論 說

THE GENETICS OF SOME MUTANT CHARACTERS IN *DROSOPHILA ANANASSAE*

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CONTENTS

Introduction	I
The First Linkage Group (X-Chromosome)	2
Descriptions of Genes	2
Determination of Loci	5
The Second Linkage Group (II-Chromosome)	8
Descriptions of Genes	8
Determination of Loci	12
The Third Linkage Group (III-Chromosome)	14
Descriptions of Genes	14
Determination of Loci	16
The Fourth Linkage Group (IV-Chromosome)	17
Descriptions of Genes	17
Determination of Loci	19
Summary.....	21
Literature Cited	22

Introduction

In my earlier paper (1935a), I reported eleven mutant characters of *Drosophila ananassae*, namely, incomplete, crumpled, Interrupted, crooked, ski, balloon, white, Plexate, retracted, lethal-1, and lethal-2, followed later (MORIWAKI 1935b, 1935c, 1936, 1937) by descriptions of thirteen more mutants. In addition to these, about thirty more mutant characters have since been found, the descriptions of which form the principal part of this paper, which will be published as a continuation of the first paper. KIKKAWA, in Kyoto, has also found more than forty mutants, the descriptions of most of which are yet unpublished, they having been reported only in the *Drosophila*

Information Service (DIS-2, 1934; DIS-3, 1935; DIS-4, 1935; DIS-7, 1937).

Before going further, I wish to record here my grateful appreciation of Prof. Y. IMAI's unceasing encouragement throughout the work, and also desire to acknowledge the assistance rendered this investigation in the form of a grant by the Foundation of Japan Society for the Promotion of Scientific Research. Finally I wish to thank Mr. K. KASAHARA for his valuable assistance in numberless ways.

The First Linkage Group (X-Chromosome)

Descriptions of Genes¹⁾

In the first paper (1935a), crooked (*ck*), Interrupted (*Ir*), lethal-1 (*l-1*), and white (*w*) were reported as sex-linked characters. Since then thirteen mutant genes have been found in the sex-chromosome, as will now be described.

Fig. 1. The achaete bristles on head and thorax. Small circles indicate the position of bristles; the black circles indicate where the bristles are missing.

1. *ac*—achaete: (X-98.8) 36b 13 (1936). One male first appeared in a line of ski-III. Many bristles are missing (Fig. 1), although the extent to which they do so somewhat varies. The dorsocentrals are however affected the most.

2. *cl*—crumploid: (X-115.8±) 35d 5 (1935a) L²⁾. In a cross of ♀ (*w f/cl*) × ♂ (*w f/cl*) seven crumploid

females were first found, all of which had also white (*w*), forked (*f*), and cut (*ct*), all homozygously, whereas during the investigation, cut were always accompanied with crumploid. The gene crumploid makes the wings crumpled (Fig. 2), but the extent of this expression, affected by certain modifiers, seems to vary from false normal to crumploid with lethal effect, although in the male the

Fig. 2. The crumploid fly.

1) According to the forms of the Drosophila Information Service (DIS), the symbols for genes are arranged alphabetically, followed by the full name, locus, date of finding (a=Jan., b=Feb., c=March, etc.), year of publication if published or "U" if unpublished, origin, characteristics, and accessory features.

2) The symbol "L" indicates that the mutant has been lost.

expression is reduced considerably, resulting in excess of males. When expressed well, it is like crumpled (*cr*—1935a).

3. *ct*³—cut³: (X—115.8) 36k24 (U). One mutant male was obtained from a mass culture heterozygous for *w f*² *y*. The wing margins are incised with normal antennae (Pl. I, Fig. 1). The gene forms multiple alleles with *ct* and *ct*², both of which were found by KIKKAWA. In the females raised by the cross ♀ *ct*³ × ♂ *ct*, the gene *ct*³ showed dominance to *ct*, while in the cross ♀ *ct*² × ♂ *ct*³, it is stated that the dominance of *ct*³ was not complete (Pl. I, Figs. 2, 3, 4).

4. *ex-b*—extended-b: (X—22.8) 36j 13 (U). The cross of a balloon² female with wild male produced a male with extended wings and deformed antennae. Since it resembled extended (*ex*—Fig. 12), of the second chromosome, although the antennae of *ex* were normal, we call it extended-b. The expression of characters, both wings and antennae, cannot be said to be uniform, particularly as the wings are sometimes almost normal.

5. *Gf*—Golf: (X—33.9) 37e21 (U). The tips of almost scutellars and dorsocentrals are knobbed like golf-club (Fig. 3). In a few cultures of the cross ♀ (*w f*²/+;+/CHIL) × ♂ (*w f*²), some females of Golf (not *w f*²) appeared successively. Outcrossing them with normal males resulted in the female offspring segregating into Golf and + in almost equal numbers, while in males we could find only a small number of Golf (*w Gf* and *Gf*) flies, besides many wild and *w f*² and a few *f*², whence it is supposed that Golf was a sex-linked dominant located near *f*² and that it had mutated in the chromosome bearing *w f*². Upon further tests being made, these points were verified. It was also found that the females carrying the genes homozygously could be alive (Tables 1 and 2).

Fig. 3. The Golf fly.

Table 1. ♀(*w Gf f*²/+) × ♂(+)

Phenotype	Females	Males
<i>w f</i> ²	/	89
+	166	113
<i>w</i>	/	14
<i>f</i> ²	/	21
<i>w Gf</i>	/	8
<i>Gf</i>	146	0
Total	312	245

Table 2. ♀(*w Gf f*²/+) × ♂(*w Gf f*²)

Phenotype	Females	Males
<i>w f</i> ²	86	105
+	/	91
<i>w</i>	/	9
<i>f</i> ²	27	27
<i>w Gf</i>	24	8
<i>Gf</i>	100	2
Total	237	242

In Tables 1 and 2, the *f*² flies in phenotype may include *Gf*, the character of which must be covered by *f*².

6. *l-3*—lethal-3; (X-?) 36d? (1936) L. Three females of scute (*sc*) were mated with one male of white yellow (*w y*) and the F_1 flies inbred, when the F_2 offspring showed approximately the ratio 2:1. The distribution of characters of 227 males in monohybrid were

$\begin{cases} +^{w} & 172 \\ w & 55 \end{cases}$	$\begin{cases} +^y & 124 \\ y & 103 \end{cases}$	$\begin{cases} +^{sc} & 103 \\ sc & 124 \end{cases}$
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This shows that a lethal gene (*l-3*) occurred in the X-chromosome which carried *w y*, and that it is located between *w* and *y*, but nearer *w*.

7. *l-4*—lethal-4: (X-45.4) 37a? (U). An exceptional sex-ratio of 2:1 was found in the offspring of the cross $\text{♀}(+/w f^2)1 \times \text{♂}(w f^2)2$, as shown in Table 3.

From this data, it may be presumed that a lethal gene (*l-4*) mutated in the + chromosome.

8. *ph*—purplish: (X-66.2) 35d23 (1935b). Two males with this character appeared first in a bobbed (bobbed-IV) culture. The gene *ph* exhibits an eye

color almost like the “purple” of *D. melanogaster*.

Fig. 4. The scute bristles on head and thorax.

9. *sc*—scute: (X-91.9) 35g7 (1936) L. In an experiment with purplish character, two males of scute appeared in a bottle. The posterior scutellar, all the orbitals, the posterior vertical, and the other bristles are always missing, with sometimes also the anterior scutellar (one or both) missing (Fig. 4). In the absence of the posterior and anterior scutellars, there occurs the following sexual difference:

	Only posterior scutellar missing	Without anterior and posterior scutellars	Total
Females	142 (40%)	209 (60%)	351
Males	320 (86%)	51 (14%)	371

10. *sc*²—scute²: (X-91.9) 36j26 (U). From a pedigree of cardinal Plexate (*cd Pt*), eight males with scute² were obtained. The gene is an

allele of scute, manifesting the omission of scutellars (the anterior is sometimes present) and anterior and middle orbitals (Fig. 5). In female flies raised from the cross $sc^2 \times sc$, the sc^2 character seems to dominate.

11. sc^3 —scute³: (X-91.9) 37c20 (U). Three males with scute³, another allele of scute, were first found in the bobbed (bobbed-IV) stock. Usually the mutant flies lack the orbitals, scutellars (both anterior and posterior), anterior supra-alar, and posterior post-alar, and sometimes also the

Fig. 6. The scute³ bristles on head and thorax.

Fig. 5. The scute² bristles on head and thorax.

posterior vertical (Fig. 6). The character of sc^3 seems to be recessive to that of sc^2 , but the heterozygous females for sc^3 and sc showed an intermediate form, that is, manifesting an sc -type in the head but an sc^3 -type in the scutellum. As to the other bristles, no inspection had been made, with the unfortunate result that the relation cannot be studied owing to loss of the sc stock.

12. vs —vesiculated: (X-62.0±) 37a22 (U) L. In the line of cardinal, one mutant male was found. By vesiculated is meant that condition in which the wings of the females are sometimes inflated as in the “vesiculated” of *D. melanogaster*. However, the mutant usually has curved and thin wings. The stock was lost before it could be sketched.

13. y —yellow: (X-93.7) 36b21 (1936). One yellow fly appeared in a culture derived from flies treated with x-rays. Like the “yellow” of *D. melanogaster*, its body color is yellow. KIKKAWA (DIS-7) independently discovered the same mutant.

Determination of Loci

The loci of the mutants described above were calculated in the X-chromosome. Some of them have already been determined by KIKKAWA (DIS-7), together with the mutants which he found. I take this opportunity of recording my indebtedness to him for allowing me to refer to his results and for using some of the mutants he had found.

Before coming to the map, I should like to say in connection with the matter of determining the loci. In studying the loci of *ex-b*, *Gf*, and *l-4*, using flies of a line $w f^2$, I frequently had cause to wonder whether the $w f^2$ flies did not sometimes carry something that suppressed the crossing over, a

small inversion perhaps, which would reduce nearly by half the recombination value between w and f^2 . As the recombination value between w and f , an allele of f^2 , I once obtained, upon counting 2943 flies (1935b), a value of 25.4 per cent, while in other experiments recently made I again obtained nearly the same value between w and f , which leads me to conclude that the suppressor must be carried in the $w f^2$ stock, though not always so. Whether the suppressor is a small inversion or not cannot be ascertained, seeing that the specific figure in the salivary gland chromosomes has not yet been found. As just mentioned, the suppressor cannot always be associated with every fly in the $w f^2$ stock, but in the stock of lethal-4, which was perpetuated by selective crossing of $\varphi(w f^2/l-4) \times \delta(w f^2)$, the suppressor seems to be always associated with $w f^2$, since in every progeny of the above cross from

mass culturing, the recombination value of $w \sim f^2$ was reduced by nearly half, as shown in Table 4.

Table 4. $\varphi(w f^2/l-4) \times \delta(w f^2)$

Phenotype	Females	Males
$w f^2$	200	210
+	244	1
w	24	0
f^2	40	25
Total	508	236

Recombination values of $w \sim f^2$:

Females 12.6%

Males 10.6%

From the above data, we can suppose that $l-4$ lies to the right of f^2 , and upon calculating the recombination value of $f^2 \sim l-4$, obtain 0.4 per cent. Since it may be assumed moreover that the suppressing power affects the value of $f^2 \sim l-4$ with almost the same force, it could be modified in proportion to the ratio of $w \sim f^2$ and $w \sim f$, that is, to 1.0 per cent.

In the next case, $w \sim ex-b \sim f^2$, the same tendency was found, but the recombination value of $w \sim f^2$ was slightly larger than that of the case of $l-4$, due probably to the fact that the suppressor could not always be present in the $w f^2$ flies used. The cross of $\varphi(w f^2/ex-b) \times \delta(w f^2)$ produced 280 females and 248 males, the segregation in the latter giving the values as under:

Recombination value of $w \sim ex-b$ 3.8%

Recombination value of $ex-b \sim f^2$ 13.9%

Recombination value of $w \sim f^2$ 15.7%

Similar to the $l-4$ case, the value of $w \sim ex-b$, namely, 3.8 per cent, was modified in proportion to the ratio of $w \sim f^2$ and $w \sim f$, that is, to 6.1 per cent.

The third case, $w \sim Gf \sim f^2$, gave nearly the same result as the preceding. From the data given already in Tables 1 and 2, only the segregation in the

males will be given next (Table 5), the classification, however, having been revised by dividing the phenotypically f^2 flies into true f^2 and Gf .

Table 5. ♀(*w Gf f²*/+)× ♂(+or *w Gf f²*)

Region of crossing over	Phenotype	Males
0 {	<i>w Gf f²</i> +	192 } 396 204 }
1 {	<i>w</i> <i>Gf f²</i>	23 } 55 32 }
2 {	<i>w Gf</i> <i>f²</i>	16 } 32 16 }
1,2 {	<i>Gf</i> <i>w f²</i>	2 } 4 2 }
Total		487

Recombination values :

<i>w</i> ~ <i>Gf</i>	12.1%
<i>Gf</i> ~ <i>f²</i>	7.4%
<i>w</i> ~ <i>f²</i>	17.9%

From the preceding form, the modified value of $Gf \sim f^2$ can be calculated, for example, $7.4 \times \frac{25.4}{17.9} = 10.5$ (per cent). Similarly the value of $w \sim Gf$ is 17.2 per cent.

The map of the X-chromosome is given in Fig. 7, the recombination values from which the loci were directly determined being listed below, with certain reference data (marked *).

Interval	Recombination value	Number of flies
dwarf (<i>dp</i>)~Notch (<i>N</i>)	15.5%	(KIKKAWA's data)
Notch~white (<i>w</i>)	1.2%	(KIKKAWA's data)
white~extended-b (<i>ex-b</i>) ...	6.1% (modified)	248
white~Golf (<i>Gf</i>).....	17.2% (modified)	487
*extended-b~forked ² (<i>f²</i>) ...	22.1% (modified)	248
Golf~forked ²	10.5% (modified)	487
*white~forked (<i>f</i>)	25.4%	2943
forked ² ~lethal-4 (<i>l-4</i>)	1.0% (modified)	236

Fig. 7. The map of the X-chromosome. The genes underlined were found by KIKKAWA.

Interval	Recombination value	Number of flies
forked~vermilion (<i>v</i>)	9.0%	619
forked~miniature (<i>m</i>).....	9.6%	1065
forked~vesiculated (<i>vs</i>)	17.6%	91
forked~purplish (<i>ph</i>)	21.8%	800
purplish~scute (<i>sc</i>).....	25.7%	479
scute~yellow (<i>y</i>)	1.8%	227
yellow~achaete (<i>ac</i>)	5.1%	452
achaete~Interrupted (<i>Ir</i>) ...	7.6%	(KIKKAWA's data)
achaete~cut ³ (<i>ct</i> ³)	17.0%	452
cut (<i>ct</i>)~clumploid (<i>cl</i>)	0.0%	2143

The Second Linkage Group (II-chromosome)

Descriptions of Genes

Succeeding ski (*sk*), Plexate (*Pt*), retracted (*rt*), and lethal-2 (*l-2*), which have already been described (MORIWAKI 1935a), fifteen additional genes mutated in the second chromosome, as follows:

14. *Bd*—Beaded: (II-?) 37d 8 (U) L. One female was first found in a pair culture of Dichaete (*D*). The margins of the wings were scalloped (Pl. I Fig. 5), as in the “Beaded” of *D. melanogaster*. The character of Dichaete, which accompanied the first Beaded, had always been associated with Beaded, but before we could continue our observations the stock was lost this summer. Whether the homozygous flies could be alive or dead, was not determined. Its linkage relation to other genes in the second chromosome will be discussed later.

15. *bn-b*—broken-b: (II-?) 37a17 (U). In a culture of cut (*ct*) one male expressed the mutated broken-b character. It manifested that the posterior, and sometimes the anterior, crossveins are missing or broken (Pl. I, Fig. 6), as in Interrupted (*Ir*) or KIKKAWA's broken (*bn*—DIS-7), which is, however, reported to belong to the third chromosome. There seems to be present an interaction of genes between this mutant character and the Plexate (*Pt*) gene, that is to say, homozygous flies of broken-b when joined by one *Pt* gene cannot be recognized, they being covered by the expression of the latter.

Fig. 8. The chilblained fly.

16. *ch*—chilblained: (II—near *Pt*) 37e21 (U). In Minute-IVa (*M-IVa*) stock a single chilblained

female appeared. The tarsi of the mutant are conglutinated, just like chilblained legs (Fig. 8). The classification is fairly good.

17. *cnt*—contracted: (II-?) 36i16 (U) L. One female was first found in cardinal (*cd*) stock. The wings of the mutant are contracted, and sometimes, when intensely expressed, are like the “vestigial” of *D. melanogaster*. Moreover nearly all the scutellars and dorso-centrals are bent upward (Fig. 9). This viability and fertility were so poor that the females could not produce any progeny when mated with *cnt* males, so the stock was perpetuated by mating the homozygous flies with the heterozygous ones, but it was lost this summer.

Fig. 9. The contracted fly.

Fig. 10. The crippled fly.

18. *cp*—crippled: (II- near *Pt*) 36l31 (U) L. Two females and one male characterized with crippled legs were found in a line of white. The mutant had not only crippled legs with deformed tarsi, but also slightly upturned wings (Fig. 10). The manifestation was indistinct sometimes, especially in flies obtained

by back-crossing.

19. *D*—Dichaete: (II-?) 36l25 (U). Dichaete (*D*) was found as three females and two males in a mass culture derived from flies heterozygous

Fig. 11. The Dichaete bristles on head and thorax.

Fig. 12. The extended fly.

for wf^2y . Its outstanding character is the omission of the anterior dorso-central, but some of the other bristles of the thorax and of the head are missing, along with or without the anterior dorsocentral (Fig. 11). The fly that carries the Dichaete genes homozygously seems to be viable. Concerning this mutant, it was concluded that a modifying gene had arisen in a culture, but the question how that gene modifies the expression of the Dichaete has not yet been completely worked out.

20. *ex*—extended: (II-?) 36a22 (1936) L. Extended first appeared in the Minute-IIIc (*Mc-IIIc*) stock as one female and one male. One or both wings are extended (Fig. 12). It is not always completely separable from the wild type, especially the males. The mating between well expressed flies resulted as follows:

	One or both wings extended	Unextended	Total
Females	168 (86%)	27 (14%)	195
Males	82 (38%)	136 (62%)	218

21. *hk*—hooked: (II-?) 37a8 (U). One female and two males of hooked mutated in a culture of the Minute-IIIc stock. All the scutellars (at times the anterior only) are bent downward, like hooks (Fig. 13). As the expression is not constant, its classification is uncertain.

Fig. 13. The hooked fly.

22. *ms*—missing: (II-68.5) 35k13 (1936) L. In the white Plexate stock, nine females and six males appeared, all of which lacked both side of the anterior scutellar. In some of the offspring, the bristles were

absent only one side of the anterior scutellar; and in others bristles on other parts were missing additionally (Fig. 14).

Fig. 14. The missing bristles on head and thorax.

23. *ms-b*—missing-b: (II-?) 36h24 (U). One female missing-b was found in a culture derived from flies heterozygous for wf^2y . Similarly to missing (*ms*), the anterior scutellar was missing, usually, however, with no omission of the other bristles (Fig. 15). But the character is not favorable

Fig. 15. The missing-b bristles on head and thorax.

for linkage work, as it often overlaps the wild type, especially in males. Here again I encountered another example of sexual difference in the expression of the genes, the examples usually showing that the female manifests the character nearly always more pronouncedly than the male.

24. *M-I/b*—Minute-IIb: (II-?) 35h8 (1937). In an experiment where females of purplish bobbed (bobbed-IV) were mated with x-rayed males of the same characters, one Minute-IIb male resulted from 2130 male offspring. The gene Minute-IIb, which manifests minute bristles, has a lethal effect when homozygous, and partially so when heterozygous; and the flies carrying the gene generally emerge a few days later than other flies of the same culture. It is supposed that some power enhancing the crossing over in the second chromosome accompanies this gene (MORIWAKI, 1937).

25. *Off*—Off: (II-40.1) 36b22 (1936) L. One mutant male was first obtained in a line of ski-III. The fly was heterozygous. Nearly all the bristles are frizzled and clipped, and the homozygous flies (Fig. 16), which are viable can be distinguished from the heterozygous ones, showing the frizzled and clipped

Fig. 16. The Off fly.

character more prominently.

26. *Pu*—Puffed: (II-?) 37g5 (U). One Puffed male was produced by the mating ♀(+/*cd Pt e*) × ♂(*cd e*), which expressed no *cd Pt e* phenotypically. In view of the knowledge that the + chromosome of the heterozygous mother had carried an inversion *CIIL* (MORIWAKI, 1937), the first male must have carried a constitution, such as *Pu CIIL/cd e*.

The gene, which seems to have a lethal effect when homozygous, manifests a character in which the compound eyes are small and reddish, puffed and inflamed (Fig. 17; Pl. I, Fig. 8), like the "Puffed" of *D. virilis*.

27. *rf*—roof: (II-?) 36i28 (U). Two females and one male of roof character first appeared in a cross of ♀(+/*w f*²) × ♂(+). The wings slope down sharply at the sides (Fig. 18), although this

Fig. 17. The Puffed eye.

Fig. 18. The roof fly.

expression cannot be constant. Even during temporary anaesthetizing of the flies, the expression seems to change every time the ether is applied.

28. *ro*—rough: (II-?) 37b23 (U) L. Two females and one male expressing a Plexate character, which were raised from a cross of ♀(*cp*) × ♂(*Pt/cp*), manifested also rough eyes. In the F_1 generation from outcrossing the Plexate rough flies with the wild ones, the rough character never appeared, and by inbreeding them F_2 flies were produced. Among the F_2 , this character segregated again, but only when accompanied with Plexate, whence we conclude that the gene rough must be recessive and that its manifestation would not be recognized, even in a homozygous condition, unless with a Plexate gene; that is, only a fly with a constitution such as *Pt ro/ro* can express rough eyes (Pl. I, Fig. 9). The fact that the gene *ro* belongs to the second chromosome could not be determined directly before the stock was lost, although it was known that it could not belong in the X-, III-, or IV-chromosome.

Determination of Loci

Fig. 19. The map of the II-chromosome.

In the second chromosome, the loci of the genes were not satisfactorily determined, partly because most the dominant genes could not be used satisfactorily, some of which had been lost before they could be used, while the others were accompanied with inversion, the power to suppress crossing over, or some power to enhance crossing over. That is to say, excepting Plexate, the most available dominant genes for determining loci, Off and Beaded, were early lost, whereas either Puffed or Dichaete seemed to carry an inversion CHIL, while Minute-IIb exhibited a peculiarity as if it possessed a certain power of enhancing crossing over.

At any rate a map of the second chromosome has been drawn as shown in Fig. 19, based on the determined genes, the linkage data used for it being as given below :

Interval	Recombination value	Number of flies
cardinal (<i>cd</i>)~Plexate (<i>Pt</i>).....	25.9%	4147
Plexate~ski (<i>sk</i>)	0.0%	1171
Plexate~spineless (<i>ss</i>)	0.8%	4147
Plexate~Off (<i>Off</i>)	14.2%	268
Plexate~ebony (<i>e</i>)	26.3%	973
Off~retracted (<i>rt</i>).....	21.1%	133
Plexate~retracted	34.0%	1939
Off~missing (<i>ms</i>).....	28.4%	141

Besides these, there are several genes, the recombination values of which with Plexate alone are already known, although it has not yet been determined whether they were located to the right or the left of Plexate; the data are as follows:

Interval	Recombination value	Number of flies
Plexate~Beaded (<i>Bd</i>)	0.0%	102
Plexate~broken-b (<i>bn-b</i>)	> 50.0%	212
Plexate~chilblained (<i>ch</i>)	0.7%	690
Plexate~crippled (<i>cp</i>)	1.0%	202
Plexate~extended (<i>ex</i>)	29.6%	61
Plexate~hooked (<i>hk</i>)	49.2%	197
Plexate~missing-b (<i>ms-b</i>)	39.9%	439
Plexate~roof (<i>rf</i>)	12.3%	342
Plexate~rough (<i>ro</i>)	2.5%	158

As stated above, gene *M-IIb* is believed to be related to some power of increasing in both sexes the rate of crossing over of its own chromosome, although the question whether the enhancer is *M-IIb* itself, or some other factor carried by *M-IIb*, still remains unanswered. From a cross of ♀(*M-IIb/cd Pt*) × ♂(*cd*), amounting to 540 flies, recombination values were obtained as follows:

Minute-IIb (*M-IIb*)~cardinal (*cd*)=43.7%
 cardinal~Plexate (*Pt*)=33.9%
 Minute-IIb~Plexate=47.2%

Since these values, however, are believed to have been augmented by the enhancing power of *M-IIb*, the true values are not known, all that is known being that the locus of *M-IIb* seems to be situated on the left side, considerably far from *cd*.

As to the exact situation of inversion CIIL, which should almost suppress the crossing over at the left arm of the second chromosome, that is, the extent to which it covers, remains undetermined, but its approximate position is supposed to lie to the left of *Pt*, covering *cd*, while its subterminal figure has been encountered in the salivary gland chromosomes. That the gene Puffed must be accompanied with CIIL is clear from its origin as already described. Actually, the recombination values between *Pu* and the other genes in the second chromosome are always very small, although the exact extent to which they were reduced has not been determined, the locus of *Pu* being therefore still unknown. These values are as under.

Interval	Recombination value	Number of flies
Puffed (<i>Pu</i>)~cardinal (<i>cd</i>)...	0.1%	1122
Puffed~chilblained (<i>ch</i>)	0.0%	432
Puffed~broken-b (<i>bn-b</i>).....	1.1%	182
Puffed~ebony (<i>e</i>)	0.3%	654
Puffed~missing-b (<i>ms-b</i>) ...	1.3%	465
Puffed~Plexate (<i>Pt</i>)	0.0%	113
Puffed~roof (<i>rf</i>).....	0.0%	244

It was recently found that Dichaete, like Puffed, seemed also to carry inversion CIIL, there having been no crossover in either Dichaete~Plexate or Dichaete~cardinal. Consequently the linkage datum of Plexate~Beaded, which was 0.0 per cent (102 flies), might be influenced by the CIIL that is included in the Beaded chromosome, since the gene Beaded mutated in the culture of Dichaete and had not been separated from the latter before it was lost.

The Third Linkage Group (III-chromosome)

Descriptions of Genes

In addition to gene balloon reported in my first paper (1935a), there have appeared nine mutants in the third chromosome, descriptions of which follow.

Fig. 20. The crooked-b fly.

29. *ck-b*—crooked-b: (III-?)
37a6 (U) L. A female and a male mutated first in a stock of *cut*³. The tarsi, which almost like crooked, previously appeared (1935a) as a sex-linked recessive, were crooked mostly in the hind-legs (Fig. 20).

The stock, however, after having shown that the gene *ck-b* behaved as a recessive in the third chromosome, was lost.

30. *er*—erect: (III-?) 37b23 (U). Several flies of both sexes mutated in a culture derived from a cross of cut with extended-b. The posterior scutellar of this mutant is erect (Fig. 21). The viability and fertility of erect are good, but the fact that it overlaps the wild type limits the usefulness of the type.

Fig. 21. The erect fly.

Fig. 22. The Minute-IIIc fly.

31. *M-IIIc*—Minute-IIIc: (III-?) 3516 (1936). Minute-IIIc was first found as a single male in a culture descended from a line that was irradiated by x-rays. As shown in Fig. 22, it is characterized with minute bristles, a different Minute from *M-II/a* and *M-IIIb* of the third chromosome which were found by KIKKAWA (DIS-4). Flies of homozygous Minute-IIIc seem to die, while the heterozygous ones, emerging a few days later than the other flies in the same culture, show less viability.

32. *M-IIId*—Minute-IIId: (III-?) 36d22 (U). Several mutant flies of both sexes were found in a wild stock. Minute-IIId is dominant, and lethal when homozygous. The heterozygotes seem to be of better viability and fertility than the other Minutes.

33. *rm*—rumpled: (III-?) 37c11 (U). In bobbed (bobbed-IV) stock appeared a female and a few males of rumpled. The wings are crumpled (Fig.

Fig. 23. The rumpled fly.

Fig. 24. The rippled fly.

23) with somewhat variable expressions and the viability somewhat poor. Even expressed weakly, the fly can be separated from the normal by the opaqueness of its wings.

34. *rp*—rippled: (III-91.4) 37b27 (U). Rippled was found in several females and males in an F_2

count from a cross of Minute-IVa with wild. They have slightly warped wings, just showing a rippled surface (Fig. 24). At times, however, this character overlaps the wild type.

Fig. 25. The ski-III fly.

36, *wp*—warped: (III-37.3±) 36k28 (U). Warped was found in two males from a small mass culture. Most the parents of this culture carried some or all the genes, *wf²y*. The wings of the mutant are warped and curved downwards (Fig. 26). The fertility

Fig. 27. The wavy fly.

manifest the character phenotypically.

35. *sk-III*—ski-III: (III-0.0) 35l6(1936)L. Ski-III was first found as a single female in a wild stock from Formosa. The wings are up-turned like a ski (Fig. 25). There is a sexual difference in the expression, which in some flies is weakly expressed, more often in males than in females. The classification into weak expression is based on the characteristic of rippled wings.

Fig. 26. The warped fly.

and viability are somewhat poor, but the separability is good.

37. *wy*—wavy: (III-18.8) 37a7 (U) L. Several wavy flies appeared in a culture of *Dichaete*, descended from an experiment with *wf²y*. The gene *wy* expresses wavy wings (Fig. 27), sometimes so faintly that the homozygotes cannot

Determination of Loci

Loci of nearly all the mutants described above have generally been determined in the same manner as in the X- and II-chromosomes, calculated directly from the recombination values without any corrections. The map of the third chromosome is given in Fig. 28, with a list of the recombination values, including values of the genes of which the loci have not been determined.

Fig. 28. The map of the III-chromosome.

As will be seen from the last group, most of the recombination values between Minute-IIIc and the other genes in the third chromosome approach fifty per cent, which could be explained by supposing that the gene *M-IIIc* might be situated near the end, either right or left, and far from the region between ski-III and plexus. Recently, however, I have obtained a result that there happened male crossing over between Minute-IIIc and plexus in natural condition, unaffected by any agency, from which I concluded that the gene *M-IIIc*, the same as *M-IIIb*, might have been associated with a certain power for enhancing the crossing over in both sexes, always resulting in increasing the recombination values.

The Fourth Linkage Group (IV-Chromosome)

Descriptions of Genes

No mutant gene had been found in the fourth chromosome until the appearance of bobbed-IV (*bb-IV*). The gene *bb-IV* was first described as a

sex-linked character bobbed (MORIWAKI 1935b), which could not be expressed in the male owing to the presence of the normal allele in Y-chromosome. Later, in his preliminary report (1936), KIKKAWA stated that the fourth chromosome (small V-shaped) could be assumed to be partly homologous to a section of the Y-chromosome. Recently, after further studies, he (KIKKAWA 1937) suggested that the short arm of the Y-chromosome is homologous to the distal part of an arm of the fourth chromosome. He (DIS-7) further states that the bobbed gene was found to be located in the fourth chromosome, at a region homologous to the Y-chromosome.¹⁾

At all events, the gene bobbed-IV (bobbed) has long been only a mutant found in the fourth chromosome, while many mutants were known in the other chromosomes. This fact could be explained by assuming that the fourth chromosome must have been "inert," seeing that the number of strands radiating from the chromocenter in the salivary gland nuclei was six. KIKKAWA (1936) and KAUFMANN (1936) determined, independently, that the six strands represent the arms of the four longer autosomes and the X-chromosomes, the fourth chromosomes being reduced to a small heterochromatin mass forming a part of the chromocenter. More recently KAUFMANN (1937) wrote:

"In salivary gland nuclei, however, the fourth chromosomes are represented by a sizeable mass of heterochromatin, plus the satellite, contrasting thereby with the more restricted expression of such "inert" chromosomes as the Y of this and other species. If the amount of banding is an indication of the genetic content of heterochromatic regions, as FROLOWA (1936) has suggested, it is probable that further genetic studies will reveal genes in the fourth chromosomes. The satellite alone possesses at least ten bands, and many others exist in the arms which form part of the chromocenter."

Meanwhile, besides bobbed-IV, I obtained three mutants which are believed to belong to the fourth chromosome, as will now be described.

38. *bb-IV*—bobbed-IV: (IV-o.o) 34k28 (1935b). As just stated, the mutant bobbed-IV originated as bobbed, one bobbed female appearing from a wild stock. It was characterized by minute bristles in the females, and often by scaly scerites; the males, however, being entirely normal in regard to these characters. Besides, the females, which are relatively infertile, generally emerge from two to five days later than the males. Sometimes, as exceptions, the males show minute bristles, but it has not yet been ascertained

1) In a recent paper (1937), I reported an abnormal inheritance in connection with the "bobbed" character of *D. ananassae*, regarding the character as sex-linked. KIKKAWA's idea that the gene "bobbed" belongs to the fourth chromosome, notwithstanding that the Y-chromosome possesses the ability to suppress its expression in males, may generally explain the abnormalities, but there remain a few examples that it cannot explain.

whether there was a pedigree, in which the males with minute bristles would appear more frequently than in the general case.

39. *mo*—mottled: (IV-?) 36k24 (U). A mating of ♀(*cd*) × ♂(*M-IIIb/cd Pt*) produced a single female of mottled accompanied with Plexate. Later, the same mutant flies often appeared also in the stock of cardinal. The compound eyes of the mutant are mottled with dark spots that can scarcely be distinguished in the younger stage or when accompanied with *cd/cd*. That the gene belongs to the fourth chromosome was confirmed by the result of the cross ♀(*mo*) × ♂(*Pt/+ ; Bb/+ ; +/mo*), which produced every class of phenotypes in almost equal numbers in both sexes. Another test made by using Minute-IVa, also led us to the same conclusion, excepting however a peculiar point to be referred to later.

40. *M-IVa*—Minute-IVa: (IV-?) 36f11 (U) L. The same experiment as that with purplish bobbed (bobbed-IV), in which *M-IIIb* mutated, was repeated in 1936. During the experiment, three males of Minute-IVa appeared in a culture obtained by crossing ♀(*ph bb-IV*) with x-rayed ♂(*ph bb-IV*). The character was dominant, and the homozygous Minute-IVa are probably not viable. From the fact that the gene *M-IVa* inherited independently with every of *cd* (II), *Pt* (II), *sk-III* (III), and *px* (III), its subject chromosome was determined as being the fourth.

41. *Sv*—Shaven: (IV-?) 37b1 (U). In a culture of ♀(*wf²/l-4*) × ♂(*wf²*), a single Shaven female (*wf²*) mutated. Shaven is dominant, and lethal when homozygous. The heterozygote generally manifests omission of bristles with various expressions, that is, achaete-like with good separability (Fig. 29), or losing only a few bristles, while at times it overlaps the wild type. The manifestation moreover seems to be stronger in females than in males, although Shaven is not a sex-linked mutant. Seeing that Shaven inherited independently with *Pt* (II) and *Bb* (III), it was believed to belong to the fourth chromosome, which confirmation was strengthened by the fact that there was a linkage relation in each of Shaven ~ Minute-IVa and Shaven ~ mottled.

Fig. 29. The Shaven bristles on head and thorax.

Determination of Loci

The loci of the genes in the fourth chromosome have not yet been satisfactorily determined. Minute-IVa, which stock was lost this summer, was used in studying its relation to bobbed-IV and mottled. In my stock

the gene Minute-IVa, however, was believed to have accompanied bobbed-IV, but owing to its loss, the relation between them could not be ascertained. In the second place, two crosses ♀(*M-IVa/mo*) × ♂(*mo*) and ♀(*mo*) × ♂(*M-IVa/mo*), were made, with the result as shown in Tables 6 and 7.

Table 6. ♀(*M-IVa/mo*) × ♂(*mo*)

Phenotype	Females	Males	Total
0 { <i>M-IVa</i> <i>mo</i>	38 123	44 102	82 225 } 307
1 { <i>M-IVa mo</i> +	1 1	1 2	2 3 } 5
Total	163	149	312

Recombination value of *M-IVa*~*mo*. 1.6%

Table 7. ♀(*mo*) × ♂(*M-IVa/mo*)

Phenotype	Females	Males	Total
0 { <i>M-IVa</i> <i>mo</i>	90 159	129 187	219 346 } 565
1 { <i>M-IVa mo</i> +	2 2	1 0	3 2 } 5
Total	253	317	570

Recombination value of *M-IVa*~*mo*. 0.9%

It may be supposed from these data that something which enhances the crossing over may be associated with Minute-IVa, as in the cases of *M-IIIb* and *M-IIIc*, in which case the recombination value in the female cannot be regarded as being true.

Besides, a recombination value between Shaven and mottled was calculated and found to be 0.0 per cent, but as the number of flies counted was too small, it also is not a satisfactory result.

In my first paper (1935a), I reported two genes, crumpled (*cr*) and incomplete (*ic*), both of which were lost after having shown that they behaved as autosomal recessives. Here is another gene, Engrailed (*Eg*), the subject chromosome of which was not determined before it was lost.

Fig. 30. Three forms of various expressions of Engrailed.

42. *Eg*—Engrailed: (?) 36125 (U) L. Two females of Engrailed were found in a culture descended from a stock of Minute-IIId. Usually the scutellum of the mutant is nicked, but the character Engrailed manifests itself

in various ways, even in being nearly normal. Three forms of the expression are given in Fig. 30. As to gene *Eg*, which inherited independently of *Pt* (II), all that is known is that it is not in the second chromosome.

Summary

1. Forty-two mutant characters of *Drosophila ananassae*, which were newly found, following the first eleven mutants, are described, with their origins, characteristics, and linkage data.

2. Of these mutants, thirteen are sex-linked. They are achaete (*ac*), clumploid (*cl*), cut³ (*ct*³), extended-b (*ex-b*), Golf (*Gf*), lethal-3 (*l-3*), lethal-4 (*l-4*), purplish (*ph*), scute (*sc*), scute² (*sc*²), scute³ (*sc*³), vesiculated (*vs*), and yellow (*y*). Although not separable from the heterozygous flies, the homozygotes of Golf, a dominant character, are viable.

3. Beaded (*Bd*), broken-b (*bn-b*), chilblained (*chl*), contracted (*cnt*), crippled (*cp*), Dichaete (*D*), extended (*ex*), hooked (*hk*), missing (*ms*), missing-b (*ms-b*), Minute-IIb (*M-IIb*), Off (*Off*), Puffed (*Pu*), roof (*rf*), and rough (*rv*) are described as mutants in the second chromosome. Among the dominant genes, Off was known to be viable when homozygous. As to the rough gene, it was peculiar in that the character could be expressed only when accompanied with a Plexate gene.

4. In the third chromosome, there newly appeared nine mutants, such as crooked-b (*ck-b*), erect (*er*), Minute-IIIc (*M-IIIc*), Minute-IIId (*M-IIId*), rumpled (*rm*), rippled (*rp*), ski-III (*sk-III*), warped (*wp*), and wavy (*wy*).

5. Bobbed-IV (*bb-IV*), which was first described as bobbed, has long been known to be only a mutant found in the fourth chromosome. Three mutant genes are newly added, namely, Minute-IVa (*M-IVa*), mottled (*mo*), and Shaven (*Sv*).

6. A certain power to enhance crossing over, affecting both sexes, seems to be associated with every Minute-IIb, Minute-IIIc, and Minute-IVa, with the result that provided any one of these Minutes are associated, the male crossing over occurs in the natural condition, whereas in the female associated with any one of these Minutes, crossing over is increased.

7. Various kinds of inversion seem to appear quite often in this species. Puffed, perhaps also Dichaete and Beaded, should be accompanied with inversion CIIL, a subterminal inversion having the power to suppress crossing over in the left arm of the second chromosome, while a small inversion may be associated with the X-chromosome of lethal-4 or *wf*², which, however, has not yet been recognized cytologically, only showing that it may suppress crossing over slightly at the region near *wf*².

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Explanation of Plate I

- Fig. 1. The cut³ wing.
- Fig. 2. The cut³/cut wing.
- Fig. 3. The cut³/cut² wing.
- Fig. 4. The cut² wing.
- Fig. 5. The Beaded wing.
- Fig. 6. The broken-b wing.
- Fig. 7. The "sump" (a microprinting technique devised by Mr. J. SUZUKI) of a normal eye.
- Fig. 8. The "sump" of Puffed eye.
- Fig. 9. The "sump" of rough eye.

Fig. 1

Fig. 4

Fig. 2

Fig. 5

Fig. 3

Fig. 6

Fig. 7

Fig. 8

Fig. 9

アナナス猩々蠅の突然變異形質に関する遺傳

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摘 要

先に發表したアナナス猩々蠅の 11 の突然變異形質に續いて發見された 42 の突然變異に就て、起原・特質・遺傳性狀等を記述した。その中伴性遺傳のものが 13, 第 2 染色體に屬するもの 15, 第 3 染色體が 9, 第 4 染色體に屬すると思はれるものが 4, その他に所屬不明のもの 1 があつた。

以上の中で優性に遺傳するものは 11 あるが、Golf と Off とは明らかにホモが生存することが知れた。

遺傳子間の相互關係で特に著しかつたのは rough と Plexate との關係で、rough 遺傳子はホモの状態にあつても Plexate が加はらねば形質を表現しない。

Minute-IIb, Minute-IIIc, Minute-IVa の夫々には、その屬する染色體に於ける交叉を高めると思はれる何等かの力が伴ふらしい。即ち之等の Minute のどれかが關係すると雄に於ても若干の交叉が見られ、雌に於ては交叉が高められる結果となる様である。

本種に於ては各種の逆位が屢々現はれる。Puffed には CIIL (第 2 染色體の左腕に於ける交叉を抑制すると思はれる一逆位) が伴つて居るし、Dichaete にも Beaded にも同じく CIIL が伴ふらしい。この他に lethal-4 又は wf^2 に伴つて小さな逆位が X 染色體にあると考へられる。即ちこの系統では wf^2 の近くの交叉が幾分抑制される傾向がある。併しこれは唾腺染色體の方からは未だ證明されて居ない。