Linkage studies in *Pharbitis Nil.* III

by

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With 1 Text-figure

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Contents

Introduction

The haploid chromosomes of *Pharbitis Nil* are 15 in number. According to U (1932), these chromosomes remain as univalents at the meiosis of the haplont; or in other words, 15 chromosomes constitute together one genome. Therefore, gene-analysis may reveal 15 linkage groups in this plant. In the last publication (IMAI 1931 a) of this series, 10 linkage groups with 50 loci were described. Recent studies advanced to establish 12 linkage groups, including 70 loci in the respective chromosomes. The determination of the other three groups is the problem of a future investigation.

Variegated linkage group

Hitherto the variegated linkage group was known to include seven genes, variegated (v), crumpled-1 (c 1), Blown-1 (B 1), fasciated-3 (f 3), brown (br), faded (fd) and couple (cu) (Imai 1931a). The relative distance of the loci of variegated, crumpled-1 and Blown-1 in the chromosome is 14·9 between v and c1 and 17·8 between c1 and B1, in the order of arrangement v—c1—B1, with the recombination of 30·8 per cent for v and B1. The recombination percentage is roughly 20—25 for v and f3, about 31·0 for v and fd, and about 37·7 for v and cu. The locus br is present not far from those of v and c1.

Last season, male-sterile-1 (ms1) was found to be linked with variegated. The new gene male-sterile-1 results in abortive anthers. The effect seems to be limited to the male gametes only, so that the plant bears fruits by the pollination of insects. The data showing linkage between ms1 and v are indicated in Table 1.

Table 1. F_2 from the cross of male-sterile-1 by variegated

Cross	+	v	ms1	v ms1	Total
D 110 × WT	109	40	42	11	202

The frequency of recombination for v and ms1 is 45·1 per cent. Therefore, under the variegated linkage group we gather eight genes, including male-sterile-1.

A backcross experiment involving v and f3 was made, the results obtained being shown in Table 2.

Table 2. Backcross involving fasciated-1, fasciated-3 and variegated; (+ + + × f1 f3 v) × f1 f3 v

Cross	+	v	f	v f	Total
(220 × DF) × IF	122	93	13	61	289

Fasciated-1 is located in the pear chromosome, therefore it is regarded to be independent of f3 and v, which are linked together. Under this condition, the fasciated segregates are crossovers and the variegated fasciated segregates are non-crossovers, whereas both normal and variegated segregates are of the mixture of the two. From the observed numbers of the two classes, fasciated and variegated fasciated segregates, recombination frequency of v and f3 is calculated to be 17·6 per cent. The formerly estimated rough value, 20—25 per cent, is corrected by this figure determined by the backcross experiment.

Cordate linkage group

Six genes, cordate (co), feathered (fe), semi-contracted (sc), precocious (pc), palmate (pl) and crêpe (cp), were regarded as to constitute the cordate linkage group. In the former publication, the writer, in relation to this, stated as follows: "The former three genes seem to be located in the cordate chromosome, in the linear arrangement, as probably being co—fe—sc, with a distance of 1·2 between co and fe, and 17·7 between fe and sc. Precocius is linked with co, the recombination being about 24·6 per cent. The recombination percentage is about 34·6 for pl and cp, about 31·3 for pc and pl, and about 38·8 for pc and cp." To this linkage group newly two genes were found as its membership; the one is Restricted (Rt), a dominant allelomorph, restricting the distribution of hairs on calyx, and the other is bobbed-1 (bb1), one of the bobbed genes shortening hairs. In a cross three genes, crêpe, Restricted and bobbed-1, were segregated in linked combinations with the simultaneous independent assortment of bobbed-2, as shown in Table 3.

Table 3. F_2 from the cross of bobbed-2 by Restricted bobbed-1 crêpe

Cross	Rt	+	Rt bb	Rt cp	bb	cp	Rt bb cp	bb cp	Total
RL × KN	86	46	0	0	0	0	84	14	230

Crêpe plants were always characterized by bobbed, bobbed-1 in reality, showing close linkage between cp and bbl. The recombination percentage of Rt and bbl-cp is 38·6. Therefore, at present the cordate linkage group gathers eight genes, including the newly found 2 loci.

Yellow linkage group

Five genes named yellow (y), dusky (dy), light-1 (lt1), deformed (de) and speckled-reduced (sp-r), were known to constitute the yellow linkage group. Recently maple (m) was brought in this linkage group. A provisional map of the yellow chromosome with six genes, including maple, was prepared by IMAI and TABUCHI (1933). Their relative loci in the chromosome are as follows: de (0), y (20·1), dy (21·4), lt1 (29·7), m (48·2) and sp-r (48·6).

A new experiment adds a member called bushy (bs) to this group. Bushy is a recessive gene manifesting a bush growth of the plant with smal lleaves. The gene is linked with yellow, and the data showing this relation are given in Table 4.

Table 4. F_2 from the cross of yellow bushy by normal

Cross	+	y	bs	y bs	Total
TW × SK	110	23	21	18	172

The recombination of y and bs is 32·0 per cent. Therefore,. the yellow linkage group is composed of seven genes, including maple and bushy.

Acuminate linkage group

Since the discovery of the three linked genes, acuminate (ac), Margined-2 (Mr 2) and magenta (mg), the acuminate linkage group had remained in that condition for some years. In this season, a new member called Blizzard-1 (Bz 1) was found to be gathered under this group. The data collected in Tables 5 and 6 show the fact that Blizzard-1 is linked with acuminate and magenta.

Table 5. F_2 from the cross of acuminate by Blizzard-1 Blizzard-2

Cross	Bz	+	Bz ac	ac	Total
RL × D 108	48	43	18	26	135

Table 6. F_2 from the cross of magenta by Blizzard-1 Blizzard-2

Cross	Bz	+	Bz mg	mg	Total
RL × D 108	99	69	21	31	220

Owing to the simultaneous segregation of Blizzard-2, which is complementary with Blizzard-1 in the manifestation of a Blizzard character, the data were not simple. The segregation of Bz *versus* + is a 9 : 7 in ratio, which makes complicate the distribution of the segregates. From the data we clearly recognize linkage between Bz 1 and ac, and Bz 1 and mg. In this cross, acuminate and magenta were linked as expected, the data, however, being not cited here.

At present the acuminate linkage group is known to contain four genes, acuminate, Margined-2, magenta and Blizzard-1. The determined recombination percentage is about 0·5 for ac and Mr 2, and 21·2 for ac and mg.

Contracted linkage group

The contracted linkage group was known to include Rayed (Ry), cream (cr), interaxil-green (ig), shrubby (sh), contracted (ct), Margined-1 (Mr 1)[1], flecked (fl), tube-white (tw), intense (i), Margined-reduced (Mr-r) and duskish (dk). Experimental data made possible to construct a provisional map of the contracted chromosome by the following relations: Ry (0), cr (± 1·2), ig (10·3), sh (10·3 ± 3·1), ct (15·9), Mr1 (16·9), fl (16·9 ± 1·2), tw (21·9), i (46·5) and Mr-r (46·5 ± 3·0). In regard to the gene duskish, it was asumed to be located in the right part of the chromosome. A recent investigation made on rather a large scale showed, however, that duskish is independent of the genes of the contracted linkage group, therefore duskish is excluded from the group. Formerly intense flower colours were regarded as due to the manifestation of a single gene called intense, but new data revealed the fact that the character may be presented by the two different genes, giving apparently the same phenotype. The newly discovered gene intense is independent of interaxil-green, shrubby and Margined-1 of the contracted linkage group, and is linked with pear and the other genes of the pear linkage group. The two intense may be called intense-1 (i1) and intense-2 (i2) respectively, the former being located in the contracted chromosome and the latter in the pear chromosome. Intense-2, however, seems sometimes to have been segregated in the writer's hybrid progenies, and gave some ambiguous segregations. Some of the data published may contain such cases. In Table 7 is presented the linked segregation of intense-1 and Margined-1.

Table 7. F_2 from the cross of normal by Margined-1 intense-1

Cross	Mr 1	+	Mr1 i1	i 1	Total
RL × A24	173	93	79	6	351

The recombination frequency is 22·5 per cent. This figure is a correct value for the relation Mr1 ~ i1, but not an accurate one owing to the repulsion data, from which the calculation was made.

A backcross involving three genes, Margined-1, shrubby and interaxil-green, was made, and the data collected are shown in Table 8[2].

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[1] Expanded is possibly allelomorphic to Mr1.

[2] In this backcross, intense was also segregated and showed quite independent segregation of Mr1, sh and ig, indicating the fact that the character is due to intense-2.

Table 8. Backcross involving Margined-1, interaxil-green and shrubby; (Mr1 + + × + sh ig) × + sh ig

Backcross	$\frac{\mathrm{Mr1}\ +\ +}{+\ \mathrm{ig\ sh}}$		$\frac{\mathrm{Mr1} \mid \mathrm{ig\ sh}}{+ \mid +\ +}$		$\frac{\mathrm{Mr1}\ + \mid \mathrm{sh}}{+\ \mathrm{ig} \mid +}$		$\frac{\mathrm{Mr1} \mid \mathrm{ig} \mid +}{+ \mid + \mid \mathrm{sh}}$		Total
	Mr1	ig sh	Mr1 ig sh	+	Mr1 sh	ig	Mr1 ig	sh	
(ID × SH) × SH	190	173	5	5	5	7	1	1	387
	363		10		12		2		

The recombination calculated from the data is 5·7 per cent for Mr1 and sh, 3·1 per cent for Mr1 and ig, and 3·6 per cent for sh and ig. The results indicate the relative loci of the three genes to be sh—ig—Mr1, with an interval of 3·6 between sh and ig, and 3·1 between ig and Mr1. The former situation (IMAI 1931a), however, was a distance of 6·6 units between ig and Mr1, and the locus sh is considered to be 3·1 units apart from ig. The locus sh is now determined to be present on the left side of ig; therefore, according to the former data, the interval sh ~ Mr1 is of 9·7 (3·1 + 6·6) units. The new data obtained by a backcross shortened the distance into 6·7 (3·6 + 3·1), which is the most reliable value at present.

Another proof for their relative loci was obtained by observing F_2 of the same cross, the data of which are shown in Table 9.

Table 9. F_2 of cross ID × SH

Cross	Data				Total	Recombination
+ + × sh ig	+ 426	sh 6	ig 7	ig sh 128	567	2·4% (sh ~ ig)
Mr1 + × + ig	Mr1 363	+ 7	Mr1 ig 10	ig 110	490	3·6% (ig ~ Mr1)
Mr1 + × + sh	Mr1 358	+ 12	Mr1 sh 15	sh 105	490	5·8% (sh ~ Mr1)

The recombination frequency shown in Table 9 is approximately the same to that obtained by the backcross. At present the figure calculated from the backcross experiment may be regarded as the standard.

As described elsewhere (IMAI 1931b), lilliptian (lp)[1] is a recessive dwarf form appeared by mutation under the writer's observation.

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[1] Formerly called pigmy.

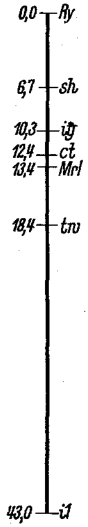
Lilliptian is found to be linked with flecked, the proof being presented by the data in Table 10.

Table 10. F_2 from the cross of lilliptian flecked by normal

Cross	+	fl	lp	fl lp	Total
Het-SK 6 × A 50	180	45	26	28	279

As the lilliptian seedlings cannot grow further, the cross was made actually by hybridizing normal with flecked heterozygous for lilliptian, and the record was taken by observing the F_2 families segregating lilliptians. The deficit of the lilliptian seedlings is considerable. The recombination frequency estimated from the segregates of 26 lp : 28 lp fl is 28·0 per cent, which shows roughly the relative position of the locus lilliptian in the contracted chromosome.

At present, therefore, the contracted linkage group includes eleven genes, Rayed, cream, interaxil-green, shrubby, contracted, Margined-1, flecked, tube-white-1 [1], intense-1, Margined-reduced and lilliptian. The corrected loci of these genes are the following: Ry (0), cr (± 1·2), sh (6·7), ig (10·3), ct (12·4), Mr1 (13·4), fl (13·4 ± 1·2), tw1 (18·4) [2], i1 (43·0) [3], Mr-r (43·0 ± 3·0) and lp (13·4 ± 1·2 ± 28·0). In the accompanying diagram is presented a preliminary map of the contracted chromosome, including 7 loci.



A provisional map of the contracted chromosome

Speckled linkage group

The speckled linkage group includes three genes, speckled (sp), white-1 (w1) and Margined-fluctuated (Mr-f), the recombination frequency being about 0·8 per cent for sp and w1, and roughly 20 per cent for w1 and Mr-f.

Recent experiments add two genes to this group. The one is Striated (Sa), which was found to be linked with speckled rather closely.

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[1] Two tube-white genes are detected. See the section "Speckled linkage group".

[2] 18·4 = 13·4 (Mr1) + 5·0 (Mr1 ~ tw1). For the figure 5·0 see p. 321, Imai 1931 a.

[3] 43·0 = 18·4 (tw1) + 24·6 (tw1 ~ i1). The figure 24·6 (tw1 ~ i1) seems to be more reliable than the new figure 22·5 (Mr1 ~ i1). For the figure 24·6 see p. 236, Imai 1929.

Striated is a dominant flower character[1], manifesting fine blushes of higher intensity on the ground colour of lower intensity. In Table 11 are presented the data showing linkage between Striated and speckled.

Table 11. F_2 from the cross of Striated by speckled

Cross	Sa	Sa sp	+	sp	Total
401 × A 23	113	0	0	35	148

Preliminary investigations showed the fact that A 23, one of the parents of this cross, carries no Striated gene, and therefore we may expect also normal and Striated speckled segregates in F_2 derived from the F_1 hybrid heterozygous for Striated and speckled, when crossing over takes place between two loci. However, non of these segregates appeared under observation, the data presenting rather close linkage between Sa and sp.

Another cross also shows close linkage occurring between Striated and tube-white. The gene manifesting a white flower-tube was known under the name of tube-white, and is considered to be located in the contracted chromosome. The tube-white character now segregated is linked with Striated, according to which we have two different genes manifesting a similar character. For identification we may call them tube-white-1 (tw1) and tube-white-2 (tw2) respectively, the former being located in the contracted chromosome and the latter in the speckled chromosome. In Table 12 are presented the data showing linkage between Striated and tube-white-2.

Table 12. F_2 from the cross of Striated tube-white-2 by normal

Cross	Sa	Sa tw2	+	tw2	Total
401 × ID	125	71	61	0	257

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[1] Formerly this was considered as a recessive to be linked with Lined (V, p. 91, IMAI 1930). But the conclusion is incorrect. Owing to the occurrence of the predominant Lined stripes on the F_1 flowers of the cross, Lined × Striated, the simultaneous manifestation of Striated was overlooked and its dominant nature was misregarded as to be recessive. According to this view, Lined and Striated segregate independently.

The segregating ratio is practically a 2:1:1, showing high repulsion.

The speckled linkage group, therefore, includes five genes, speckled, white-1, Margined-fluctuated, Striated and tube-white-2.

Pear linkage group

Four genes, pear (p), fasciated-1 (f1), fasciated-2 (f2) and Blown-2 (B2), were known to be gathered under the pear linkage group. The recombination frequency is roughly 20—25 per cent for p and f2, about 2·5 per cent for p and f1, and 23·5 per cent for p and B2. Recent experiments bring in the other five genes, intense-2, chestnut, striped-2, light-2 and Margined-3, to this group which therefore contains nine loci alltogether.

The writer's observation made last season determined the location of intense-2 (i2). In Table 13 are presented the data showing linkage between i2 and p.

Table 13. Backcross involving pear and intense-2; (+i2 × p+) × p i2

Cross	+	p	i2	p i2	Total
(220 × DF) × IF	46	109	88	46	289

Of these segregates, p and i2 are non-crossovers, and + and p i2 are crossovers. The recombination percentage is 31·8. Fasciated-1 being linked very closely with p, it is expected also to be linked with i2. In Table 14 is given the proof by the data obtained by the same backcross.

Table 14. Backcross involving fasciated-1 fasciated-3 intense-2;
(+ +i2 × f1 f3+) × f1 f3 i2

Cross	+	i2	f	i2 f	Total
(220 × DF) × IF	105	110	50	24	289

Of these segregates, f is a non-crossover between f1 and i2, and i2 f is a crossover, whereas both + and i2 are of the mixture of the two. The recombination frequency calculated on the basis of the observed numbers of the former two classes is 32·4 per cent, which is very near to that for p and i2. On this occasion a short statement will be given in connection with linkage between p and fl. Formerly the recombination frequency was estimated to be 2·5 per cent. In the hybrid progeny, a few not-pear fasciated segregates may appear, and they are considered as produced by crossing over. A later investigation reveals the fact that they cannot be regarded as so simple. The degree of linkage between p and fl may be higher than it was formerly presumed, or less than 2·5.

A seed-colour gene chestnut (cn) is linked with i2, the proof being shown by the data in Table 15.

Table 15. F_2 from the cross of intense-2 chestnut by normal

Cross	+	i2	cn	i2 cn	Total
D104a × 410M	87	9	5	27	128
220 × DF[1]	54	8	7	16	85
Total	141	17	12	43	213

The recombination frequency for i2 and cn is 13·9 per cent.

A recessive variegation was known as striped, which is collected in the duplicated linkage group. Another gene, manifesting a similar recessive variegation, is found to be included in the pear linkage group. Therefore we may call them striped-1 for that of the duplicated linkage group and striped-2 (st2) for that of the pear linkage group. In Table 16 are copied the data showing linkage between st2 and p.

Table 16. F_2 from the cross of striped-2 by pear

Cross	+	st2	p	st2 p	Total	wl
700 × SK	101	33	34	5	173	56

The frequency of recombination is 40·1 per cent. This striped-2 is linked with light-2[2], the location of which has not yet been determined. Table 17 includes its proof by the data.

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[1] In this cross, both parents are not-chestnut, and the segregating gene chestnut occurred by mutation.

[2] The writer (IMAI 1931a) obtained fragmental data showing close linkage between light-2 and ivory. It is not clear whether this light-2 is the same with that described in the text or not.

Table 17. F_2 from the cross of light-2 by striped-2

Cross	+	lt2	st2	lt2 st2	Total
D25 × KD	103	52	59	7	221

The two genes are segregated with the recombination frequency of 26·9 per cent.

A new gene Margined-3 (Mr 3), which works as complementary with Margined-1 of the contracted linkage group and Margined-2 of the acuminate linkage group in the manifestation of a white margin on the corolla, is detected by a recent investigation, and is found to be linked with pear, striped-2 and light-2. The data collected in Table 18 will show their linkage relations.

Table 18. F_2 showing linkage for Margined-3 *versus* pear, light-2 and striped-2

Cross	Data				Total	w1
Mr1 Mr3 + × + + p	Mr	Mr p	+	p		
700 × SK	87	15	47	24	173	56
+ + lt2 × Mr1 Mr3 +	Mr	Mr lt2	+	lt2		
D25 × KD	105	30	57	29	221	—
Mr1 Mr3 st2 × + + +	Mr	Mr st2	+	st2		
700 × SK	64	38	71	0	173	56
D25 × KD	70	65	86	0	221	—
Total	134	103	157	0	394	(56)

On account of the simultaneous segregation of another Margined gene, probably Margined-1, the data are not simple. Roughly speaking, Margined-3 is linked with p and lt2 rather weakly, and with st2 rather strongly.

Retracted linkage group

The retracted linkage group was established in 1929, when foliate (fo) had been found to be linked with retracted (r). In this season, dragonfly-suppressed (dg-s), which results in a normal recessive to dragonfly, was detected to be gathered under this group. In Table 19 are shown the linked data for retracted and dragonfly-suppressed.

Table 19. F_2 from the cross of retracted dragonfly dragonfly-suppressed by dragonfly

Cross	+	r	dg-s	r dg-s	Total
800 × SA	112	19	23	17	171

Since both parents of this cross contained the gene dragonfly, the segregation of the gene dragonfly-suppressed can be detected phenotypically. The recombination of retracted and dragonfly-suppressed is 31·6 per cent.

Therefore the retracted linkage group includes three genes, retracted, foliate and dragonfly-suppressed. Retracted is linked with dragonfly-suppressed at about 31·6 per cent of recombination and is linked with foliate closely.

Delicate and duplicated linkage groups

No new genes are found for the delicate and duplicated linkage groups, remaining in the condition described two years ago (Imai 1931a). "Two genes, delicate (dl) and crumpled-2 (c2), are known to constitute the delicate linkage group. The recombination frequency for dl and c2 is roughly 5 per cent." "Six genes, duplicated (dp), striped-1 (st1)[1], Dilute (D), white-2a (w2a), dragonfly (dg) and extended (e), are found to constitute the duplicated linkage group. The recombination is 13·7 per cent for dp and st1, 25·6 per cent for dp and D, 10·1 per cent for st1 and D, less than 1·4 per cent for D and w2a, 23·3 per cent for w2a and dg, and 38·3 per cent for dg and e. Their order in the chromosome may be dp—st1—D ± w2a—dg, with a distance of 13·7 units between dp and st1, 10·1 units between st1 and D, and 23·3 units between w2a and dg. The locus extended is situated at a distance of 38·3 units in the right side or in the left of the locus dragonfly."

Duskish linkage group, newly established

Last season, Blizzard-2 (Bz2) was analysed to be linked with duskish (dk), as is given by the data in Table 20.

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[1] This was described as striped.

Table 20. F_2 from the cross of duskish by Blizzard-1 Blizzard-2

Cross	Bz	+	Bz dk	dk	Total
RL × D108	96	66	24	34	220

Owing to the simultaneous segregation of Blizzard-1, the data are complicated, but the dependent relation between Bz2 and dk is evident. Duskish seems to be linked with purple (pr) loosely. As stated before (Imai 1931a), purple is linked with crisscrossed (cs), the recombination frequency being about 19·0 per cent. The figure, however, is not much reliable, because of the fact that it was calculated from repulsion data. Crisscrossed, in turn, was detected to be linked with dk, the data being presented in Table 21.

Table 21. F_2 from the cross of duskish by crisscrossed

Cross	+	cs	dk	cs dk	Total
RL × ID	101	53	52	0	206

No double recessives are obtained, showing rather high repulsion. According to Hagiwara (1930), side-reduced (sr) and duskish are linked each other, the recombination frequency being 6·6 per cent. With these results and those showing independent relations to some genes of the known ten linkage groups together, we may conclude that the genes above cited may constitute a new duskish linkage group, which includes five genes, duskish, Blizzard-2, crisscrossed, purple and side-reduced. Owing to rather fragmental data, a definite conclusion as to the relative loci of these genes in the duskish chromosome cannot be drawn.

Polymorphic linkage group, newly established

Polymorphic (py) is independent of the genes of the known linkage groups, so far our experiments went. Last summer, a gene called bobbed-2 (bb2) was found to be linked with polymorphic, the dependent segregation is shown by the data in Table 22.

Table 22. F_2 from the cross of bobbed-2 by polymorphic

Cross	+	bb2	py	bb2 py	Total
RL × KN	95	46	35	7	183

Actually this hybrid progeny showed the simultaneous segregation of bobbed-1; but, owing to its perfect accompanyment with crêpe, all crêpe (bobbed at the same time) segregates were omitted in the compilation of Table 22. From this table the recombination of bb1 and py is calculated to be 37·3 per cent. Therefore, this newly established linkage group includes two genes, polymorphic and bobbed-2.

Conclusion

The haploid chromosomes of *Pharbitis Nil* are 15 in number, acting together as one genome. In this plant, there are expected to be 15 linkage groups. At present, however, 12 linkage groups are registered, including 70 loci in the respective chromosomes.

1. *Variegated linkage group.* The group includes eight loci variegated (v), crumpled-1 (c1), Blown-1 (B1), fasciated-3 (f3), brown (br), faded (fd), couple (cu) and male-sterile-1 (ms1). The former three genes are located in the chromosome with a distance of 14·9 between v and c1, and 17·8 between c1 and B1, in the order of arrangement v—c1—B1, with the recombination of 30·8 per cent for v and B1. The recombination percentage of v is 17·6 for f3, 31·0 for fd, about 37·7 for cu and about 45·1 for ms1. Brown is present not far from the loci v and c1 in the chromosome.

2. *Cordate linkage group.* This group is composed of eight loci, cordate (co), feathered (fe), semi-contracted (sc), precocious (pc), palmate (pl), crêpe (cp), Restricted (Rt) and bobbed-1 (bb1). The former three genes are located in the chromosome as probably being co—fe—sc, with a distance of 1·2 between co and fe, and 17·7 between fe and sc. Precocious is linked with co, the recombination being about 24·6 per cent. Three genes, pl, cp and pc, are linked each other, with the recombination percentage of about 34·6 for pl and cp, about 31·3 for pc and pl, and about 38·8 for pc and cp. Bobbed-1 is linked with cp closely, and both of them are segregated with the recombination frequency of about 38·6 per cent for Rt. Crêpe is located farther than pc from co.

3. *Yellow linkage group.* Seven genes, deformed (de), yellow (y), dusky (dy), light-1 (lt1), speckled-reduced (sp-r), maple (m) and bushy (bs), are found in this group. Deformed is linked with the recombination percentage of 20·1 for y, 23·9 for dy, 25·8 for lt1, and nearly independent of sp-r and m. Yellow is linked with the recombination percentage of 1·3 for dy, 9·6 for lt1, 28·5 for sp-r, and 28·1 for m.

Dusky is also linked with lt1 rather closely, with the recombination of 24·8 per cent for sp-r and 31·6 per cent for m. On the basis of these relations, a provisional map may be drawn with a distance of de (0), y (20·1), dy (21·4), lt1 (29·7), m (48·2), sp-r (48·6) and bs (20·1 ± 32·0).

4. *Acuminate linkage group.* Four genes, acuminate (ac), Margined-2 (Mr2), magenta (mg) and Blizzard-1 (Bz1), are known to be collected in this group. The recombination percentage is about 0·5 for ac and Mr2, and 21·2 for ac and mg. Linked segregation of Bz1 was also observed for ac and mg.

5. *Contracted linkage group.* Under this group, eleven genes, Rayed (Ry), cream (cr), shrubby (sh), interaxil-green (ig), contracted (ct), Margined-1 (Mr1), flecked (fl), tube-white-1 (tw1), intense-1 (i1), Margined-reduced (Mr-r) and lilliptian (lp), are gathered. Experimental data make possible the drawing of a provisional map of the contracted chromosome of the following relations: Ry (0), cr (± 1·2), sh (6·7), ig (10·3), ct (12·4), Mr1 (13·4), fl (13·4 ± 1·2), tw1 (18·4), i1 (43·0), Mr-r (43·0 ± 3·0) and lp (13·4 ± 1·2 ± 28·0).

6. *Speckled linkage group.* Five genes, speckled (sp), white-1 (w1), Margined-fluctuated (Mr-f), Striated (Sa) and tube-white-2 (tw2), are known to constitute this group. The recombination frequency is about 0·8 per cent for sp and w1, and roughly 20 per cent for w1 and Mr-f. The three genes, sp, Sa and tw2, are linked each other closely.

7. *Delicate linkage group.* Only two genes, delicate (dl) and crumpled-2 (c2), are registered under this group. The recombination frequency for dl and c2 is roughly 5 per cent.

8. *Pear linkage group.* Nine loci, pear (p), fasciated-1 (f1), fasciated-2 (f2), Blown-2 (B2), intense-2 (i2), chestnut (cn), striped-2 (st2), light-2 (lt2) and Margined-3 (Mr3), are found to be gathered under this group. The recombination percentage is roughly 20—25 for f1 and f2, less than 2·5 for p and f1, about 23·5 for p and B2, 32·4 for f1 and i2, 13·9 for i2 and cn, 31·8 for i2 and p, 40·1 for p and st2, and 26·9 for st2 and lt2. Margined-3 is linked with st2 rather closely, and with p and lt2 rather loosely.

9. *Duplicated linkage group.* Under this group six genes, duplicated (dp), striped-1 (st1), Dilute (D), white-2a (w2a), dragonfly (dg) and extended (e), are known with the following dependent relations. The recombination percentage is 13·7 for dp and st1, 25·6 for dp and D, 10·1 for st1 and D, less than 1·4 for D and w2a, 23·3 for w2a

and dg, and 38·3 for dg and e. Their order in the chromosome may be dp—st1—D ± w2a—dg, with a distance of 13·7 between dp and st1, 10·1 between st1 and D, and 23·3 between w2a and dg. The situation of e is dg ± 38·3.

10. *Retracted linkage group.* Three genes, retracted (r), foliate (fo) and dragonfly-suppressed (dg-s), are found to compose this group. Retracted is linked with dg-s at about 31·6 per cent of recombination and is linked with fo closely.

11. *Duskish linkage group.* This newly established group contains five genes, duskish (dk), side-reduced (sr), Blizzard-2 (Bz2), crisscrossed (cs) and purple (pr). Duskish is linked with cs rather closely, and cs with pr at about 19·0 per cent of recombination. Purple seems to be linked with dk loosely. Duskish is also linked with Bz2. According to Hagiwara, sr is linked with dk, the recombination frequency being 6·6 per cent.

12. *Polymorphic linkage group.* This is another group newly found, including two genes, polymorphic (py) and bobbed-2 (bb2). The recombination frequency of py and bb2 is about 37·3 per cent.

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Summary

The 12 linkage groups contain the following 70 loci:

1. Variegated linkage group (8 loci) ...... variegated, cumpled-1, Blown-1, fasciated-3, brown, faded, couple, male-sterile-1.
2. Cordate linkage group (8 loci) ...... cordate, feathered, semi-contracted, precocious, palmate, crêpe, Restricted, bobbed-1.
3. Yellow linkage group (7 loci) ...... deformed, yellow, dusky, light-1, speckled-reduced, maple, bushy.
4. Acuminate linkage group (4 loci) ...... acuminate, Margined-2, magenta, Blizzard-1.
5. Contracted linkage group (11 loci) ...... Rayed, cream, shrubby, interaxil-green, contracted, Margined-1, flecked, tube-white-1, intense-1, Margined-reduced, lilliptian.
6. Speckled linkage group (5 loci) ...... speckled, white-1, Margined-fluctuated, Striated, tube-white-2.
7. Delicate linkage group (2 loci) ...... delicate, crumpled-2.

8. Pear linkage group (9 loci) . . . . . . pear, fasciated-1, fasciated-2, Blown-2, intense-2, chestnut, striped-2, light-2, Margined-3,
9. Duplicated linkage group (6 loci) . . . . . . duplicated, striped-1, Dilute, white-2a, dragonfly, extended.
10. Retracted linkage group (3 loci) . . . . . . retracted, foliate, dragonfly-suppressed.
11. Duskish linkage group (5 loci) . . . . . . duskish, side-reduced, Blizzard-2, crisscrossed, purple.
12. Polymorphic linkage group (2 loci) . . . . . . polymorphic, bobbed-2.

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