* and *lg* is 30.9 in an average, though varying from 24% to 32% in the coupling phase. Linkage intensity between d_2 and *Pl* amounts to 38.1 through two crosses, in which leaf color segregates 9 colored vs. 7 colorless, indicating that besides *Pl*, an activator gene *A*, is concerned with the character expression of leaf color. As will be mentioned in the next paragraph, *A* belongs to an another linkage group, this result means a linkage between d_2 and *Pl*. The linear order of three genes, d_2, *Pl* and *lg* will be given by examining linkage intensity between *lg* and d_2. In five crosses an average recombination value of 47.2 was calculated, indicating that the possible order is d_2-*Pl-lg*.

Linkages between *Ph* and *lg*, between *Ph* and *Pr*, and between *Pr* and *lg*, are given as 7.4%, 24.2% and 28.2% respectively, suggesting that the sequence of these genes is *lg-Ph-Pr*.

Thus two sets of gene maps, d_2-*Pl-lg* and *lg-Ph-Pr* are provided. In connecting these two groups, linkage between d_2 *and Pr* should be examined, since *lg* is considered to be the base point in the two maps. In this respect two crosses were made, and a 52.8% recombination value was obtained, indicating that d_2 and *Pr* are located apart. Based on these results, sequences of five genes would be as ; d_2-*Pl-lg-Ph-Pr*.

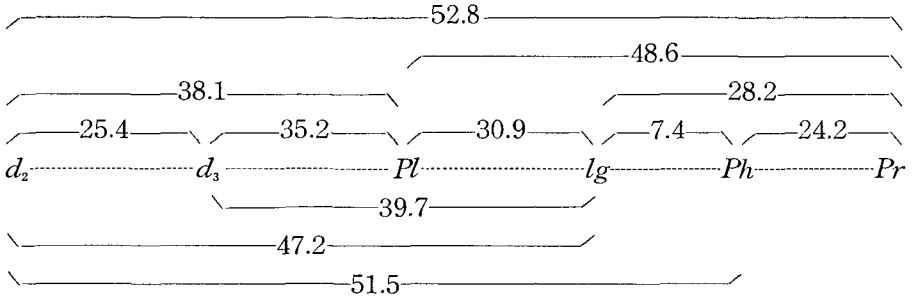
For further verification of this assumption examination of such linkage as between d_2 and *Ph*, or between *Pl* and *Pr* was made. Recombination values of 51.5% and 48.6% were given, respectively, by testing three cross combinations. As mentioned above, linkage intensities between d_2 and *lg*, and between *lg* and *Ph* are 47.2% and 7.4% respectively, the gene sequence of d_2-*lg-Ph* is natural to consider. The value of 48.6% between *Pl* and *Pr* may also be an additional evidence of the linear order of genes, *Pl-lg-Pr*.

In regards to a linkage between d_2 and d_3, a cross of two genotypic plants, $+d_3$ d_4 d_5 ("tillering" dwarf form) and d_2+ d_4 d_5 ("Ebisu" dwarf form) was made. In this cross the genes d_4 and d_5 have nothing to do with the mode of segregation ratio, and therefore two dwarf forms should be monogenically inherited. The observed result is in close accordance with expectation based on an approximate 25.4% recombination value in repulsion phase. From this

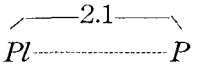
result it follows that d_3 might be assigned to the present linkage group.

In this connection, a linkage between d_3 and *Pl* was ascertained, the recombination value between them being 35.2%. As the cross over between d_2 and *Pl* was 38.1%, d_3 might be located between d_2 and *Pl*. This supposition was proved to be right, by examining another linkage, viz. between d_3 and *lg*, of which linkage intensity being 39.7%, varying 31% to 47%. The possible order of d_2, d_3 and *lg* is d_2-d_3-*lg*.

On the whole therefore, the order and distance of the above mentioned six genes, d_2, d_3, *Pl* *lg*, *Ph* and *Pr* might be diagramatically indicated as follows.



As for an another possible gene to be assigned to this group, *P* is worth to note. Two crosses of *C A P*+ × *C A*+*Pl* give segregation that undoubtedly shows the occurrence of close linkage between the genes *P* and *Pl*, with a recombination value of 2.1%.



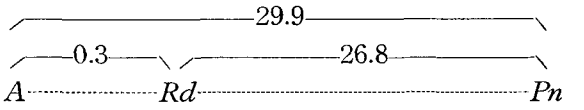
c. "*A*" linkage group (Group III)

The members of this group are *A* (anthocyanin activator), *Rd* (red pericarp) and *Pn* (purple node). Before going further some considerations on gene interaction between *A* and *Pn* should be recalled. The action of *Pn* is expressed only in the coexistence of *C A*, and in this connection such crosses as *C*+ + × *C A Pn* and *C A*+ × *C*+*Pn* are inappropriate in examining linkage intensity between *A* and *Pn*, since there is no way of discriminating two genotypes of +*Pn* and + +, both of them being colorless in their stem nodes. Linkage between *A* and *Pn* is observable through the cross combination in which both the parents are different from each other in *A*-locus in such a way as *A* vs. A^a, but not in a way as *A* vs. +.

Crosses were made between two genotypic plants of C^B *A Pn* and C^B A^a +, and a linkage was found out in the coupling phase.

In addition to this linkage, another linkages of this group, between *A* and *Rd* and between *Rd* and *Pn*, were examined by studying a cross combination of C^{Bp} *A*+*Rc Rd* (purple apiculus with green node and red pericarp) and C^{B} A^{d} *Pn* ++ (red apiculus with red node and white pericarp). Three recombination values regarding the linkages of *A-Pn*, *A-Rd* and *Rd-Pn* are given as 32%, 0.2% and 30% respectively. This result indicates a possible order of these as ; *A-Rd-Pn*.

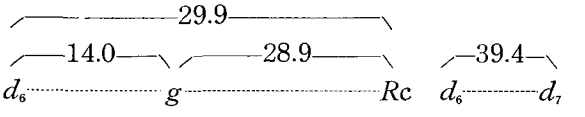
For further verification of the close linkage between *A* and *Rd*, additional crosses were made, and in all of F_2 segregations approximately 0.3% recombination value, which is of about the same magnitude as those shown the above, was recognized. By adding some data on these linkages a diagramatic expression of the gene order and the magnitude of gene distance may be as ;



d. "*g*" linkage group (Group IV)

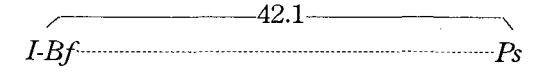
This group consists of linkages among d_6 ("lop-leaved" dwarf), g (recessive long empty glumes), *Rc* (brown pericarp) and possibly d_7 ("cleistogamous" dwarf). The gene d_6 gave a 14.0% recombination value with *g*, *g* gave a 28.9% recombination value with *Rc*, while *Rc* gave a 29.9% recombination value with d_6, suggesting that these genes are situated in the order of d_6-*g*-*Rc*.

An additional gene, d_7, possibly is assigned to this group, by adapting a linkage between d_7 and d_6, with a 39.4% recombination value. Due to the lack of sufficient data of linkages between d_7 and other genes, the location of d_7 is not determined yet.



e. "*I-Bf*" linkage group (Group V)

This goup is based upon a single weak linkage with a 42.1% recombination value between *I-Bf*, an inhibitor for dark brown furrows in lemma and palea, and *Ps*, a gene for purple stigma color.

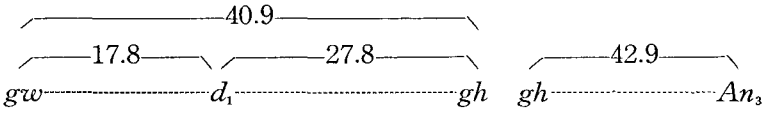


f. "d_1" linkage group (Group VI)

This group includes three genes, namely, d_1 for "Daikoku" dwarf, *gh* for

gold hull, and *gw* for green and white striped leaves and panicles. The recombination values are calculated as ; 17.8% for d_1 and *gw*, and 40.9% for *gw* and *gh*, and 27.8 for d_1 and *gh*, suggesting that the possible order of the concerning genes would be *gw*-d_1-*gh*. To set up accurate magnitude of gene distances of the above, however, further studies should be made, because of the reason, that, in estimating the abov linkages certain correction methods were applied under the repulsion phases of gene combination concerned.

A possibility that one of genes for awnedness may be inserted in this group exists. This is based upon a linkage between gold hull and awnedness with an intensity of 42.9% recombination value.



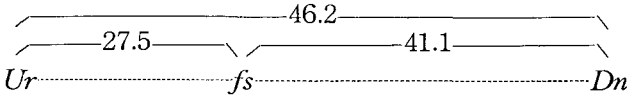
g. "*fs*" linkage group (Group VII)

This is a group of which postulated members are *fs* (fine stripes of young leaf), *Ur* (Undurate rachis) and *Dn* (Dense panicle). The gene *fs* shows linkages with *Ur* and *Dn*, in the intensity of recombination values of 27.5% and 41.1% respectively.

Linkage would be also expected between *Ur* and Dn. In this connection it should be mentioned that besides an action of *Dn*, a dense panicle is also resulted as a pleiotropic effect of *Ur*. The former behaves as epistatic over the latter in their character expression, thus the discrimination between two genotypes, *Dn Ur* and *Dn*+are difficult. In the present examination of combined segregation of *Ur* and *Dn*, F_2 plants were assorted into four classes as shown below, where 46.2% of a recombination value between *Ur* and *Dn* was computed by FISCHER's Maximum Likelihood Method.

1	2	3	4
Dn Ur *Dn* +	+ *Ur* (*Ur* homo)	+ *Ur* (*Ur* hetero)	+ +

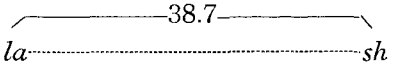
Based on these results, gene sequences would be as follows.



h. "*la*" linkage group (Group VIII)

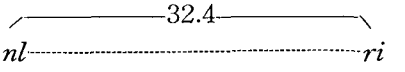
Prostrated or lazy growth habit governed by *la* and shattering of grains caused by *sh* are found to be linked with each other with an intensity of 38.7% recombination value. This constitutes the linkage group termed as

"*la*" linkage group.



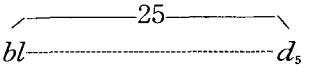
i. "*nl*" linkage group (Group IX)

Based on a linkage between *nl* (neck leaf) and *ri* (whorled arrangement of rachises), and with results that these two genes are independent of many other genes of known linkage groups, the "*nl*" linkage groups has been postulated. The linkage intensity between *nl* and *ri* is 32.4%. Though this value was obtained in the repulsion phase, considerable small variation of recombination values, 28% to 34% are presented throughout crosses examined.



j. "*bl*" linkage group (Group X)

This group comprises two genes, *bl* (brown mottled discoloration of leaves and panicles) and d_5 ("tillering" dwarf). The *bl* is linked with d_5 with a 25.1 % recombination value. The numerical value of this linkage intensity itself is not so trustworthy in that; i) segregation of normal vs. dwarf is 15 : 1 and ii) only a single cross combination was available in estimating this linkage. Therefore to obtain a more precise value, further examination which involves such a cross as $+d_3\,d_4+ \times bl\,d_3\,d_4\,d_5$ should be made.

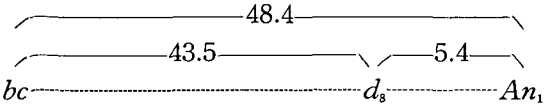


k. "*bc*" linkage group (Group XI)

Insofar as the writers have examined, the gene *bc* for brittle culm shows no linkage with almost all genes which belong to the aforesaid linkage groups, indicating that *bc* would be one of the marker genes of the new linkage group. As regards possible genes of this group, d_8 for "Nohrin 28" dwarf and An_1 one of multiple genes for awnedness, may be worthy of note.

The genes d_8 and An_1 show a striking linkage in which the recombination value is approximately 5.4%, though some variation, from 3% to 10%, were presented in crosses examined. As to linkage intensities of *bc* with d_8 and with An_1, recombination values of 43.5% and 48.4% were given respectively.

These results may be the indication of the gene sequence, as shown below.



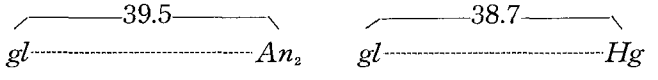
l. "*gl*" linkage group (Group XII)

The *gl*, which is responsible for glabrous floral glumes and leaves, is a gene that shows no linkage with genes located in the linkage groups mentioned above. A single dominant gene for awnedness, An_2, and a gene *Hg* for pubescence in floral glumes seem to be linked with *gl*. Thus these three genes appear to be members of 12th linkage group.

Recombination value between *gl* and An_2 comes to 39.5% which is similar to the value reported by BREAUX NORRIS (1940) in crosses of U. S. varieties. Between *gl* and *Hg*, a recombination value of 38.7% was given. Here, it must be mentioned that the action of *Hg* and *gl* are opposite in expressing pubescence in the floral glumes, and therefore the classification of four genotypes $+Hg$, $++$, *gl Hg* and $gl+$ are difficult when it is done by glume hair types. The *gl* exerts its effect not only on the floral glumes but also on the leaves, and in contrast with this, the effect of *Hg* is limited to the floral glumes. Thus the discrimination of the above four genotypes should be made by the following mode of character expression.

	Phenotype	
genotype	glume hair	leaf hair
$+Hg$	++	+
$++$	+	+
gl Hg	+	—
gl +	—	—

As to the expected linkage between An_2 and *Hg*, no trustworthy numerical value of recombination has been given yet.



On the whole therefore, about 35 genes, of which character expressions were analysed by the writers, have been assigned to different linkage groups, and the relative position of these genes on each of the twelve groups has been postulated. Fig. 42 is a diagramatic presentation of the results mentioned above.

Based on this, a trial construction of rice linkage maps, which is as presented in Fig. 43, is possible to advocate.

C. Other rice linkages reported in Japan and the adjacent countries.

Among the reports of rice linkages in Japan and Taiwan, the following will be mentioned.

According to OKA (1953), his postulated genes X_1 and Y_1, which are said

to be responsible for gametic development, are assumed to be linked with *wx* in group I, in the sequence of X_1-Y_1-*wx*. To this group NAGAMATSU and OHMURA (1961 & 1962) added two genes, *dp* for depressed palea, and *v* for virescent seedling. The linear order of four genes concerned in their experiment, was concluded as *wx-dp-C-v*.

To the group II, two additional genes, *Xa*, a gene for resistance to *Xanthomonas oryzae*, and *lop*, a gene for lopped leaf may be inserted. These results are based on two sets of linkages obtained by NISHIMURA (1960) and NAGAMATSU and OHMURA (1961); these are shown as *Xa-lg-Ph-* and *Pl-lop*. HSIEH (1961) in Taiwan reported additional genes in this group. They are *Ps*, for stigma color, *d* for dwarfness, and *Pi* for *Piricularia* resistance. Linkage relations of these genes are *lg-Pr*, *Ps-Pr*, *Ps-Ph*, *d-Pl* and *Pi-lg*. Thus in total, eleven or twelve genes may possibly assigned in this group.

Three genes were added by HSIEH (1960) to the next group, group III. They are *lgt*, *d* and *ts*, which are responsible for the expression of such characters as long twisted grain, a type of dwarf plant, and twisted stem, respectively. The arrangement of these genes is assumed to be *lgt-d-ts-A*. He also reports a possiblility of linkage between *A* and I-Ps_2, one of the inhibitors for stigma coloration, though it should be confirmed by further tests. On the whole therefore, in this group, at least six genes, are possible to exist.

NAGAMATSU and OHMURA's (1961) finding that the so-called "long stemmed Daikoku" (a Daikoku type dawrf similar to JODON's intermediate dwarf) is linked with *la* (lazy) indicates the existence of a dwarf gene in the group VIII.

D. Linkage groups summarized by JODON

JODON (1948) summarized linkage data and tentatively proposed eight linkage groups. They are mainly based on work in the United States and India. RAMIAH (1953) in India placed genes for anthocyanin coloration in different plant parts, along with some other genes, into three linkage groups. JODON (1955, 1956) modified his earlier paper of 1948 and suggested seven linkage groups which are briefly presented in Table 4.

Following his report of 1956, additional experimental findings as mentioned below have been made.

According to JODON's later report (1957), a gene for white hull (*Wh*) is linked with a gene for liguleless (*lg*) and it also appears to be linked with a gene for apiculus coloration (*Apb*). By adding some other data of his experiments, he concluded the following gene sequence of his group II: *gh-Apb-lg-Wh*.

TABLE 4. Linkage groups of rice, according to JODON

Group	Gene	Character expression
I	*C* (*Ap*)	Colored apiculus (Chromogen)
	**Lmp* (*Pla*)	Colored leaf margin
	**d*$_3$	dwarf
	Hf	Colored hull-furrows (Dark furrows)
	**Anr*	Red apiculus (Modifyer)
	wx	waxy
	Fl$_1$	Maturity
	v	virescent
	Cl	Clustered spikelets
	fm (*sf*)	sterile ?
	**Fl*$_3$	Maturity
	**Lp*	Colored leaf blade
II & III	*A* (*Apb*)	Colored apiculus (Activator)
	Pr (*Rd*)	Red pericarp
	Sp	Purple stigma
	Np (*Pn*)	Purple node
	Pa	Purple auricle ?
	Lax	Colored leaf axil
	Lsp	Purple sheath
	hg (*gh*)	gold hull
	Ntp	Colored internode
	Gp	Purple empty glumes
	Lgp	Purple collar (ligule)
	Lmp	Purple leaf margin
	Hp	Purple hull (caryopsis and lemma)
	Hw (*Wh*)	White hull
	lg	liguleless
	Ph	Phenol staining
	Lbp (*Pl*)	Purple leaf blade
	**d*$_2$	dwarf
	**sk*	semi sterile ?
IV	*Pbr* (*Rc*)	Brown pericarp (bran)
	g	long empty glumes
	**d*$_6$	dwarf
	Ntp (*Pin*)	Colored inter node (same as *Pn* ?)
	Fl	Maturity

* Gene of which location is estimated by Japanese data alone.

Group	Gene	Character expression
V	*Jp*	Purple junctura or collar
	Prp	Purple pericarp
	Lsp	Purple sheath
	O	Scent or aroma in grain
VI	*Hb*	Colored hull (black)
	Ntv	Purple internode
	An	Awn
	d	dwarf
VII	*Lh* (*gl*)	Pubescence
	An	Awn
VIII	*Ce*	Cercospora resistance
	d	dwarf

RICHHARIA, MISRO, BUTANY and SEETHARAMAN (1960) reported two sets of linked genes, in which the concerned genes are *Lsp* (colored sheath, *Psh*), *Lxp* (colored leaf axil, *Px*), *Ntp* (colored internode, *Pin*), and *Ap* (colored apiculus). These are assigned a position in the combined (II and III) group of JODON in the order of *Lsp-Lxp-Ntp-Ap*.

G, one of the duplicate genes for short glumes, and *Kra*, one of the complementary genes for round shape of spikelets are reported to be linked with the gene *A* which is presumed to be an activator of anthocyanin coloration (KADAM and D'CRUZ 1960). These three genes are arranged in the sequence of *A-G-Kra*, and are considered to belong to JODON's group IV, instead of group I or II.

In addition to the above, two sets of linkages between color genes involving the stigma color gene are reported. They are *Psh* (purple sheath) *-Ap-Ps* (purple stigma) (MOHAMMAD and MOHAMMAD 1959) and a close linkage between a glume color gene and a stigma color gene (D'CRUZ 1960).

IV. Considerations

A. Identification of linkage groups

In this section the writers will give a critical identification of two series of the linkage groups, viz. the groups summarized by JODON and the groups proposed by the writers.

As can be seen through Figure 42 and Table 4, thesee two series of linkage groups do not coincide with respect to the loci or some genes, and thus can not be brought together under one general series of rice linkage

groups. Especially, the differences are seen in the location of *A*, *P*, *Pl*, *Pn*, *Pr* and *gh*. In Japanese rice, these genes belong to three different linkage groups, viz. (*P*, *Pl*, *Pr*), (*A*, *Pn*) and (*gh*), while in the other varieties genes which are probably identical with those genes in Japanese rice have been assigned positions in the linkage group termed as combined (II. III) group of JODON.

This discrepancy cannot be satisfactorily explained at present, because of the fact that little information has been accumulated in the identification of gene systems in distantly related rice varieties. However, as to the probable nature of such differences, the following presumptions may be considered.

i). It may be due partly to the existence of some structural differences of chromosomes between different varieties. In this connection, MIZUSHIMA and KONDO (1959, 1960, 1961, 1962) made crosses between Japanese and Indian varieties and observed an anomalous mode of segregation on characters governed by *wx*, *C*, *A*, *Rc* and *Rd*. To explain this, they proposed a hypothesis saying that this might be due to minor structural differences of chromosome between parental varieties.

ii). JODON (1955) suggested that anthocyanin color characters may be controlled by different gene systems in different varieties. This is also worthy of consideration and in this respect further studies should be made.

iii). Other difficulties lie in the proper identification of characters and the causal genes involved. It is highly probable that in some of the reported data, where linkage involves color character, different workers have found the same linkage relationships although their classification is based on different plant parts. And on the other hand, in some reports, recombination data account for the correlation of two characters only and, without further analysis on their gene systems, linkage is postulated. In this respect, it should be recalled that, as already mentioned in the introduction part of the present paper, if the reported data merely indicate that a certain character shows association with leaf color, for example, it is actually impossible to determine which gene, chromogen (*C*), activator (*A*), localization (*Pl*) or inhibition (*I-Pl*), is linked with the causal gene of the said character.

As already mentioned in the introduction of the present paper, linkage studies in rice have not been subjected to systematic work and only a fraction of the possible paired combinations between recognizable characters has been tested. It is desirable, in carrying on linkage studies to make systematically planned hybridization so that complete genic analysis of characters is obtainable, especially when dealing with those affecting coloration. Linkage work would be complicated by inadequate genic information on complex characters.

B. Future problems

As the first steps in comprehensive and systematic research, the following proposals and approaches should be discussed and strengthened in the future.

1. Exchange of gene stocks between workers or some kind of a pooling system along the blood bank line of thought—This would facilitate identification of genes and the comparison of genic systems and linkage groups. Consolidation and summarization of available information (including pictures) on characters and their causal genes would be desirable too.

2. Building up multiple markers and induced mutants—The former would be of much benefit in the assignment of new or untested genes to their respective linkage groups. Viable, easily identified mutants would be valuable for use in linkage studies. Information on effective irradiation methods should be exchanged, together with the actual products of mutation.

3. Utilization of reciprocal translocations—By using known genetic stocks, a complete set of reciprocal translocation homozygotes should be prepared. According to NISHIMURA's finding (1960), the chromosomes VI and XI, designated by him, bear two series of genes which belong to the Japanese linkage groups I and II, respectively.

4. Acceleration of further research on sterility of intervarietal hybrids—without adequate knowledge of this importtant phase of rice genetics, introduction of genes from distantly related varieties would be markedly sampered.

5. Finding of correlation between marker-genes and agronomic characters —Though this may not be an urgent problem at present, we have to bear this in mind constantly. TORIYAMA's results (1960), in which he reported that one of the effective factors (a polygene) for cold tolerance in Japanese varieties is located in Group II, are worthy of mention. This may well be the first step in this area of Japanese rice breeding.

Through the efforts mentioned above, a set of linkage maps, within the Japanese rice, within the Indian rice, and within the "Bulu" type rice, will be possible to obtain respectively. And by examining the relative location of apparently identical genes in the distantly related rice varieties, an actual comparison of each set of linkage maps will be realized as the second step of the linkage studies in cultivated rice plant in the world-wide scale.

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VI. Explanation of Figures

Fig. 1. Diagramatic illustration of the gene scheme on anthocyanin and its related color, the so-called tawny.

Fig. 2. Histological location of color governed by *Pl* gene.
J, stem node; K, midrib of blade; K′, enlarged figure of (K); K″, leaf margin; M, internode; Q, midrib of sheath; Q′, enlarged figure of (Q).

Fig. 3. Histological location of color governed by *Pn* gene.
J-Q, refer to the illustrations of Fig. 2.

Fig. 4. Histological location of colors due to *C*, *Rc*, *Rd* and Pl^{w}.
a, self-colored floral glume, with "Tawny" coloration; b, brown pericarp (*Rc* gene); c, red pericarp (coexistence of *Rc* and *Rd* genes); d, purple pericarp (Pl^{w} gene, in cooperation with *C* and *A* genes).

Fig. 5. Histological location of coloration, in the dark (or brown) furrows of lemma and palea, and in the gold hull characters.
a, dark furrows (*Bf* gene); b, gold hull (*gh* gene).
Note that cell walls are colored.

Fig. 6. Brown pericarps with reddish brown speckles, of which the causal gene is *Rc*.

Fig. 7. Red pericarp, of which the causal genes are *Rc* and *Rd*.

Fig. 8. Dark (or brown) furrows in lemma and palea, of which the genotype is *Bf I-Bf*$^{+}$.

Fig. 9. White hulls.
a, white hulls caused by *Wh* gene; b, normal straw color.

Fig. 10. Glabrous floral glume and leaf, caused by *gl* gene.

Fig. 11. Long pubescence, governed by *Hg* gene.

Fig. 12. Recessive long emply glumes.
a, even long empty glumes (*g* gene); b, uneven long empty glumes (*Su-g* gene, coexistent with the *g*).

Fig. 13. Dominant long empty glumes, governed by *Gm* gene.

Fig. 14. Clustered spikelets, governed by *Cl* gene.

Fig. 15. Original mutant of the Japanese barnyard grass-like dense panicle, of which causal gene is *Dn*.

Fig. 16. Undulated rachises, governed by *Ur* gene.

Fig. 17. Neckleaf character caused by *nl* gene.
This is a different trait from the "sathy" type which means an enclosed panicle.

Fig. 18. Floral glume of "cleistogamous" dwarf.
a, cleistogamous spikelet, showing a single anther exerts, though it is a

rare case, from the sprit of the apiculus; b, normal spikelet showing anthers exerted after blooming.

Fig. 19. Dense panicles of which the responsible major gene is *Dn*, except the right most one.

Fig. 20. Verticilate arrangement of rachis, of which the causal gene is *ri*.

Fig. 21. Lazy growth habit, caused by *la* gene.

Fig. 22. Liguleless character caused by *lg* gene.

Fig. 23 Panicle and leaf of "Daikoku" dwarf, caused by d_1 gene.

Fig. 24. Panicle and leaf of "Ebisu" dwarf, caused by d_2 gene.

Fig. 25. Panicle and leaf of "cleistogamous" dwarf, caused by d_7 gene.

Fig. 26. Panicle and leaf of "Nhorin 28" dwarf, caused by d_8 gene.

Fig. 27. Panicle and leaf of "tillering" dwarf, caused by d_3, d_4 and d_5 genes.

Fig. 28. "Tillering" dwarf, showing its general appearance.
The triple recessive gives this form of dwarf appearance.

Fig. 29. Panicle and leaf of "lop-leaved" dwarf, caused by d_6 gene.

Fig. 30. General appearance of the so-called "single" dwarfs, governed by genes, from d_1 to d_7.
a, d_1; b, d_2; c, $d_3 d_4 d_5$; d, d_6; e, d_7.

Fig. 31. Panicles of the so-called "single" dwarfs, governed by genes, from d_1 to d_7.
a, normal; b, d_2; c, d_7; d, d_6; e, d_1; f, $d_3 d_4 d_5$.

Fig. 32. General appearance of the so-called "double and multiple" dwarfs.
a, $d_1 d_2$; b, $d_2 d_6$; c, $d_1 d_6$; d, $d_2 d_3 d_4 d_5$; e, $d_1 d_3 d_4 d_5$.

Fig. 33. General appearance of the so-called "double and multiple" dwarfs (continued).
a, $d_3 d_4 d_5 d_6$; b, $d_2 d_7$; c, $d_6 d_7$; d, $d_1 d_7$; e, $d_3 d_4 d_5 d_7$.

Fig. 34. Endosperm character.
a, non-waxy (or non-glutinous); b, waxy (or glutinous).

Fig. 35. Shattering, governed by *sh* gene.

Fig. 36. Brittleness in leaf and stem.
a, non-brittle, the normal; b, "brittle culm" caused by *bc* gene.

Fig. 37. Phenol staining of pericarp, in which the causal gene is *Ph*.

Fig. 38. The fine striped leaf, caused by *fs* gene.

Fig. 39. The green-and-white-striped leaf, caused by *gw* gene.

Fig. 40. The JODON's virescent seedling caused by *v* gene.

Fig. 41. Brown or blackish mottled discoloration caused by *bl* gene.

Fig. 42. Diagramatic presentation of recombination values between recognized genes in each linkage group of Japanese rice.

Fig. 43. Trial construction of linkage maps in Japanese rice.
In the parentheses are the genes reported by other workers.

Fig. 1

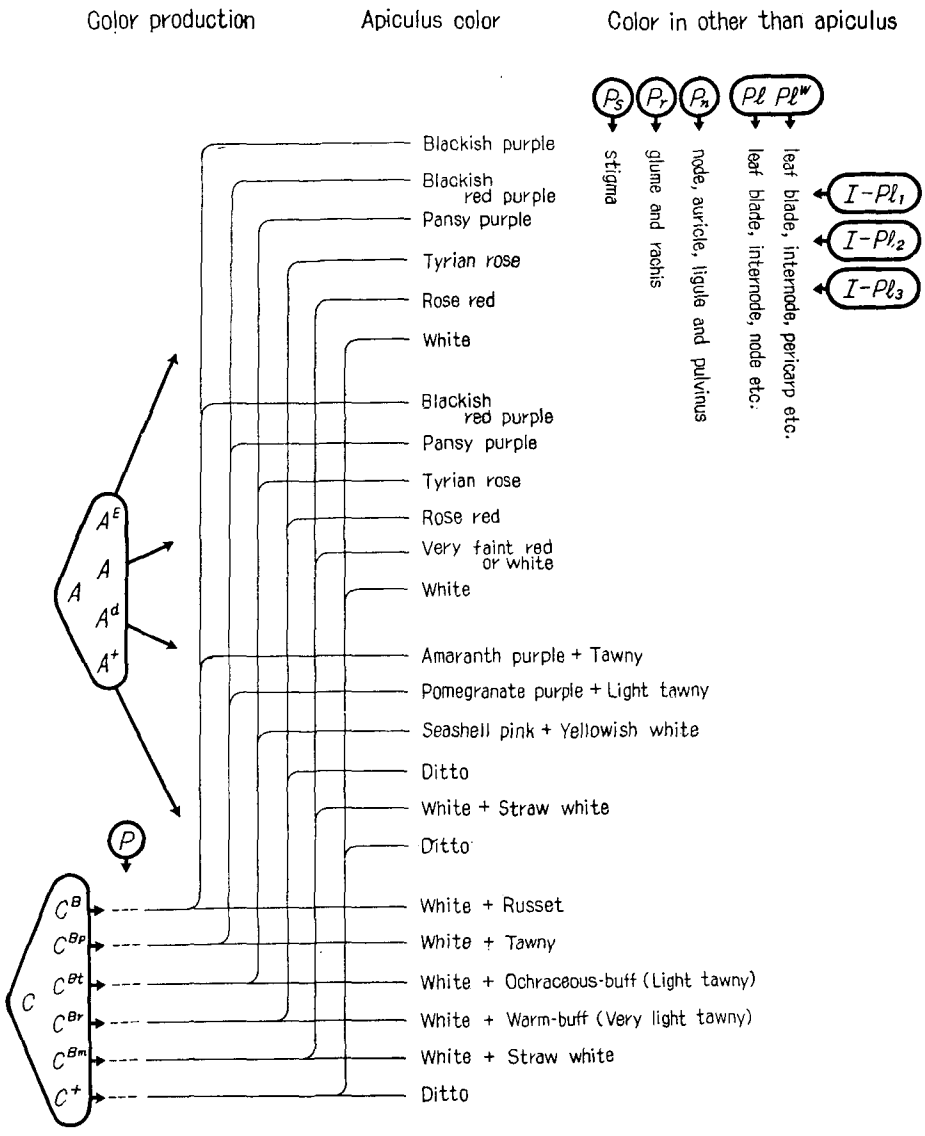
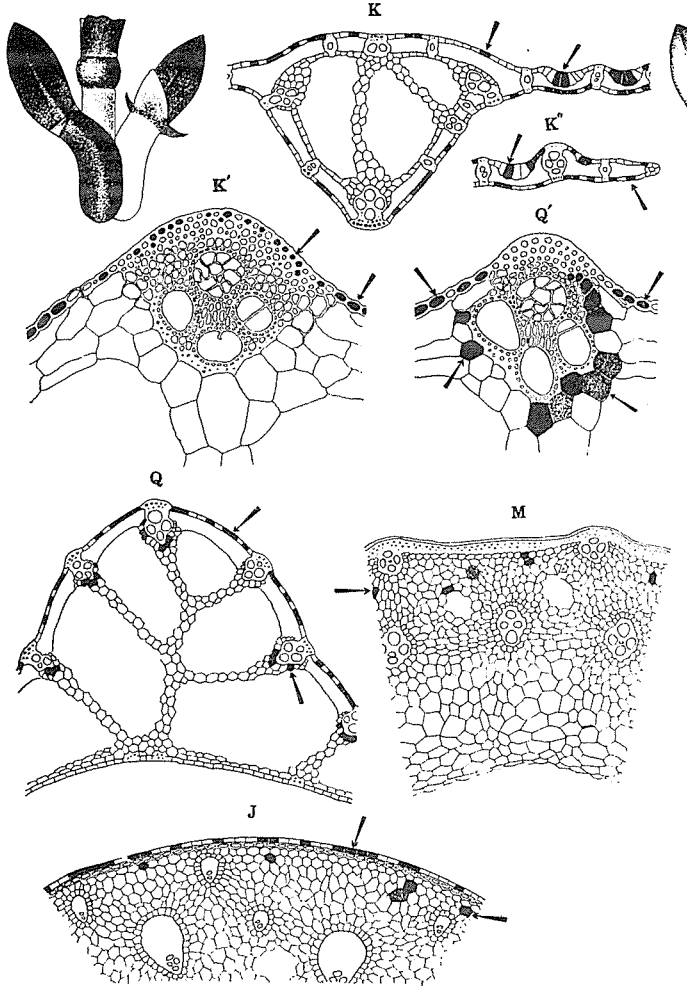

Color production
Apiculus color
Color in other than apiculus
P_s
P_r
P_n
Pl Pl^w
stigma
glume and rachis
node, auricle, ligula and pulvinus
leaf blade, internode, pericarp etc.
leaf blade, internode, node etc.
I-Pl_1
I-Pl_2
I-Pl_3
Blackish purple
Blackish red purple
Pansy purple
Tyrian rose
Rose red
White
Blackish red purple
Pansy purple
Tyrian rose
Rose red
Very faint red or white
White
Amaranth purple + Tawny
Pomegranate purple + Light tawny
Seashell pink + Yellowish white
Ditto
White + Straw white
Ditto
White + Russet
White + Tawny
White + Ochraceous-buff (Light tawny)
White + Warm-buff (Very light tawny)
White + Straw white
Ditto
A^E
A
A^d
A^+
A
P
C^B
C^{Bp}
C^{Bt}
C^{Br}
C^{Bm}
C^+
C

Fig. 2



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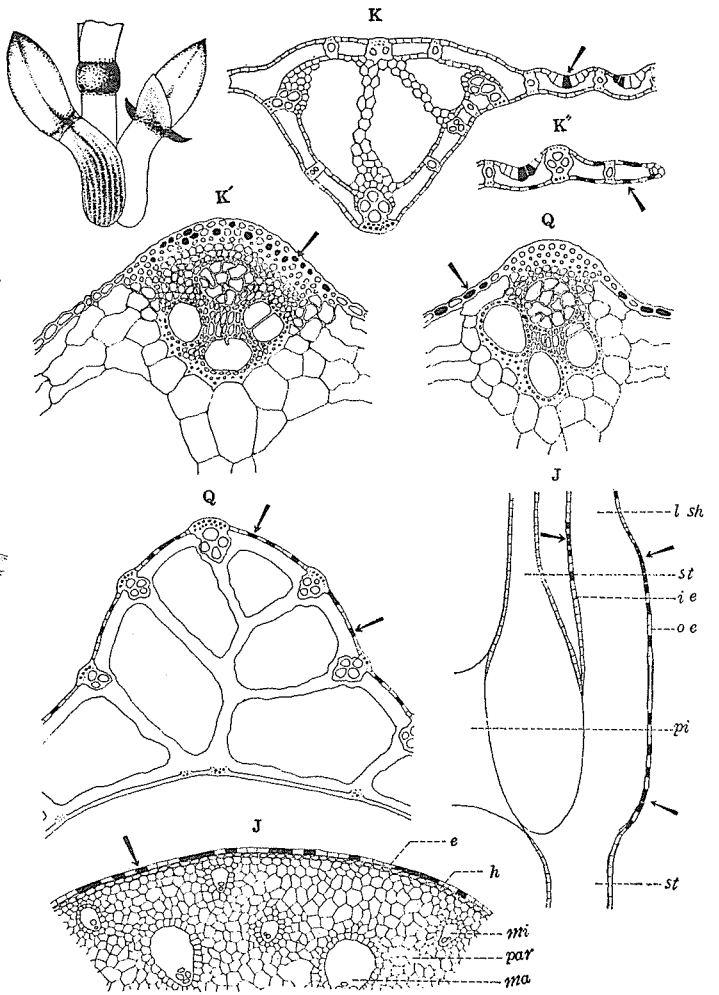

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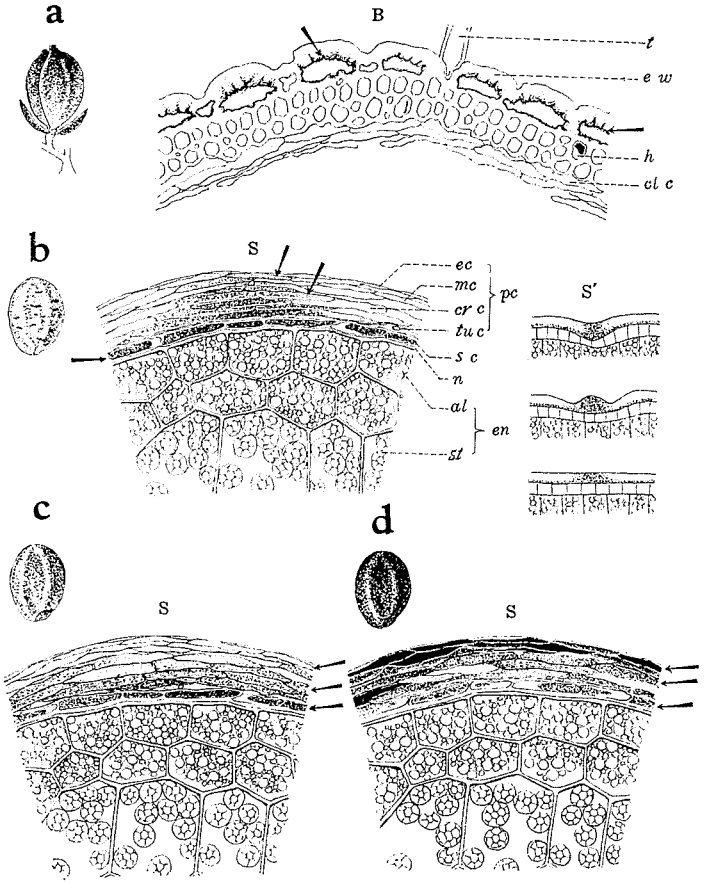

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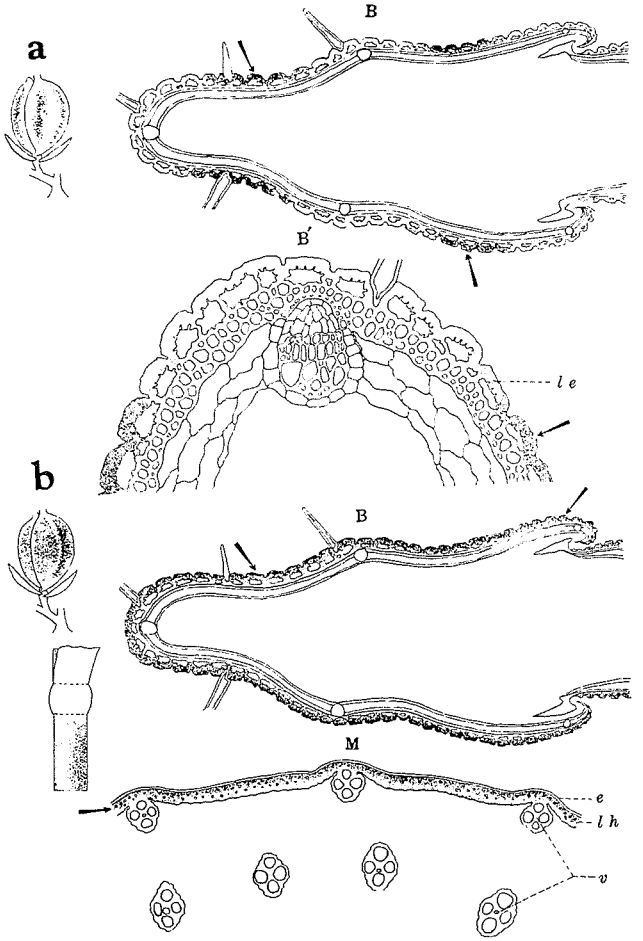


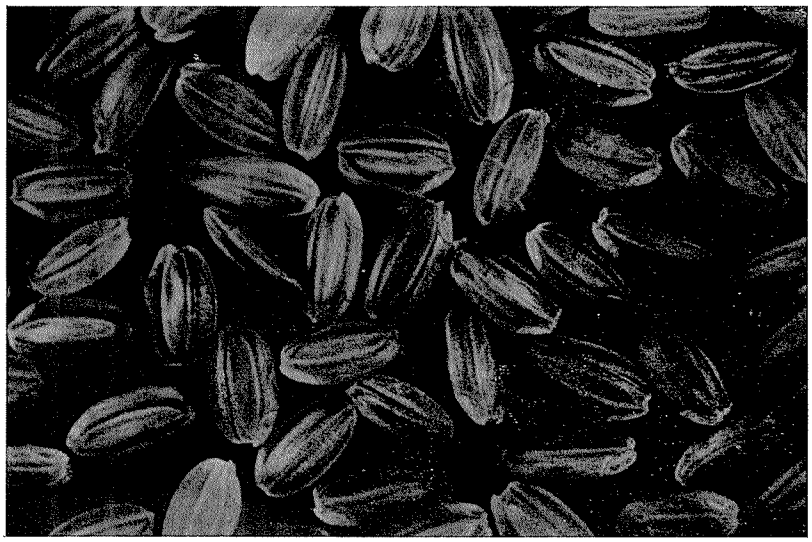
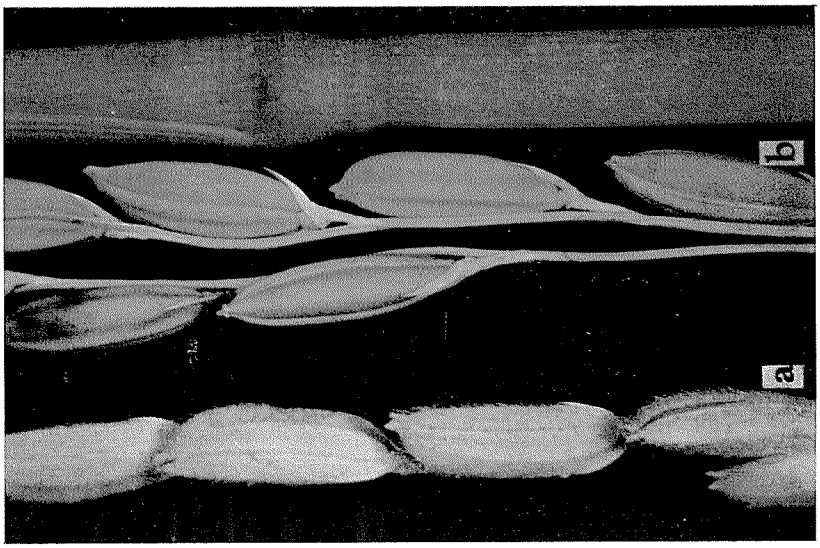


Fig. 7

Fig. 6



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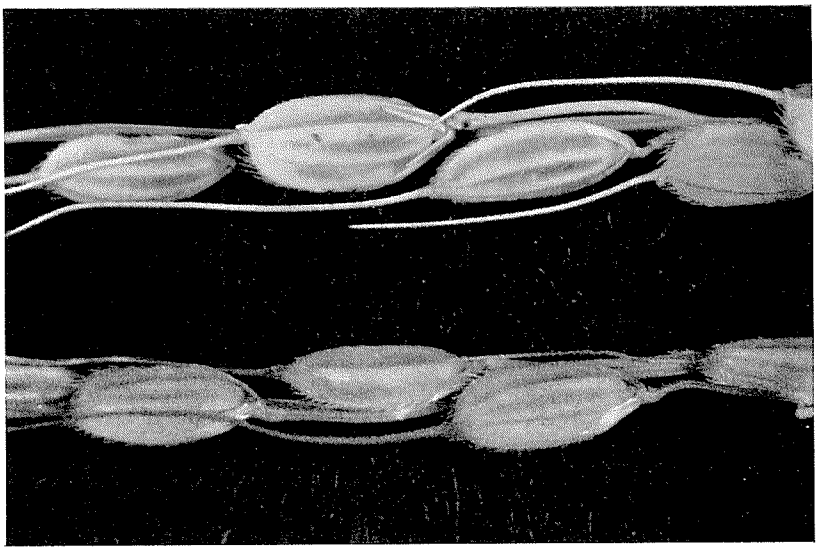
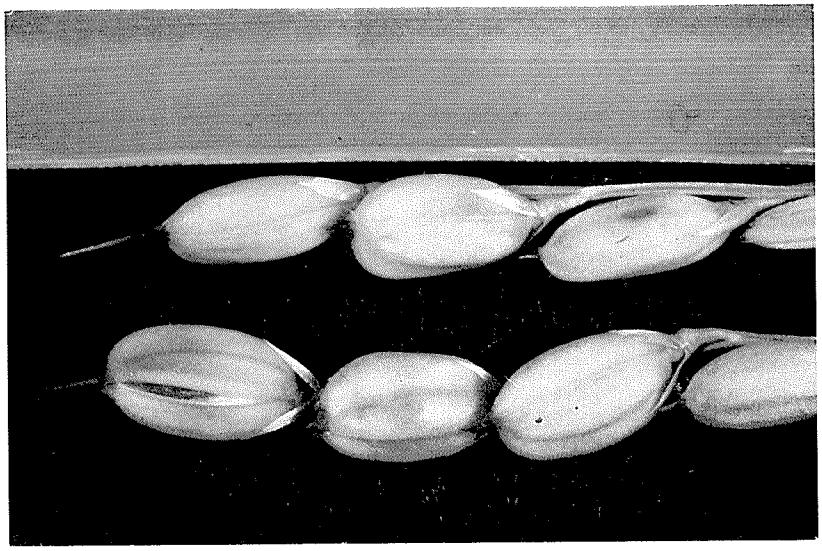


Fig. 8

Fig. 11



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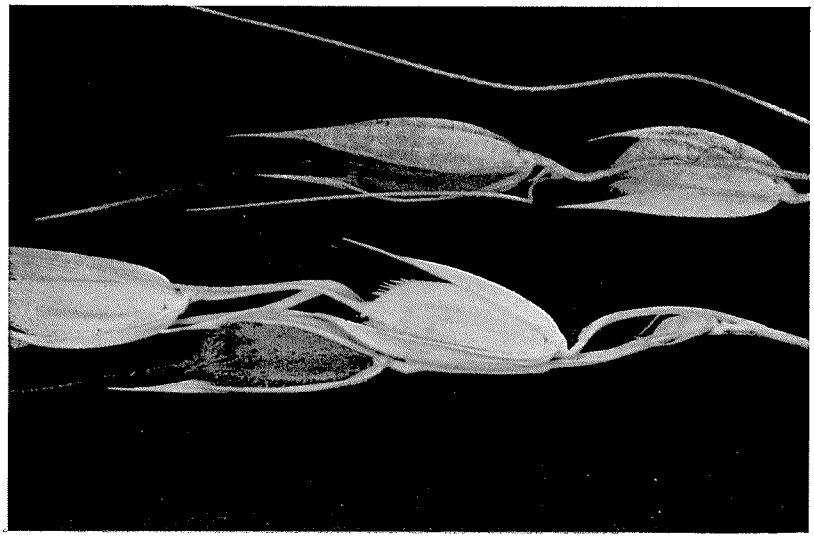

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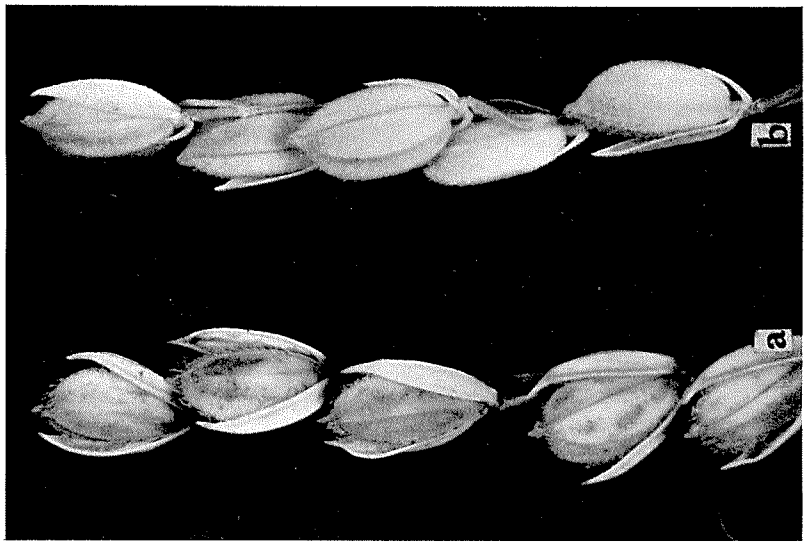


Fig. 12

Fig. 15

Fig. 14

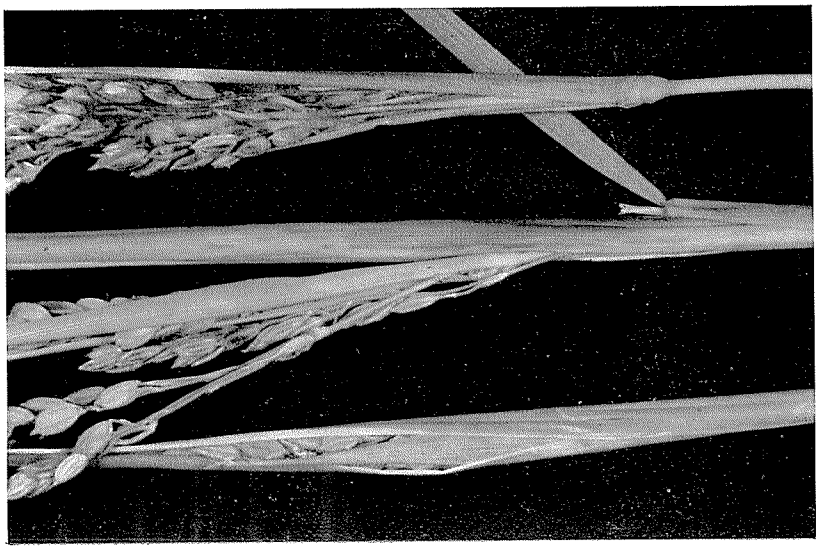


Fig. 17

Fig. 16

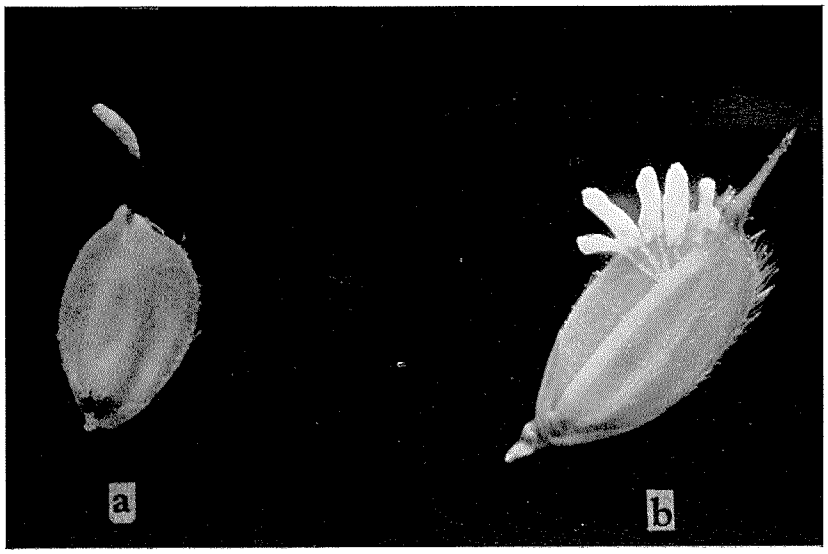
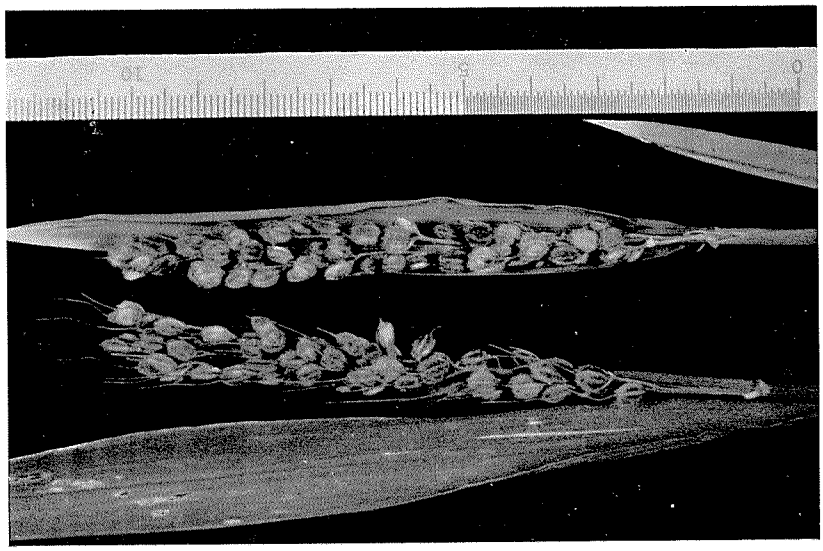


Fig. 18

Fig. 19

Fig. 20

Fig. 21



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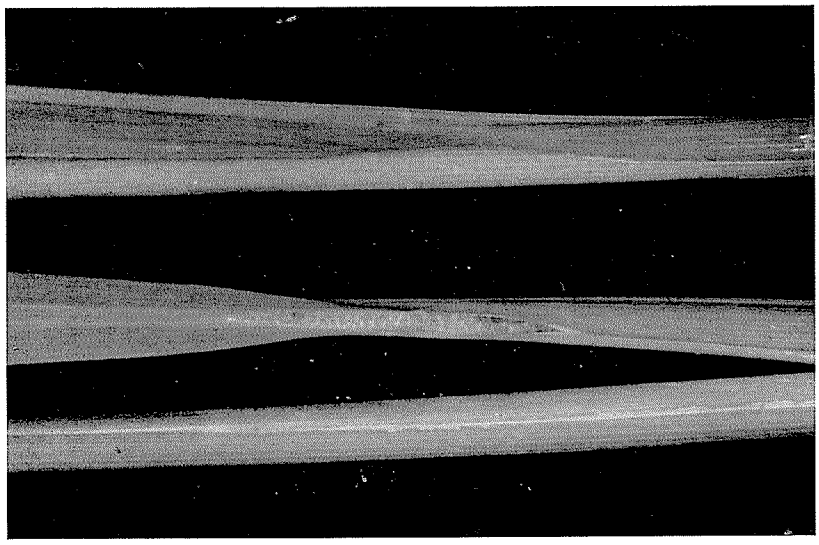

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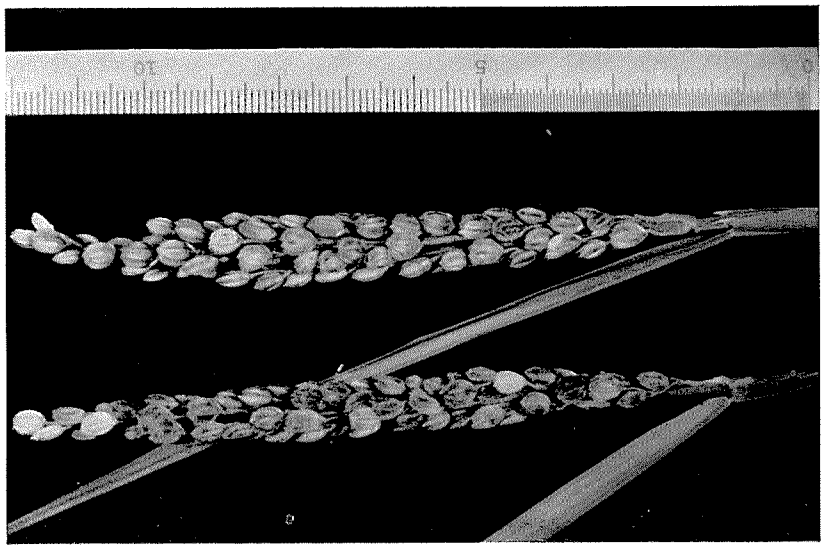
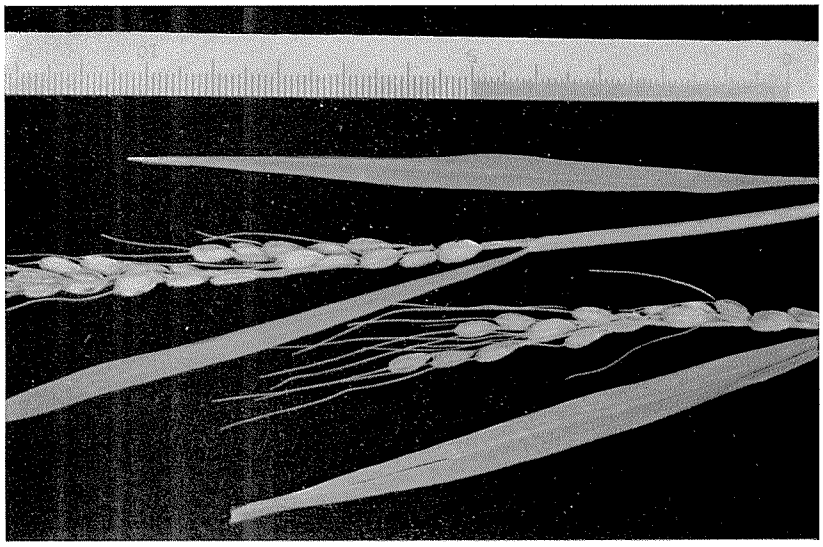


Fig. 25

Fig. 24



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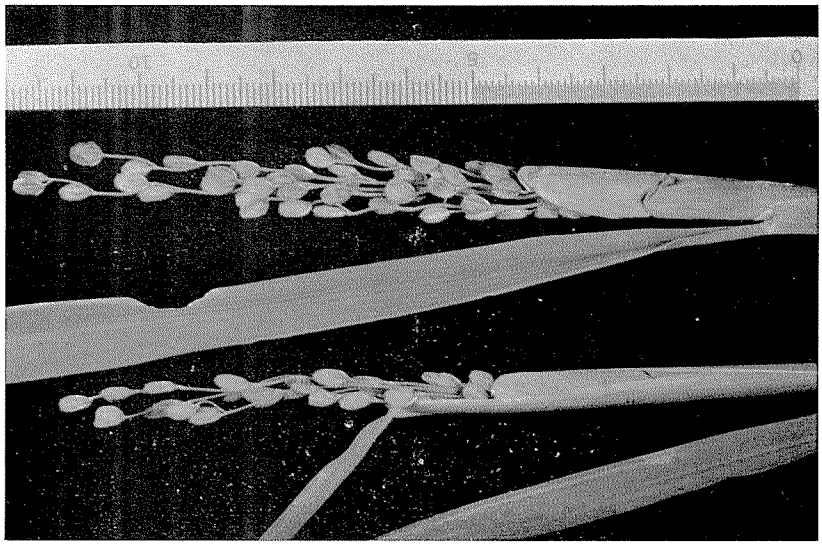


Fig. 26

Fig. 29

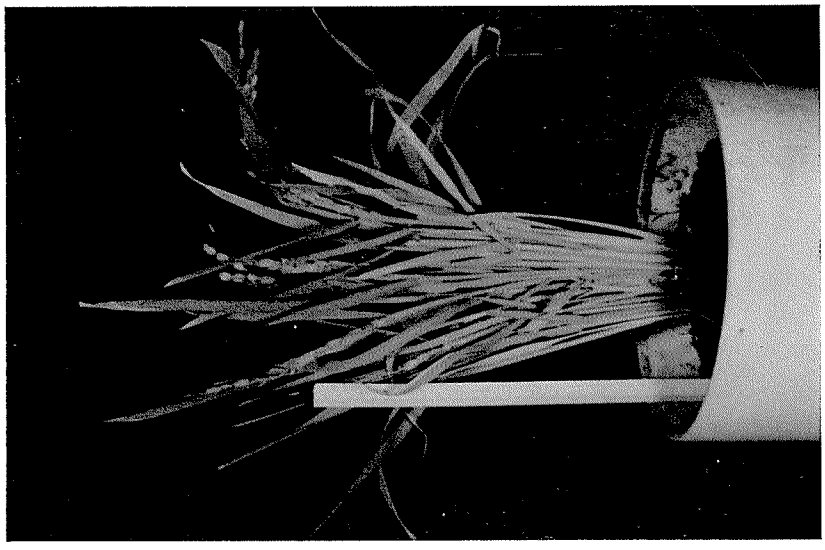


Fig. 28

Fig. 30

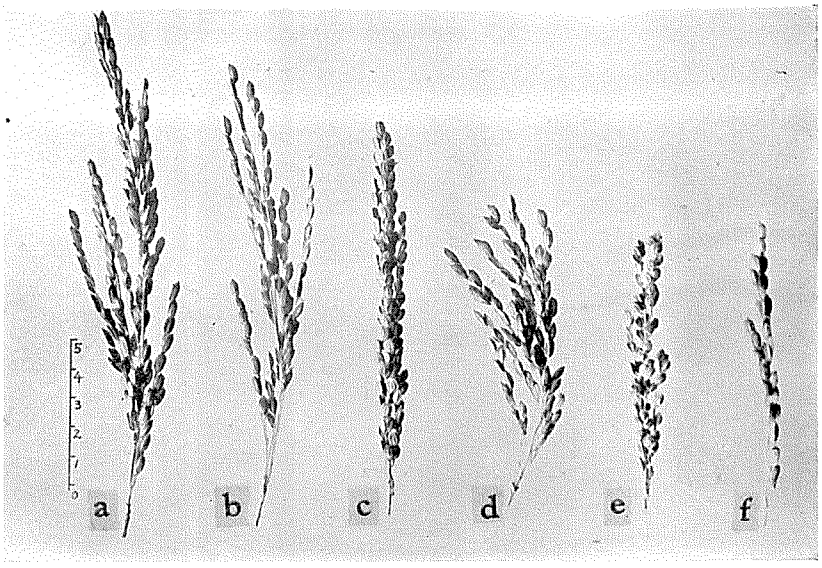
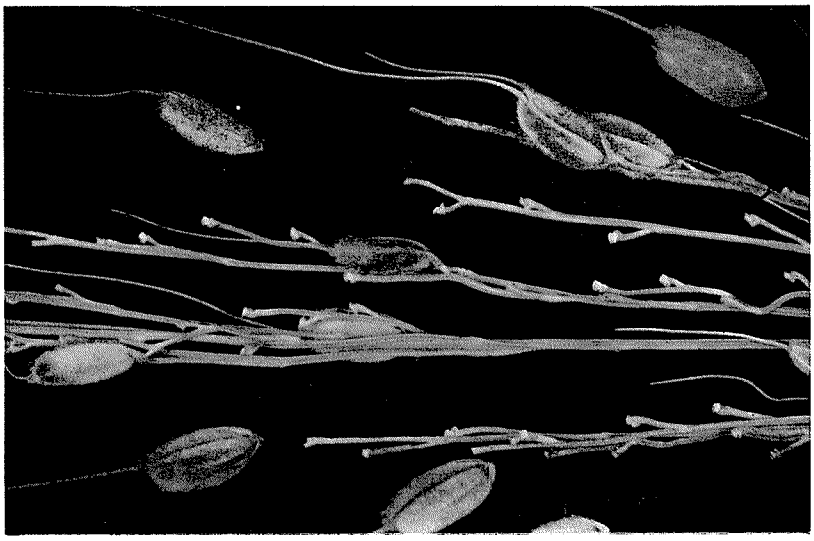


Fig. 31

Fig. 32

Fig. 33



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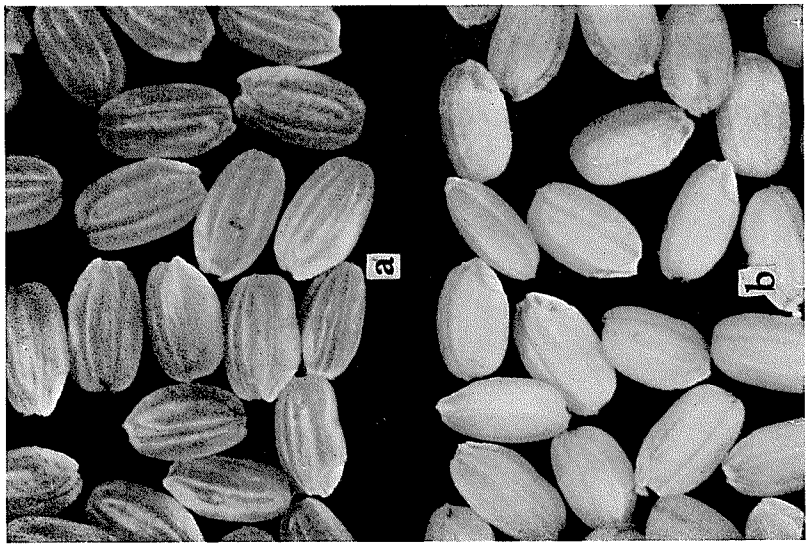
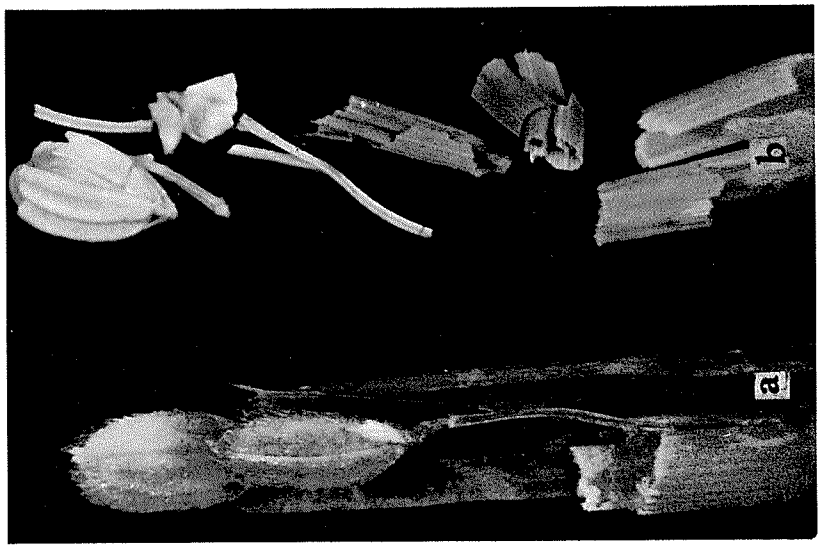


Fig. 34

Fig. 37



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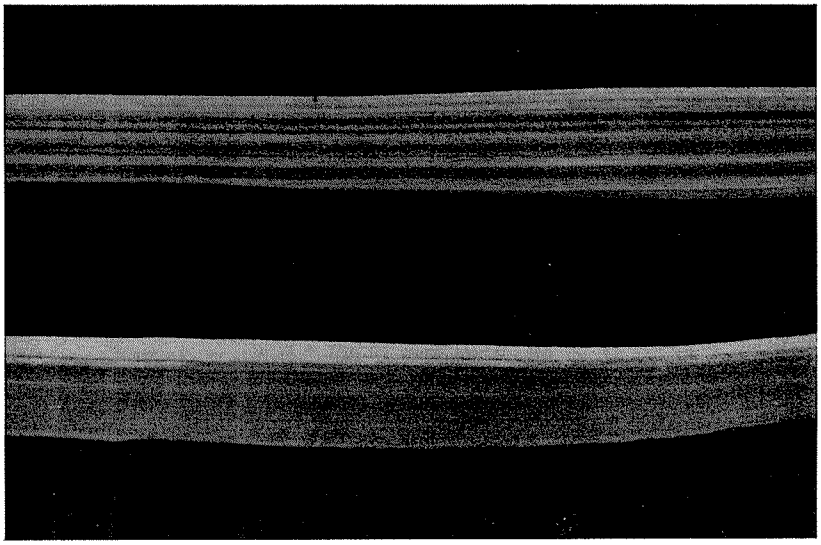

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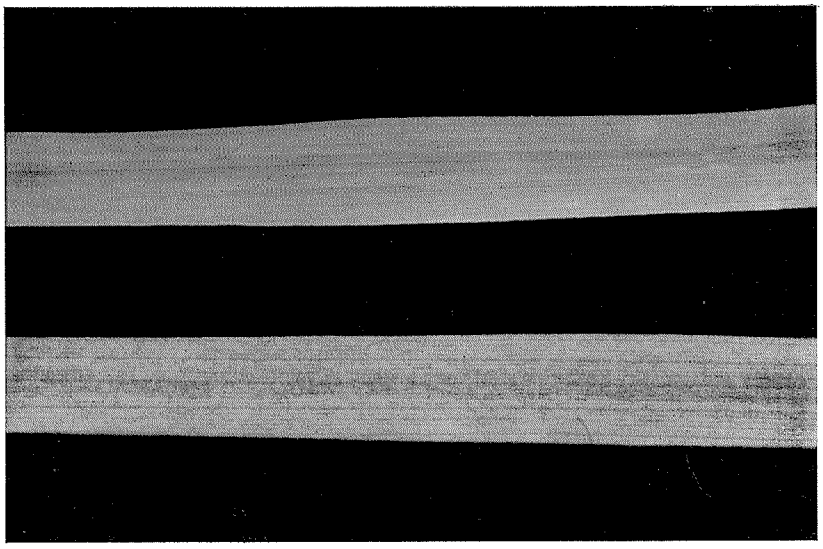

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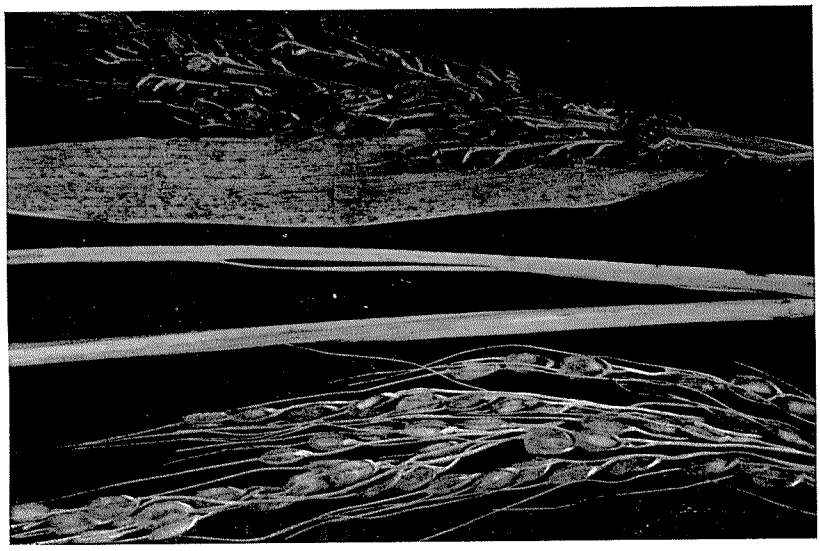

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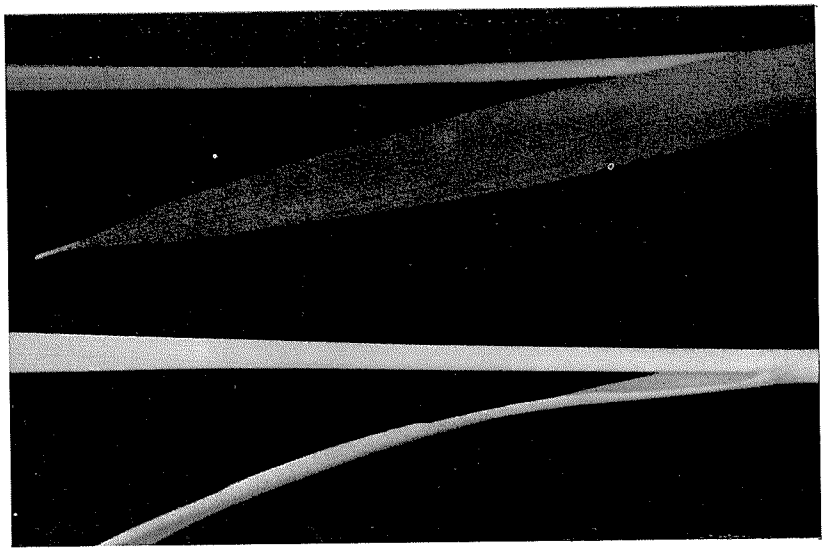

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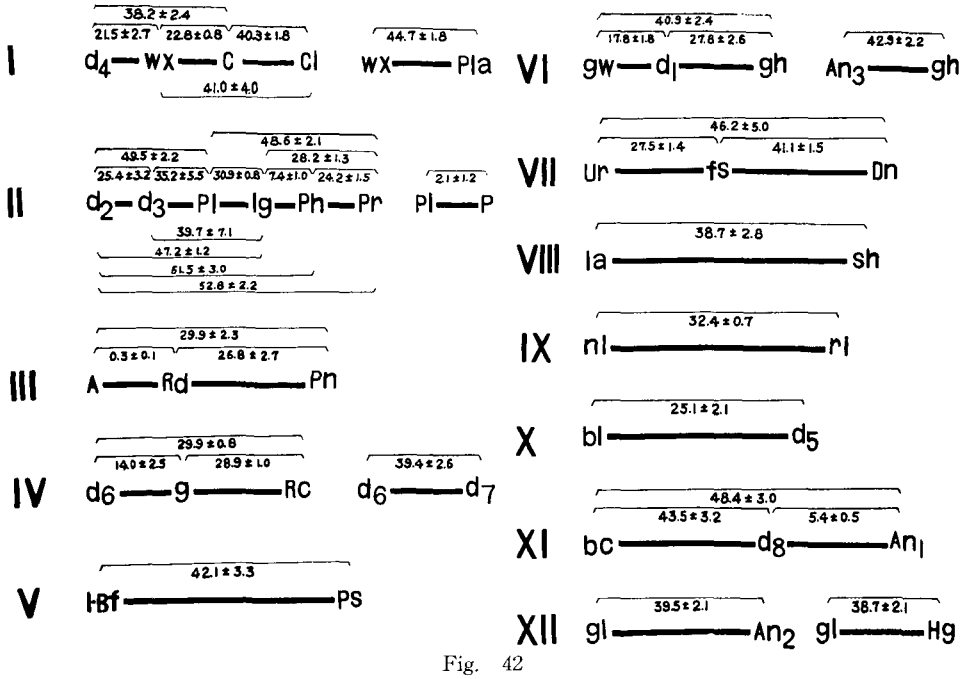
I
38.2 ± 2.4
21.5 ± 2.7
22.8 ± 0.8
40.3 ± 1.8
41.0 ± 4.0
d4 WX C Cl
44.7 ± 1.8
WX Pla
II
48.6 ± 2.1
49.5 ± 2.2
28.2 ± 1.3
25.4 ± 3.2
35.2 ± 5.5
30.9 ± 0.8
7.4 ± 1.0
24.2 ± 1.5
d2 d3 Pl Ig Ph Pr
2.1 ± 1.2
Pl P
39.7 ± 7.1
47.2 ± 1.2
51.5 ± 3.0
52.6 ± 2.2
III
29.9 ± 2.3
0.3 ± 0.1
26.8 ± 2.7
A Rd Pn
IV
29.9 ± 0.8
14.0 ± 2.5
28.9 ± 1.0
d6 g RC
39.4 ± 2.6
d6 d7
V
42.1 ± 3.3
lBf Ps
VI
40.9 ± 2.4
17.8 ± 1.8
27.8 ± 2.6
gw d1 gh
42.3 ± 2.2
An3 gh
VII
46.2 ± 5.0
27.5 ± 1.4
41.1 ± 1.5
Ur fs Dn
VIII
38.7 ± 2.8
Ia sh
IX
32.4 ± 0.7
nl rl
X
25.1 ± 2.1
bl d5
XI
48.4 ± 3.0
43.5 ± 3.2
5.4 ± 0.5
bc d8 An1
XII
39.5 ± 2.1
gl An2
38.7 ± 2.1
gl Hg

Fig. 42

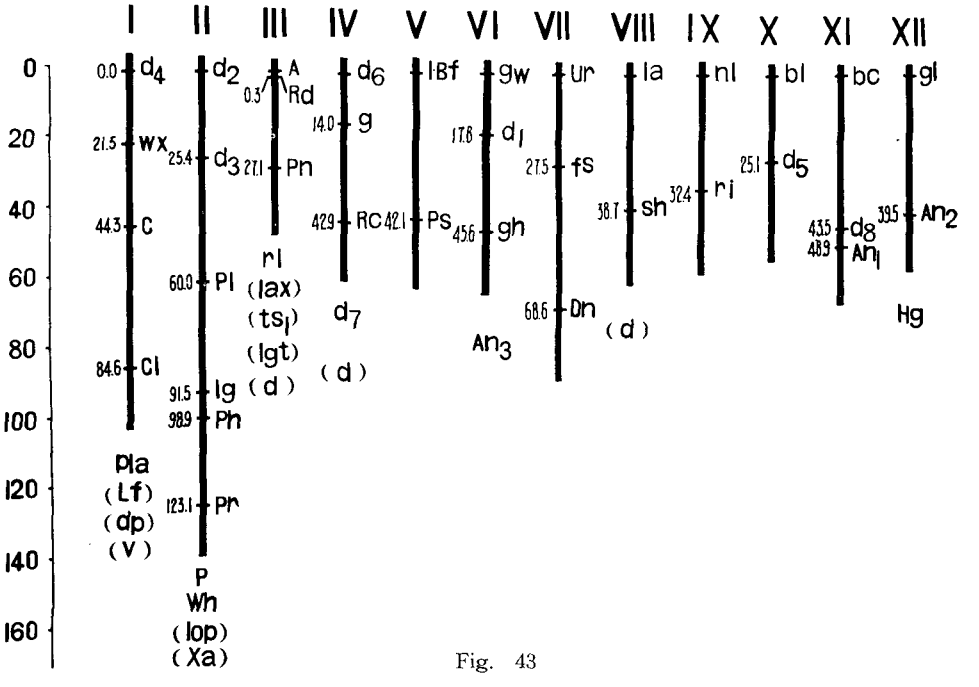
I II III IV V VI VII VIII IX X XI XII
0
20
40
60
80
100
120
140
160
0.0 d4
21.5 WX
44.3 C
84.6 Cl
Pla
(Lf)
(dp)
(V)
25.4 d2
d3
60.0 Pl
91.5 Ig
98.9 Ph
123.1 Pr
P
Wh
(lop)
(Xa)
0.3 A
Rd
27.1 Pn
rl
(lax)
(ts1)
(lgt)
(d)
14.0 d6
g
42.9 RC
d7
(d)
42.1 lBf
Ps
17.8 gw
d1
45.6 gh
An3
27.5 Ur
fs
68.6 Dn
38.7 Ia
sh
(d)
32.4 nl
rl
25.1 bl
d5
43.5 bc
d8
48.9 An1
39.5 gl
An2
Hg

Fig. 43