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Genetic Studies on *Crippled*, a Mutant Character of *Drosophila melanogaster*.

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With Plates XVI–XX and one Textfigure.

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Contents.

INTRODUCTION

This work was begun in the Zoological Department of Columbia University in October 1923 and continued in the Woods Hole Laboratry during the summer of the next year, until I left America in the middle of September. Thus I had to drop the work unfinished and incomplete in some respects. However, since I have no prospect of taking it up again in future, I thought it best to publish it so far as the results I had got go. Before going any further, I feel it my pleasant duty to express here my sense of gratitude for the hospitality extended to me by the staffs of those institutions. Especially are my best thanks due to Professor T. H. MORGAN, Doctor A. H. STURTEVANT and Doctor C. B. BRIDGES to whom I am indebted for invaluable advice and suggestions. The main results obtained from the work have been written for "Genetics." The present paper contains more detailed accounts of the same data.

ORIGIN AND DESCRIPTION OF CRIPPLED

The fly which became the ancestor of the strain on which the present study was carried out, was a female from the *black purple cinnabar* stock. She had the tarsus of one of her hind legs curved sharply forward (Pl. XVII, fig. 1). This fly was crossed with one of her brothers, and gave some offspring with a similar abnormality. The strain of this new mutant character was thus established and named *crippled*. Some time afterwards, the original stock of *black purple cinnabar* was found to contain some flies with a similar abnormality. The character of these flies, when examined, revealed to be genetically the same as the character previously found. It is therefore very likely that this mutant character had appeared in that stock some time before it was first discovered.

There are some striking features of this *crippled.* The character appears either in one of the hind or middle leg and practically never in the front leg. As a rule, only one leg of those two pairs becomes abnormal. Further, the abnormality of the middle leg belongs to a type entirely different from that of the hind leg. When the character appears in the hind leg, some of the segments are shortened, or broadened, or swollen, or curved, or twisted. Sometimes, this occurs only in one segment, but more commonly in two or more at the same time, thus disfiguring often the entire leg; even cases are met with in which some of the distal segments are gone (Pl. XVII). When the middle leg is affected, on the other hand, the leg may be forked, or dwindle as a whole, or may disappear entirely (Pls. XVIII, XIX). And what seems interesting is that the state of food apparently determines whether the middle or the hind leg is to become abnormal. For the sake of description, I shall hereafter discriminate those two types of *crippled* by calling them *crip-h* and *crip-m* respectively, according as the character appears in the hind or the middle leg; but when there is no need of discrimination, the character will be called *crippled* simply.

CRIP-H

Description

As mentioned above, *crip-h*, the abnormality of the hind leg, is a character liable to much variation. The fly having the factor for this character in the homozygous state, may be quite normal in every respect, but may have its one hind leg more or less deformed. The abnormality may appear in any segment from the coxa to the tarsus; and the segment is shortened, swollen, straightened, crooked, or twisted. This may occur in only one segment; but more commonly more than one segment is deformed at the same time. Frequently also the leg lacks some of the distal segments. In extreme cases the entire leg is missing, leaving scarcely any trace whatever. In Pl. XVII some of such crippled hind legs are shown. Fig. 1 shows the leg of the fly in which the abnormality was first found. In figs. 2 and 3 the tibia, as well as the proximal segments of the tarsus, is somewhat disfigured. In figs. 3 and 7 the entire leg is shaped something like a cork-screw, some of the segments being twisted more or less. In figs. 8 to 10, 12 and 14 the entire leg is folded up, and practically every segment is abnormal in shape. In figs. 14, 21 and 22 the segments are swollen and much deformed. Lastly, in figs. 18 to 20 and in figs. 23 and 24 the leg lacks some of the distal segments.

Except in cases where the abnormality is very slight, the crippled leg is apparently useless to the fly, the fly usually drags it while walking. Moreover, such a fly often has one of the wings folded, evidently owing to the hind leg of the same side being crippled and incapable of extending it.

As mentioned already, this character appears usually in only one hind leg, the right or the left, but flies may be found with both legs crippled. In such cases there is little similarity between the two legs—fig. 15 is an example of this kind.

Exceptionally, the middle leg shows the same kind of abnormality (figs. 16 and 17). In these cases the hind leg of the same side is also abnormal, practically without exception. Such abnormality of the middle leg belongs to a category different from *crip-m* to be described later.

Influence of Environment on Character Crip-h

Age of parents

Before working on the influence of the environment on the character *crip-h*, a sort of preparatory experiment was carried out, to see if the age of parents had any influence on the character of the offspring. Thus, a pair of flies homozygous for the factor *crip-h* were put in a bottle and left for eight days; and before any F1 fly came out, the parents were transferred to a second bottle, and left there for the next eight days. Sometimes, the same thing was repeated for a third bottle. These two (or three) bottles were put in the same 25° C. incubator and the percentages of the *crip-h* flies which came out were compared. Altogether a dozen sets of such bottles were prepared. The result is shown in table I.

TABLE I.

Age and percentage of *crip-h* flies.

Culture No.	*Brood No.*	*Total number*	*Percentage of crip-h*
19	1	278	6·1
	2	298	8·1
	3	101	11·9
140	1	291	6·9
	2	174	5·8
212	1	548	11·4
	2	361	15·5
	3	248	27·4
219	1	505	11·4
	2	333	9·8
213	1	610	12·7
	2	334	15·6
252	1	278	*D** 18·2; *d* 29·5
	2	303	*D* 23·4; *d* 41·8
231	1	340	*D* 29·6; *d* 21·7
	2	85	*D* 40·0; *d* 36·0
281	1	137	*bprcn* 40·7; *prcn* 47·4
	2	226	*bprcn* 44·4; *prcn* 41·5
2132	1	164	14·6
	2	275	12·7
2134	1	103	7·8
	2	260	5·8
2137	1	155	8·4
	2	61	21·3
2138	1	206	*bpr* 13·4; *bprcn* 5·9
	2	268	*bpr* 6·5; *bprcn* 11·8

**D*—flies with the third-chromosome dominant character *Dichaete*; *b*—*black*, *pr*—*purple*, *cn*—*cinnabar*, all second-chromosome recessive characters.

In the table, Nos. 19, 212, 213, 231, 252 and 2137 show that the percentage of *crip-h* is higher in the later broods than in the earlier, whereas, Nos. 140, 219, 2132 and 2134 show that the percentage is higher in the earlier broods than in the later. In the remaining two sets, Nos. 281 and 2138, the result is self-contradictory, that is, in some classes (*b pr cn* in Nos. 281 and 2138) the percentage of the *crip-h* fly is higher in the later broods than in the earlier, whereas, in the other classes (*pr cn* in No. 281, *b pr* in No. 2138) the reverse is true. It seems unlikely then that the age of parents has any definite influence on the character *crip-h* of the next generation.

High temperature

Of the two bottles prepared in the manner described above, one was put into the incubator in a temperature of 29°–30°C. while the other was left in the ordinary temperature, 25°C. High temperature accelerates the development of the larvae and shortens the larval period more or less, sometimes by two days; so that the counting of the fly was finished on the eighth day from the day the first fly appeared in the bottle. The result of this experiment is shown in table 2. Of all the eight sets making up each of the two bottles, seven show that high temperature produce more *crip-h* flies—the difference being 35 to 60 per cent of the percentage of *crip-h* flies reared in 25°C. Only one set, No. 246, appears to show a contrary result. But here the brood of the flies in the 25°C. bottle was much smaller than that of the higher temperature, and as will be shown later, the percentage of the *crip-h* flies varies according to the size of the brood—the larger the brood, the lower the percentage—hence, one can not say that the result of this set is really contradictory to the general result.

Low temperature

A similar experiment was carried out for low temperature. The ordinary ice-box was used to get a low temperature, which fluctuated between 8° to 15°C. Such temperature retarded the development of the larvae considerably, and the F1 flies were counted for about a month after the first fly had appeared. Most of the cultures produced less than one hundred flies during this time

Table 2.

Effect of high temperature on the character *crip-h*.

Culture No.	P	F_1 Brood No.	F_1 Total number	F_1 Percentage of *crip-h*
177	*crip-h*/*crip-h* × *crip-h*/*crip-h*	1*	27	29·6
		2	58	19·0
174	〃 〃	1*	290	20·0
		2	212	14·1
199	〃 〃	1	256	4·7
		2*	320	14·4
246	*crip-h*/*crip-h* × *S*/*scrip-h* *D*/*d*	1*	468	*D* 28·6, *d* 38·6; *SD* 0·0, *S* 0·9
		2	135	*D* 41·6, *d* 40·0; *SD* 0·0, *S* 0·0
247	〃 〃	1*	412	*D* 21·1, *d* 36·7; *SD* 0·0, *S* 0·0
		2	379	*D* 15·1, *d* 20·0; *SD* 0·0, *S* 0·0
248	*crip-h*/*crip-h* × *crip-h*/	1*	394	*bprcn* 43·4; + 0·0
		2	105	*bprcn* 32·1; + 0·0
249	〃 〃	1*	366	*bprcn* 33·3; + 1·1
		2	300	*bprcn* 23·3; + 0·0
251	*crip-h*/*crip-h* × *S*/*s-crip-h* *D*/*d*	1*	290	*D* 31·3, *d* 42·0; *SD* 0·0, *S* 0·0
		2	303	*D* 29·0, *d* 23·3; *SD* 0·0, *S* 0·0

* Brood reared in high-temperature incubator·

S—Flies with second-chromosome dominant character *Star;* +—Wild-type flies

Of the two bottles which contained two successive broods reared from the same pair of flies, usually the first bottle, but occasionally the second bottle, was kept in the ice-box. In all, ten sets of such pairs of bottles were prepared.

As shown in table 3a, the bottles kept in the ice-box yielded a relatively higher percentage of *crip-h* flies than the corresponding bottle that had been left in the 25°.C incubator. The percentage of such flies in the former bottle is in most cases 65 to 75 per cent, whereas, in the latter it is usually 20 to 30 per cent. Thus, it is clear hat, even if due allowance is made for the difference in the size of the broods of the cold and ordinary

TAABLE 3 a.

Effect of low temperature on character *crip-h*.

Culture No.	P	F_1 Brood No.	F_1 Total number	F_1 Persentage of Crip h.
244	$\frac{crip\text{-}h}{crip\text{-}h} \times \frac{crip\text{-}h}{crip\text{-}h}$	1 2*	377 6	35·8 100·0
273	$\frac{crip\text{-}h}{crip\text{-}h} \times \frac{crip\text{-}h}{}$	1* 2	165 178	71·7 27·5
230	$\frac{crip\text{-}h}{crip\text{-}h} \times \frac{crip\text{-}h}{crip\text{-}h} \frac{d}{D}$	1 2*	409 37	D 21·8, d 15·7 D 66·7, d 100·0
285	$\frac{crip\text{-}h}{crip\text{-}h} \times \frac{crip\text{-}h}{crpi\text{-}h}$	1* 2	142 213	76·8 29·6
286	" "	1* 2 3	99 200 119	69·7 27·0 26·9
288	" "	1* 2	45 211	75·6 19·9
298	" "	1* 2	52 270	75·0 21·5
309	" "	1* 2	74 152	68·9 28·2
294	" "	1* 2	87 266	69·0 33·5
297	" "	1* 2	11 218	68·8 22·9

* Brood reared in ice-box

TABLE 3 b.

Effect of low temperature on character *crip-h* in heterozygous state.

Culture No.	P	F_1 Brood No.	F_1 Total number	F_1 Percentage of crip-h
230	$\frac{crip\text{-}h}{crip\text{-}h} \times \frac{crip\text{-}h}{} \frac{d}{D}$	1 2*	409 37	D 0·0, d 0·0 D 20·0, d 25·0
273	$\frac{crip\text{-}h}{crip\text{-}h} \times \frac{crip\text{-}h}{}$	1* 2	165 178	24·1 1·3
284	" "	1* 2	96 236	17·7 0·0
287	" "	1* 2	76 189	23·7 1·1

* Brood reared in ice-box

bottles, the difference in the percentages of *crip-h* flies from those bottles is fairly great.

Four cultures of flies heterozygous for the factor *crip-h* were reared in the same ice-box. From these there appeared 17 to 25 per cent *crip-h* flies, in all of which the abnormality was rather slight (Table 3a). A culture of *black jaunty* flies having no *crip-h* factor was reared in the same ice-box and produced no *crip-h* fly among the progeny. These experiments seem to indicate that the abnormality found in those flies reared in the ice-box is due to the presence of the factor for *crip-h*.

State of food

There is a more or less remarkable difference in the percentage of *crip-h* flies between the earlier and later counts of the same bottle, the earlier counts usually countaining more *crip-h* flies than the later counts. In table 4 the percentage of *crip-h* flies of the first four days and the same of the last five days are shown for comparison. In most of the cultures we find that there are more *crip-h* flies in the earlier count than in the later count. This difference is as a rule greater, the larger the brood.

This difference is without doubt not due to the larval or pupal period of the *crip-h* fly being shorter than that of the normal fly. Because, if the parents are transferred to a new bottle, the same change is repeated in this bottle; and the percentage of the abnormal flies from this bottle as a whole scarcely shows any difference from the percentage of the first bottle.

Thus the cause of the change is evidently not anything "internal," but is "external," and probably connected with the state of food which undergoes considerable change in the course of culture. Further consideration on this question will be deferred to the chapter in which the cause of the production of *crip-m* flies is discussed.

Inheritance of Crip-h

Crip-h, a recessive character, may be concealed in the homozygous state.

TABLE 4.

Comparison of the percentages of *crip-h* flies between the earlier and later counts of the same culture.

Culture No.	*Total number*	*Percentage of crip-h*			
		Earlier count		*Later count*	
		crip-h	*crip-m*	*crip-h*	*crip-m*
209	320	10·5	—	18·0	—
216	621	16·7	—	7·3	—
217	610	13·2	—	12·3	—
219	505	11·4	—	11·4	—
222	548	14·2	—	8·8	—
229	250	12·6	—	8·4	—
234	361	14·2	—	16·3	—
235	333	13·2	—	5·5	—
237	248	24·6	—	30·5	—
239	334	17·0	—	13·8	—
244	377	49·5	—	17·4	—
246	468	{*D* 37·3 {*d* 51·7	—	{*D* 19·2 {*d* 25·0	—
247	412	{*D* 31·6 {*d* 37·2	—	{*D* 10·5 {*d* 35·9	—
248	394	48·5	—	32·1	—
249	366	39·2	—	28·0	—
251	290	{*D* 36·9 {*d* 52·2	—	{*D* 22·6 {*d* 21·7	—
252	278	{*D* 19·4 {*d* 34·8	—	{*D* 12·5 {*d* 14·5	—
253	434	14·2	—	7·1	—
254	398	37·5	—	21·4	—
255	267	{*D* 37·0 {*d* 23·8	—	{*D* 30·4 {*d* 19·0	—
256	339	20·0	—	14·7	—
257	135	{*D* 40·0 {*d* 51·0	—	{*D* 44·4 {*d* 20·0	—
258	105	35·5	—	28·0	—
259	300	20·7	—	23·2	—
260	348	32·1	—	18·1	—
261	379	{*D* 17·9 {*d* 19·6	—	{*D* 12·0 {*d* 20·5	—
262	404	23·6	—	10·3	—
297	218	25·8	—	20·7	—
298	268	29·8	—	14·3	—
2100	119	36·2	—	14·0	—

TABLE 4. (Continud)

Culture No.	*Total number*	*Percentage of Crip-h*			
		Earlier count		*Later count*	
		crip-h	*crip-m*	*crip-h*	*crip-m*
2105	362	27·0	—	9·1	1·1
2132	164	22·6	—	5·0	1·3
2134	103	3·8	—	5·9	5·9
2135	173	7·3	—	5·2	3·9
2140	217	2·1	—	15·7	3·3
2141	273	9·0	—	3·6	2·9
2143	260	5·8	—	3·3	8·2
2144	185	3·3	2·2	3·2	14·9
2146	221	2·24	—	5·2	2·1
2147	236	10·2	—	3·7	1·9
2148	274	15·5	—	2·3	1·5
2149	275	17·5	—	6·8	1·5
2152	260	8·0	—	1·4	2·1
2154	239	6·7	—	1·8	3·7
2155	222	4·5	—	4·5	2·7
2162	190	6·6	—	7·0	10·5
2164	256	16·4	—	8·6	2·9
2165	283	34·4	—	13·0	8·1
2166	258	38·5	—	10·0	9·1
2170	204	18·2	—	12·4	1·0
2171	326	21·9	—	8·4	2·8
2189	357	36·5	—	12·7	2·0
2190	283	24·5	—	22·8	2·2
2191	377	33·1	—	10·0	0·5
2192	262	33·8	0·6	16·9	2·9
2193	327	33·1	—	16·8	2·0
2194	99	37·7	—	19·5	—
2195	401	24·5	—	15·7	4·6
2196	328	38·6	—	14·0	1·9
2197	351	36·0	—	19·2	5·3
2206	223	11·9	1.5	4·5	—
2207	186	15·2	—	16·1	4·6
2208	335	28·8	—	17·0	5·3
2217	352	8·0	—	6·5	1·4
2219	355	16·2	—	11·7	2·4
2220	322	8·6	—	8·1	1·5
2222	299	17·4	0·6*	8·0	0·7

* Flies lacking a front leg.

When a *crip-h* fly is crossed with a wild fly or a fly of any unrelated strain, most of the F1 individuals produced are normal, and very few are *crippled* (Table 5). Sometimes no abnormal individual is found among

TABLE 5.

Cross between *crip-h* and wild-type fly.

Culture No.	*P*	F_1	
		Total number	*Number of crip-h*
9	*bprcn* × *bprcn crip-h*	341	1
13	〃 〃	249	2
16	〃 〃	113	1
135	*Tdy bprc px sp** × *bpr cn crip-h*	387	1
136a	〃 〃	241	0
136b	〃 〃	205	1
137	*ru h st pp ss es*** × *bprcn crip-h*	249	1
143	*Tdy brp cpxsp* × *bprcn crip-h*	212	0
145	〃 〃	87	0
146	〃 〃	117	0
233	〃 〃	328	1

* Fly with combination of second-chromosome mutant characters: *dumpy (Tdy)*, *black (b)*, *purple (pr)*, *curved (c)*, *plexus (px)* and *speck (sp)*.

**Fly with combination of third chromosome mutant characters: *roughoid (ru)*, *hairy (h)*, *scarlet (st,) peach (pp)*, *spineless (ss)* and *sooty (es)*

the two or three hundred flies which make up the entire brood. If there are any, the number is usually only one or two. The percentage of *crip-h* flies in such a cross, therefore, is always lower than one and sometimes even zero. In other words, the factor for *crip-h* usually behaves as recessive, but can be slightly dominant in some exceptional cases.

In F1 there appear some *crip-h* flies which are homologous for the factor. The number of those flies, however, is variable and always smaller than the number expected on the basis of a simple recessive factor, since flies which should be crippled genetically, may frequently not be crippled at all. But if one breeds two such flies together, he gets quite as many crippled flies in the next generation as when two crippled flies are mated together.

The cross between two flies homozygous for the factor for *crippled* gives usually 10 to 30 per cent of abnormal flies, more rarely 5 to 10 per cent or 30 to 40 per cent the percentage never being as high as 50, unless the culture is bred in low or high temperature (Tables 1–4).

No special type inherited

Evidently no special type of the abnormality is inherited. Not only do *crip-h* flies of various types come out of one and the same bottle, but a somatically normal pair having the factor for *crip-h* in the homozygous state, may produce a number of very abnormal flies, just as much as a somatically very abnormal pair do. To examine this fact more in detail, I selected as parents, from one and the same brood, three pairs of flies which were different in the grade of abnormality, namely, normal, slightly crippled and highly crippled, and compared the percentages of the crippled flies among the F1 progeny. The result is shown in table 6a. Further, from each of these three cultures, three pairs of flies were selected again in the same manner as above, and were bred together, and Nos. 11641–11663 of table 6b were obtained. Thus, No. 11641,

TABLE 6 a.

Comparison of the results of mating of normal, slightly *crip-h*, and highly *crip-h* individuals.

Culture No	*P*	F_1				
		Total number	*Percentage of crippled*	*Percentage of slightly crip-h*	*Percentage of highly crip-h*	*Percentage of crip-m*
1164	*Normal*	256	14·5	8·2	5·5	1·2
1165	*Slightly crip-h*	283	26·9	15·9	9·2	3·5
1166	*Highly crip-h*	238	33·2	13·9	14·7	4·6

TABLE 6 b.

Comparison of the results of mating of normal, slightly *crip-h* and highly *crip-h* indivbuals of F_1 in table 6 a.

Culture No.	F_1	F_1				
		Total number	Percentage of crippled	Percentage of slightly crip-h	Percentage of highly crip-h	Percentage of crip-m
11641	*Normal*	357	27·5	15·1	11·5	0·8
11642	*Slightly crip-h*	283	23·7	14·1	9·5	1·1
11643	*Highly crip-h*	377	19·9	11·9	7·7	0·3
11651	*Normal*	262	32·7	16·8	14·1	1·5
11652	*Slightly crip-h*	327	26·3	13·5	12·2	0·9
11653	*Highly crip-h*	99	29·3	15·2	14·1	0·0
11661	*Normal*	401	21·9	11·9	8·2	2·2
11662	*Slightly crip-h*	328	27·4	11·0	15·9	0·9
11663	*Highly crip-h*	351	30·8	15·4	13·4	2·3

for instance, are offspring of two normal individuals from the F_1 generation of No. 1164 whose parents were also normal, while No. 11663 are the progeny of two highly crippled individuals among No. 1166 which came from a pair of likewise highly crippled flies. These two cultures, Nos. 11641, and 11663, accordingly, are the results of a sort of selective breeding for two successive generations of normal individuals on 'he one hand and highly abnormal individuals on the other. As shown in that table, the difference in the percentage of *crip-h* flies between those two cultures is small and insignificant. The other cultures in the same table show similar results.

Right or left determined at random.

Also there seems to be no fixed rule according to which it is determined which hind leg (right or left) is to become abnormal, this being determined apparently at random. In table 7 the head line indicates the side of the leg of the parents which is crippled: N—both legs normal, L-left leg crippled, R-right leg crippled, B-both legs crippled, while the other lines below show the numbers of the offspring in which the right, or the left, leg, or both legs are crippled. The totals at the bottom of

TABLE 7.

Correlation between parents and offspring of the side of crippled leg.

N—normal, L—left leg crippled, R—right leg crippled, B—both legs crippled.

Culture No / P / F_1	N♀×N♂	N♀×L♂	N♀×B♂	B♀×N♂	R♀×R♂	R♀×L♂	L♀×R♂	R♀×B♂	B♀×R♂	L♀×L♂	B♀×B♂
	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B
120	—	—	—	—	—	—	—	—	—	1 3 0	—
127	—	—	—	—	—	—	1 5 0	—	—	—	—
128	—	—	—	—	0 3 1	—	—	—	—	—	—
129	—	—	—	—	—	—	7 7 0	—	—	—	—
130	—	—	—	—	—	—	—	—	—	3 6 0	—
131	—	—	—	—	—	—	—	—	—	6 11 0	—
134	—	—	8 8 1	—	—	—	—	—	—	—	—
140	—	—	—	—	—	4 10 0	—	—	—	—	—
142	—	—	—	3 9 1	—	—	—	—	—	—	—
141	—	24 23 1	—	—	—	—	—	—	—	—	—
144	—	—	—	—	—	10 14 1	—	—	—	—	—
147	—	20 19 4	—	—	—	—	—	—	—	—	—
151	—	—	—	—	—	12 21 0	—	—	—	—	—
153	—	—	—	—	—	4 5 1	—	—	—	—	—
159	—	—	—	—	—	—	—	—	—	12 10 0	—
165	—	—	—	—	—	11 6 1	—	—	—	—	—
185	—	—	—	—	36 36 4	—	—	—	—	—	—

TABLE 7 (Continued)

P / F₁ / Culture No.	N♀×N♂	N♀×L♂	N♀×B♂	B♀×N♂	R♀×R♂	R♀×L♂	L♀×R♂	R♀×B♂	B♀×R♂	L♀×L♂	B♀×B♂
	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B	R L B
1103	—	—	—	—	34 36 33	—	—	—	—	—	—
1108	—	—	—	—	21 27 8	—	—	—	—	—	—
2142	—	—	—	—	—	12 12 1	—	—	—	—	—
2144	—	—	—	—	—	—	—	—	—	5 13 4	—
2145	—	—	—	—	—	9 15 0	—	—	—	—	—
2147	—	—	—	—	10 7 1	—	—	—	—	—	—
2153	4 5 0	—	—	—	—	—	—	—	—	—	—
2156	—	—	—	—	—	—	18 15 2	—	—	—	—
2162	—	—	—	—	—	—	—	—	—	7 14 4	—
2164	24 12 1	—	—	—	—	—	—	—	—	—	—
2165	—	—	—	—	—	35 36 5	—	—	—	—	—
2166	—	—	—	—	—	—	—	28 44 7	—	—	—
2167	—	—	—	—	—	—	28 19 5	—	—	—	—
2170	—	—	—	—	—	—	—	—	—	15 15 1	—
2171	—	—	—	—	27 26 2	—	—	—	—	—	—
2172	—	—	—	—	25 17 3	—	—	—	—	—	—
2173	—	—	—	—	—	—	—	—	—	5 5 1	—
2174	—	—	—	—	—	—	16 19 5	—	—	—	—
2175	—	—	—	—	22 23 0	—	—	—	—	—	—

TABLE 7 (Continued)

Culture N. \ P / F_1	N♀×N♂	N♀×L♂	N♀×B♂	B♀×N♂	R♀×R♂	R♀×L♂	L♀×R♂	R♀×B♂	B♀×R♂	L♀×L♂	B♀×B♂
	RLB	RLB	RLB	RLB	RLB	RLB	RLB	RLB	RLB	RLB	RLB
2176	18 9 1	—	—	—	—	—	—	—	—	—	—
2177	—	—	—	—	17 16 1	—	—	—	—	—	—
2179	—	—	—	—	29 11 9	—	—	—	—	—	—
2181	—	—	—	—	—	—	—	—	11 7 0	—	—
2182	—	—	—	—	—	—	45 21 8	—	—	—	—
2183	22 23 1	—	—	—	—	—	—	—	—	—	—
2189	42 34 22	—	—	—	—	—	—	—	—	—	—
2190	—	—	—	—	—	—	—	—	—	39 32 5	—
2191	—	—	—	—	—	—	—	—	34 35 6	—	—
2192	43 32 9	—	—	—	—	—	—	—	—	—	—
2193	—	—	—	—	46 29 9	—	—	—	—	—	—
2194	—	—	—	—	—	—	—	—	—	—	14 11 4
2195	41 42 5	—	—	—	—	—	—	—	—	—	—
2196	—	—	—	—	—	—	—	—	—	38 49 12	—
2197	42 53 11	—	—	—	—	—	—	—	—	—	—
Total	236 210 50	44 42 5	8 8 7	3 9 1	258 231 62	97 119 9	115 86 20	28 44 7	45 42 6	122 149 27	14 11 4

the table seem to show that there can hardly be any rule according to which the side of the leg to become abnormal is to be determined. It might be noticed, however, that, when both parents have a crippled right leg, the offspring tend to have a crippled leg on the right side a little more frequently than on the left side; and the same in principle seems to be true when both parents have a crippled left leg—in short, the offspring tend to have the deformity on the same side as the parents. But, the preponderance of the same side over the opposite side seems to be too slight to say anything further positively on the basis of it. Perhaps this is a thing altogether accidental.

Locus of crip-h factor in chromosome

Some *black purple cinnabar crip-h* flies were crosseb with *Star Dichaete* flies and several F1 *Star Dichaete* males were backcrossed to *black purple cinnabar crip-h* females. The result was that none of the *crip-h* flies that appeared in the next generation was *Star*, except a few *Star crip-h* flies which were tested and found to be heterozygous for the factor for *crip-h*. There were, on the other hand, practically as many *Dichaete crip-h* flies as there were not-*Dichaete crip-h* flies (Table 8). It is clear then that the factor for *crip-h* is in the second chromosome the same as *Star*. This fact was also proved by mating the *black purple cinnabar crip-h* fly with the wild fly and backcrossing the F1 fly with the *black purple cinnabar crip-h* fly. When the F1 male was backcrossed with the *black purple cinnabar crip-h* female, all the *crip-h* flies that appeared in the next generation were also *black purple cinnabar*, except a few heterozygotic wild-type *crippled* individuals. When, on the other hand, the female was backcrossed, most of the *crip-h* flies that appeared in the F2 generation were also *black purple cinnabar*; but there were some *purple cinnabar* (not-*black*) *crip-h* flies among them (Table 9).

The fact that the *purple cinnabar* (not-*black*) fly may be *crippled*, suggests that the factor for *crip-h* is lccated to the "right" of *black*. Accordingly, ten *black* (not-*purple* not-*cinnabar*) flies and more than eight *purple cinnabar* (not-*black*) flies that had come from the crossing-over

TABLE 8.

Backcrossing of heterozygous *Star-Dichaete* or *Dichaete* *crip-h* male with homozygous *crip-h* female.

Culture No.	P	F1 Total	Percentage of crip-h SD	Sd	sD	sd
246	$\frac{crip\text{-}h}{crip\text{-}h}$ ♀ × $\frac{crip\text{-}h}{S}$ $\frac{D}{d}$ ♂	468	—	0·9	28·6	38·6
247	″ ″ ″	412	—	—	21·1	36·7
251	″ ″ ″	290	—	—	31·3	42·0
252	″ ″ ″	278	—	—	18·2	29·5
255	″ ″ ″	267	—	—	29·0	23·3
257	″ ″ ″	135	—	—	41·6	40·0
261	″ ″ ″	379	—	—	15·1	20·0
267	″ ″ ″	303	1·3	—	23·4	41·8
230	$\frac{crip\text{-}h}{crip\text{-}h}$ ♀ × $\frac{crip\text{-}h}{crip\text{-}h}$ $\frac{D}{d}$ ♂	409	—	—	21·8	17·1
231	″ ″ ″	162	—	—	10·9	27·0
230′	″ ″ ″	340	—	—	29·6	21·7
203	″ ″ ″	96	—	—	31·0	38·9
232	$\frac{crip\text{-}h}{crip\text{-}h}$ ♀ × $\frac{}{Scrip\text{-}h}$ $\frac{D}{d}$ ♂	355	10·2	15·7	—	—
203	″ ″ ″	58	18·8	29·4	—	—
240	″ ″ ″	258	27·5	21·2	—	—

between the loci *black* and *purple* were tested for the factor for *crip-h*. It was found that the *black* (not-*purple* not-*cinnabar*) flies were never homozygous for the factor for *crip-h*, while the *purple cinnabar* (not-*black*) flies were homozygous for the factor without exception (Table 10). These experiments have shown that the factor for *crip-h* probably does not lie between the loci *black* and *purple*, but is located between the loci *purple* and *cinnabar*. Further, ten *black purple* (not-*cinnabar*) flies and seven *cinnabar* (not-*black* not-*purple*) flies that had come from the crossing-over between the loci *purple* and *cinnabar* were tested. It was found that nine of the ten *black purple* (not-*cinnabar*) flies and five of the seven *cinnabar* (not-*black* not-*purple*) flies were homologous for the factor in question. Also, two *black cinnabar* flies which had come from the double

TABLE 9.

Backcrossing of heteozygous *black purple cinnabar cirp-h* with homozygous *black purple cinnabar crip h..*

Culture No.		F_1						
		Total number	*Percentage of crip-h*					
			+	*bprcn*	*b*	*prcn*	*bpr*	*bcn*
248*	*bprcn crip-h* / *bprcn crip-h* ♀ × *bprcn crip-h* / — ♂	394	0·0	43·4	—	—	—	—
249*	〃 〃	366	1·1	33·7	—	—	—	—
248a	〃 〃	105	0·0	32·1	—	—	—	—
249a	〃 〃	300	0·0	23·3	—	—	—	—
{213 239	*bprcn crip-h* / — ♀ × *bprcn crip-h* / *bprcn crip-h* ♂	983	0·0	13·7	0·0	0·0	0·0	0·0
216	〃 〃	621	0·0	13·8	0·0	12·0	0·0	0·0
{219 235	〃 〃	808	0·0	10·7	0·0	4·2	0·0	33·3
{222 234 237	〃 〃	1157	0·0	14·5	4·1	3·0	0·0	0·0

* Broods reared ni high temperature.

crossing-over were tested, and one of them was found to have the factor in a homozygous state (Table 10). These experiments have shown that the factor for *crip-h* is located between the loci *purple* and *cinnabar*, which are known to be at about 54·5 and 57·5 respectively (BRIDGES and MORGAN, '19; CLAUSEN, '24; MORGAN, BRIDGES and STURTEVANT, '25).

Hairless—a modifying factor for crip-h?

A *Dichaete Hairless* fly was crossed with a *crip-h* fly, and five of the heterozygous *Dichaete Hairless* daughters were backcrossed with the *crip-h* males. As shown in Table 11, in all of the five cultures more *crip-h* individual were found among the *Hairless* flies than among not-*Hairless* flies. Thus, the factor for *Hairless* seems to have a tendency to make flies crippled which should otherwise be normal. The flies heterozyous for the factor for *crip-h* are not made abnormal by the presence of the factor for *Hairless* and no *crip-h* individual was found among the not-*black* not-*purple* not-*cinnabar* *Hairless* flies in those cultures.

TABLE 10.

Experiments fcr locating *crip-h* factor in ohrmosome.

Culture No.	P♀		P♂		F1								
	Hind leg	Combination of factors	Hind leg	Combination of factors	Total	Percentage cf crip-h							
						+	b	prcn	bpr	cn	bcn	pr	pbrcn
241	c	bprcn / prcn	N	— / bprcn	132	0·0	—	9·4	—	—	—	—	11·1
253	N	bprcn / bpr	N	bprcn / bprcn	434	—	—	—	0·0	—	—	—	11·2
254	N	b / bprcn	N	b / bprcn	389	—	—	—	0·0	—	0·0	—	30·6
256	N	bcn / bprcn	N	b / bprcn	339	—	—	—	—	—	0·0	—	18·2
260	N	b / bprcn	N	b / bprcn	348	—	1·1	—	0·0	—	—	—	28·4
262	N	cn / bprcn	c	bprcn / bprcn	404	—	—	10·0	—	1·0	0·0	—	15·6
263	c	cn / bprcn	N	prcn / bprcn	302	—	—	11·4	—	10·1	—	—	12·9
265	N	cn / bprcn	c	bprcn / bprcn	273	—	—	0·0	—	11·0	7·1	—	15·6

TABLE 10 (Continued)

Culture No.	P♀		P♂		F_1								
	Hind leg	Combination of factors	Hind leg	Combination of factors	Total	Percentage of crip-h							
						+	b	prcn	bpr	cn	bcn	pr	bprcn
268	c	b/bprcn	c	bpucn/bprcn	326	—	0·0	—	0·0	—	0·0	—	16·3
269	N	prcn/bprcn	N	prcn/bprcn	246	—	—	12·3	—	—	—	—	11·8
270	N	bpr/bprcn	c	bprcn/bprcn	358	—	—	—	12·7	—	—	—	18·6
271	N	b/bprcn	c	bprcn/bprcn	408	—	0·0	—	0·0	—	0·0	—	20·1
277	N	b/bprcn	N	cn/bprcn	388	0·0	0·0	—	0·0	2·2	—	—	7·0
281	N	bprcn/bprcn	c	prcn/bprcn	137	—	—	47·4	—	—	—	—	40·7
282	c	bpr/bprcn	c	bpr/bprcn	320	—	—	—	67·3	—	—	—	51·0
287	c	bprcn/bprcn	N	b/b	189	—	1·1	—	—	—	—	—	—
289	c	bprcn/bprcn	c	cn/bprcn	213	—	—	—	—	28·0	—	—	31·1
288	c	cn/bprcn	c	cn/bprcn	211	—	—	14·1	—	21·6	—	—	14·1

TABLE 10 (Continued)

Culture No.	P♀ Hind leg	P♀ Combination of factors	P♂ Hind leg	P♂ Combination of factors	F1 Total	Percentage of crip-h +	b	prcn	bpr	cn	bcn	pr	bprcn
295	N	bpr/bprcn	c	bprcn/bprcn	266	—	—	—	34·8*	—	—	—	32·0*
296	c	prcn/bprcn	c	prcn/bprcn	102	—	—	47·1	—	—	—	—	53·1
2117	N	bpr/bprcn	c	bprcn/bprcn	56	—	—	—	58·8	—	—	—	40·9
{2134, 2152}	N	bpr/bpr	N	bpr/bprcn	363	—	—	—	7·8*	—	—	—	—
2139	c	bpr/bprcn	c	bpr/bprcn	220	—	—	—	6·3*	—	—	—	13·2*
{213, 239}	N	/bprcn	c	bprcn/bprcn	983	0·0	0·0	0·0	0·0	0·0	—	—	13·7
216	N	/bprcn	N	bprcn/bprcn	621	0·0	0·0	12·0	0·0	0·0	—	—	13·8
{219, 235}	N	/bprcn	c	bprcn/bprcn	838	0·0	0·0	4·2	0·0	33·3	—	—	10·7
{222, 234, 237}	N	/bprcn	c	bprcn/bprcn	1157	0·0	4·1	3·0	0·0	0·0	0·0	—	14·5
229	c	bcn/bprcn	c	prcn/bprcn	578	—	—	10·2	—	8·8	16·2	—	16·0

N—*Normal*, *c*—*rippled*. * a few *crip-m* individuals included.

TABLE 11.

Backcrossing of heterozygous *Dchaete-Hairless crip-h* male with homozygous *crip-h* female.

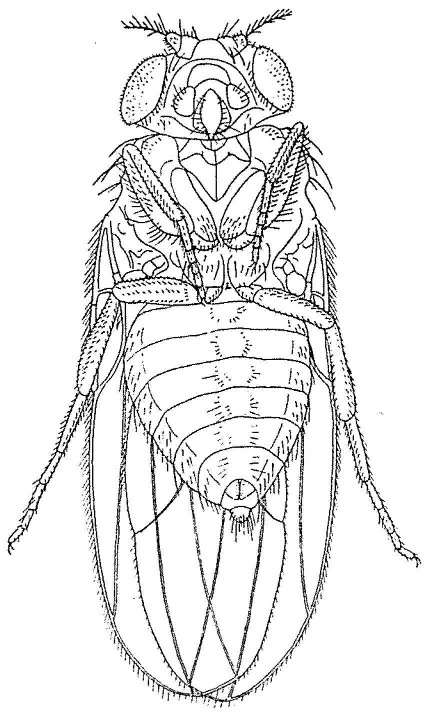
Culture No	P	F_1			
		Percentage of crip-h			
		DH	dH	Dh	dh
2107	$\frac{crip\text{-}h}{crip\text{-}h} \frac{DH}{} \times \frac{crip\text{-}h}{crip\text{-}h}$	38·1	50·0	12·9	16·4
2108	〃 〃 〃	27·8	20·8	12·0	19·0
2113	〃 〃 〃	27·6	26·0	9·5	13·7
2114	〃 〃 〃	42·9	40·9	22·7	19·2
2115	〃 〃 〃	30·6	11·0	15·0	6·0

CRIP-M

Origin and Description

In the course of the breeding experiments described in the preceding chapters, a somewhat different kind of crippled flies began to appear in some of the cultures. Such flies were first found in a certain particular strain, but appeared later in a few other strains that were somewhat remotely related to it and also to one another. In this particular kind of the *crippled*, the leg that becomes abnormal is one of the middle pair instead of the hind pair. Moreover, the abnormality belongs to a category different from the abnormality of the hind leg. The case met with most commonly, is that the leg is entirely missing. More rarely, it is represented only by the coxa, or by the coxa and trochanter, with or without a small vestige of some of the more distal segments (Pl. XVIII, figs. 1–5). Sometimes, the leg is smaller in size than the normal leg, but quite normal in proportion of segments (fig. 7). In the majority of these cases only one of the middle legs is abnormal, but rare cases are found in which both of them are missing and the fly is four-legged (Text-figure).

Reduplication of Middle Leg



In these *crip-m* flies the pleura also shows abnormality in some way or other. In the flies lacking one of the middle legs a depression usually occurs at the part of the pleura where the leg should be. This depression may be so large as to occupy the position of the sternopleural bristles which are also missing. In the flies having the middle leg smaller than normal, on the other hand, the pleura often shows a sign of doubling, as indicated by the presence of another set of sternopleural bristles beside the ordinary set (figs. 7 and 8, *b*). In such flies the part between the two sets of bristles commonly carries a rudiment of another leg. This rudiment, as a rule, is very small and imperfect, consisting of only one or a few segments (figs. 5–8); but rarely is it fairly large and quite normal in proportion of segments. There are even instances where two practically perfect middle legs occur side by side (fig. 9). There are also other instances where not a whole leg, but a part of it, is reduplicated (Pls. XVIII & XIX).

It is necessary, in all cases of reduplication of the leg, to determine whether the supernumerary limb belongs to the right or to the left side. This is not difficult if such a limb has the femoral or the tibial segment. In the femur the number of the rows of hairs is more on the external (anterior) side than on the internal (posterior) side, while in the tibia two long bristles occur near the distal end, one on the externo-dorsal side and the other on the interno-ventral side. By these criteria it is easy to tell whether the given femur or tibia is of the right or the left side. But when only the tarsus is reduplicated, it is practically impossible to determine to which side it belongs. In the diagram attached to each figure of Pls. XVIII–XX, is shown the relative situation of the parts reduplicated, as well as the side to which those parts belong; the limbs are represented in transverse section, the right limb as having a longer spur on the right side, and the left limb on the left side.

Pl. XVIII, fig. 5. Left leg; fig. 6, right leg: both have much dwindled and consist of a few segments; and with a small rudiment of a supernumerary limb (l')

Fig. 7. Left leg: much reduced in size, but practically normal in proportion of segments; a small rudiment of a supernumerary limb (l') is present. Between the two limbs is found an extra set of sternopleural bristles. b - sterno-pleural bristles; b'—extra set of the same. Such an abnormality as shown in figs. 5—7 is rather common.

Fig. 8. Left leg: reduced in size, but practically normal in proportion of segments; a rudiment of a supernumerary limb consisting of three segments, occurs above the ordinary limb. Between the two limbs is found an extra set of sterno-pleural bristles (b').

Fig. 9 (Pl. XVI, fig. 8). Two complete left limbs are present one above the other; both are a little smaller than normal size, and about equal to each other; the ventral limb has the distal end of the tibia twisted.

Fig. 10. A small supernumerary left limb is placed over the normal left limb, the former being attached to the trochanter of the latter on the dorsal side; the extra limb consists of a trochanter, femur, tibia and two tarsal segments of which the femur is very short and rudimentary.

Fig. 11. Left leg: the femur is thicker than normal and compound, i. e. composed of two limbs fused longitudinally into one; the tibia and tarsus are doubled, the ventral extra branch is as large and as complete as the dorsal ordinary limb; the extra branch is a left limb.

Fig. 12. Right leg: the femur is compound, distal parts are reduplicated; the ventral supernumerary branch which is also a right limb, is as large and as complete as the dorsal normal limb.

Fig. 13 (Pl. XVI. fig, 6). A supernumerary branch representing a right limb, is placed on the dorsal side of a normal right leg. The branch is of almost the same length and thickness as the original limb.

Fig. 14 (Pl. XVI, fig. 9). The femur is compound, and terminated in two limbs both of the left side; the dorsal supernumerary limb is half as thick as the ventral ordinary limb, and composed of a tibia and four proximal tarsal segments.

Fig. 15. Left leg: the basal part of the femur is compound, with a supernumerary branch inserted on the ventral side near the base; the branch, which is probably another left limb, is composed of a very short femur and a longer tibia.

Fig. 16. Left leg: the tibia is compound, with two supernumerary tarsal segments attached to the distal end of the tibia on the dorsal side of the ordinary tarsus.

Fig. 17. Right leg: three supernumerary tarsal segments are attached to the distal end of the tibia on the dorsal side of the ordinary tarsus.

Fig. 18. Right leg: the tibia is compound; the first tarsal segment is divided by a horizontal plane into two branches one overhanging the other the dorsal branch is compound, and the terminal tarsal segment is divided by a vertical plane into two halves attached to each other by the ventrolateral sides; the tarsal segments of the ventral branch are normal in shape and size.

Pl. XIX, fig. 1 (Pl. XVI, fig. 1). Right leg, the femur is divided at the base by a vertical plane into two branches subequal in size, of which the anterior and extra branch, a left limb, is curved sharply at the middle of the tibia.

Fig. 2. Left leg: the femur is divided at the base by a vertical plane into two branches subequal in size; the anterior extra limb, a right limb, has the femur and tibia shortened.

Fig. 3. Left leg (Pl. XVI, fig. 2): the femur is inflated and much

deformed; the distal half of the tibia is reduplicated; the anterior extra limb, a right limb, is slightly smaller than the posterior normal limb.

Fig. 4. Left leg: the femur is divided at the base by a vertical plane into two subequal branches, the anterior supernumerary limb, a right limb, is curved near the middle and folded up. Such cases of reduplication as in figs, 1, 2 and 4 are rather commonly met with.

Fig. 5 (Pl. XVI, fig. 3). Right leg: the trochanter is divided by a horizontal plane into two subequal limbs; the anterior extra limb, also a right limb, is curved sharply near the middle of the tibia, and twisted.

Fig. 6 (Pl. XVI, fig. 7). The trochanter is divided by a vertical plane; the anterior extra limb has the femur much deformed and shortened, the tibia thickend, shortened, and compound, and the tarsus subdivided at the first segment by a vertical plane, into two secondary tarsi subequal in size and facing each other with the antero-dorsal sides.

Fig. 7. Right leg: an extra leg is placed antero-dorsal to the ordinary leg; both the legs are complete, but shortened and much twisted; the anterior leg, probably a right leg, is with all the tarsal segments compound, being made up of two parts fused into one by the ventral surfaces, and with only the last segments divided.

Fig. 8. Left leg: the femur is compound; the tibia and the tarsus are reduplicated; the inner supernumerary limb has the first two tarsal segments compound, and the distal three segments doubled, the plane of the two successive divisions being vertical.

Fig. 9 (Pl. XVI, fig. 5). Right leg: the first tarsal segment is divided at the base by a vertical plane; in the posterior limb the first tarsal segment is compound, and the second is subdivided at the base by a vertical plane; all the three branches are about equal in size. Owing to a secondary rotation, it is rather hard to decide the symmetrical relation of the three branches; but the above is probably the right interpretation.

Fig. 10. Left leg: the femur is compound, the tibia and tarsus are reduplicated, the plane of division being horizontal; the tibia of the dorsal limb is curved slightly; the ventral limb is compound, with the third to the fifth tarsal segments reduplicated, the plane of the secondary division being vertical.

Fig. 11 (Pl. XVI, fig. 11). Left leg: the tibia is divided by a vertical plane one-third from the distal end; the inner branch is compound and divided at the third tarsal segment, the plane of division being vertical.

Fig. 12 (Pl. XVI, fig. 10). Right leg: the trochanter is provided with a short club-shaped process directed antero-ventrally, and articulated at the base; the coxa is divided by a vertical plane into an anterior and a posterior branch; the anterior branch is compound throughout, with a very short femur and a tibia shorter and stouter than normal.

Pl. XX, fig. 1 (Pl. XVI, fig. 4). A supernumerary right leg is present on the ventral side of the normal right leg. The leg is much smaller than normal, but has all the usual segments normal in proportion, except the femur being very short. On the left side, between the ordinary leg and the supernumerary right leg, occurs a stump-like process which probably represents a supernumerary left leg.

Rules of Reduplication

From the observations on all these examples of reduplication, as well as similar examples which have not been figured, I have formulated the following rules of reduplication of the leg: —

(1). The reduplication may occur at any part of the leg.

(2). The parts contained in the branches are only those that are distal to the point of division.

(3). In all the cases of reduplication one branch or leg is in the normal position and direction.

(4). The plane of division of the leg into two primary branches may coincide with a vertical (dorso-ventral) plane, or with a horizontal (antero-posterior) plane of the leg.

(5). When the division occurs through a vertical plane, the resulting two branches are mirror images of each other, the anterior sides facing.

(6). When the division occurs through a horizontal plane, the resulting two branches are on the same side (not mirror images of each other) and one hangs over the other.

(7). Of the two primary branches, the one in the normal position undergoes no further division, while the other may do so.

(8). When a secondary division occurs in the primary branch, the plane of division is dorso-ventral, and the two secondary branches are mirror-images of each other.*

BATESON ('94, '13) has given a comprehensive review of all the cases of reduplication found in the leg of insects described previous to the time of publication of his "Materials for the Study of Variation," and has noticed that the following features are salient in all those cases:

"They (supernumerary limbs) may arise at any point on the normal limb, being found in all situations from the base to the apex. Nor are they limited as to the surface from which they spring. .... "

"With rare and dubious exceptions, the parts which are contained in these extra appendages are only those which lie peripheral to their origin" (BATESON, '13. p. 72).

These statements have been found to hold good for practically all the cases of reduplication, not only those which are mentioned in his book, but also all other similar cases described in subsequent works, including the reduplications brought about by experiments (PRZIBRAM, '21).

Further, BATESON has noticed that the supernumerary limb is in practically every case itself a reduplicated structure, and that "it is practically certain that in no case can a single, viz. an unpaired, duplicate of the normal appendage grow from the normal limb" ('13, p. 75).

And for these extra paired appendages, according to him, the following rules hold good, with certain exceptions :—

"I. The long axes of the normal appendage and of the two extra appendages are in one plane; of the two extra appendages one is therefore nearer to the axis of the normal appendage and the other is remoter from it."

"II. The nearer of the two extra appendages is in structure and position formed as the image of the normal appendage in a plane mirror placed between the normal appendage and the nearer one, at right angles

* In my former paper I gave a little different statement for this part. But this is apparently a better presentation of the facts involved.

to the plane of the three axes, and the remoter appendage is the image of the nearer in a plane mirror similarly placed between the two extra appendages" ('94, pp. 478–479).

In fact, the extra part of the reduplicated limb is in most cases compound, and thus the whole limb is a triple structure. (PRZIBRAM. '21, has given a review of all such cases known to him). However, some unmistakable cases have been described in which the whole limb is a double structure, instead of being a triple structure, consisting of two branches placed as mirror images of each other (HARRISON, '21). In *Drosophila* too, Miss HOGE ('15) has found several cases falling into this category in her "*Reduplicated leg*" strain. HARRISON ('21), accordingly, has modified Bateson's rules as to the symmetry of the reduplicated limb mentioned above as follows:—

"1. The long axes of duplex or multiplex appendages lie in one plane."

"2. Two adjacents members form in structure and position the image of each other, as reflected from a plane mirror bisecting the angle between the respective axes and perpendicular to the common plane of the two axes." (HARRISON, '21. p. 97).

Applying these rules to the cases met with here, we find that they hold good for examples such as those in Pl. XIX, figs. 1, 2, 3 and 4, in which the plane of division coincides with a vertical plane of the leg. However, this does not hold true with such instances of reduplication as in Pl. XVIII, figs. 9, 10, 11, 12 and 14, where the plane of division is horizontal, and the resulting two limbs are of the same side, of which one limb overhang the other. These instances thus form exceptions to rule 2 above.

The latter type of reduplication of the leg is apparently extremely rare; in fact I do not know if any indubitable instance of this type has ever been reported. It is true that a few examples are known, where two limbs of the same asymmetry stand in a series on the same side of the body. In all these cases, however, the two limbs are situated one behind the other; so that the reduplication here has occurred in the antero-posterior direction. An elaterid beetle with two fore legs on the right side referred to by PRZIBRAM ('10, figs. a–c), seems to be a beautiful example of this kind. Also most of the instances of the reduplicated leg of *Amblystoma* which have been described by SWETT ('24) as exceptions to BATESON'S rules, apparently belong to this category.

The examples we have before us, on the other hand, are of the two limbs or branches of the same asymmetry situated one above the other—the doubling is therefore in the dorso-ventral direction, and not in the antero-posterior direction. PRZIBRAM ('10) recognizes the rarity of the doubling of this type; he mentions: "..............konnte ich keine Fälle finden, wo die Spaltung durch horizontale Trennung der dorsalen von der ventralen Fläche entstanden wäre. Würden solche Fälle zu Regeneration führen, so müssten die Hyperregenerate übereinander, nicht nebeneinander liegen, wie es immer zutritt." (p. 414).

GOLDSCHMIDT ('21) records some interesting cases of doubling in the copulatory apparatus of some intersexual gypsy moths. The valve of either side may be doubled or tripled. If the doubling occurs, the extra valve shows the same asymmetry as the normal valve. But the extra valve is situated outside of the normal one, so that the doubling seems to have occurred in a manner somewhat different from either of the above two categories.

If any secondary reduplication occurs in the extra leg or branch in the *crip-m* fly, the plane of division is always dorso-ventral. The plane of secondary division, therefore, may be vertical to the plane of primary division, although it may be parallel to the latter, thus violating BATESON'S rule 1.

Even where both the primary and secondary divisions occur through the dorso-ventral plane, the long axes of the resulting three limbs very rarely lie in the same plane. This is due to the torsion of the limbs which very commonly occurs.

Crip-m is a character sharply distinguishable from *crip-h*; and in no cases was the discrimination difficult. In fact, as mentioned already, *crip-h* flies may sometimes have the middle leg also somewhat abnormal. This abnormality, however, never occurs without the hind leg of the same side being concomitantly abnormal. In *crip-m*, on the other hand, only the middle leg becomes abnormal, the hind leg usually remaining quite normal.

A few cases have been met with where a fore leg is missing, without any abnormality in the middle or hind leg. These belong, without doubt, to the category of *crip-m*, but with the difference that the abnormality has appeared in the fore leg, instead of the middle leg.

Crip-m and State of Food

Another feature which characterizes *crip-m* is that these flies appear only after the cuture has become old, mostly during the last few days of counting (Table 4). As mentioned already, the percentage of *crip-h* flies shows a remarkable decrease during the latter part of the counting; and this is the time when *crip-m* flies appear. Some cultures throw relatively many *crip-m* flies, as compared with other cultures. In those cultures the percentage of *crip-h* flies is usually low from the beginning. If one keeps such cultures long enough—more than one month,—he usually finds that the *crippled* flies that come out of them after that time are mostly *crip-m*. These facts suggest that one and the same cause determines both the decrease of the number of *crip-h* flies and the appearance of *crip-m* flies. And this cause is evidently environmental, and connected with the change in the state of food, as shown by the following experiments: Two successive broods of *crip-m* flies were raised from the same parents; in all six such sets of cultures were prepared. In every set the two broods showed practically the same change in the types of the *crippled* fly from *crip-h* to *crip-m*. Further, a pair of *black purple cinnabar crip-m* flies were introduced into a bottle containing a very old culture. This culture had been yielding *black purple* flies for more than ten days and most of the *crippled* flies that were appearing then were *crip-m*. Two out of ten such bottles produced some offspring of the introduced pairs. The *crippled* flies among the offspring were mostly *crip-m*, besides being *black* *purple cinnabar*.

The banana culture medium is strongly acid at the start of the cluture; then it decreases its acidity gradually, evidently owing to the larvae feeding on it, until it becomes weakly alkaline toward the end of the counting. This change is so remarkable that I presumed that it was this phenomenon that was mainly responsible for the alteration of the types of *crippled* flies from *crip-h* to *crip-m*. I accordingly neutralized to some extent some such new acid cultures with sodium bicarbonate or with ammonia water, and also acidified some old alkaline cultures with acetic acid. But it was rather hard to keep the acidity or alkalinity of the food as desired, without doing harm to the developing larvae. Anyway, these experiments were not successful, and no apparent effect of the changed environment upon the types of *crippled* flies could be seen.

Inheritance of Crip-m

When two *crip-m* flies are mated together, there appear in the F1 generation some *crip-m* flies. The number is very small, usually 5 to 8 per cent of the whole brood. The result is the same if two *crip-h*, or normal, flies having the factor for *crip-m*, are mated together.

To find the locus of the factor for *crip-m* a few *black purple cinnabar crip-m* flies were crossed with wild flies; the cross gave normal flies only in the F1 generation. Then six F1 females were backcrossed to the *black purple cinnabar crip-m* males. From each culture appeared a few *crip-m* flies, besides a number of *crip-h* flies. All of the *crip-m* flies were *black purple cinnabar*, except one *black purple* (not–*cinnabar*) and one *purple cinnabar* (not-*black*) *crip-m* individual. This result shows that the factor for the character *crip-m* lies in the second chromosome somewhere near *purple* (Table 12).

Next, five *crip-m* females were mated each with a male from the original *black purple cinnabar* stock bottle. As mentioned at the beginning of this paper, the flies from this stock may have carried the factor for *crip-h*, but there is no ground for suspecting that the factor for *crip-m*, if any special factor for this character exists, had been present in

TABLE 12.

Backcrossing of heterozygous *black purple crip-m cinnabar* female with homozygous *black purple crip-m cinnabar* male.

Culture No.	*Total*	*Normal*							*crippled*				
									crip-h		*crip-m*		
		Wild type	*bprcn*	*b*	*prcn*	*bpr*	*cn*	*bcn*	*bprcn*	*prcn*	*bprcn*	*prcn*	*bpr*
2201	348	176	126	10	9	1	2	1	21	—	2	—	—
2202	445	234	138	16	12	9	5	—	16	2	11	1	1
2203	451	218	156	14	10	4	2	—	40	3	4	—	—
2204	392	189	153	10	8	6	3	—	20	1	2	—	—
2210	424	202	180	10	6	3	1	1	19	1	1	—	—
2211	365	171	156	5	6	1	4	—	19	—	3	—	—

them. These five females all gave a few *crip-m* offspring besides a number of *crip-h* flies (Table 13). The above two experiments seem to show that the factor for *crip-m* is the same that produces *crip-h*.

It might be suspected that the absence of the middle leg and the reduplication of the same would represent entirely different characters. But this is not altogether so. In fact, I crossed flies lacking a middle leg together, or such a fly with a fly having a reduplicated middle leg,

TABLE 13.

Cross between *crip-h* from *bpcrcn* stock bottle and *crip-m*.

Culture No.	*P*	*Total*	*Normal*		*crippled*			
					crip-h		*crip-m*	
			bpr	*bprcn*	*bpr*	*bprcn*	*bpr*	*bprcn*
2216	$\frac{bprcrip\text{-}h}{bprcncrip\text{-}h} \times \frac{bprcn\,crip\text{-}m}{bprcn\,crip\text{-}m}$	412	190	177	13	21	4	7
2217	$\frac{bprcrip\text{-}h}{bprcrip\text{-}h} \times \frac{bprcn\,crip\text{-}m}{bprcn\,crip\text{-}m}$	352	324	—	26	—	2	—
2218	$\frac{bprcrip\text{-}h}{bprcncrip\text{-}h} \times \frac{bprcn\,crip\text{-}m}{bprcn\,crip\text{-}m}$	365	154	148	29	33	1	—
2219	$\frac{bprcncrip\text{-}h}{bprcncrip\text{-}h} \times \frac{bprcn\,crip\text{-}m}{bprcn\,crip\text{-}m}$	355	—	301	—	51	—	3
2220	$\frac{bprcncrip\text{-}h}{bprcncrip\text{-}h} \times \frac{bprcrip\text{-}m}{bprcrip\text{-}m}$	322	293	—	27	—	2	—

or two flies each having a reduplicated middle leg. These crosses always gave practically the same results; flies with a reduplicated middle leg may appear out of the cross between flies lacking a middle leg, and vice versa (Table 14). Moreover, there are a series of types of abnormality of the

TABLE 14.

Correlation between the abnormality of parents and that of offspring, with special reference to the abnormality of middle leg.

Culture No.	*P*				*F*₁				
	♀		♂		*Total*	*Middle leg*			*Hind leg*
	Middle leg	*Hind leg*	*Middle leg*	*Hind leg*		*absent*	*deformed*	*reduplicated*	*abnormal*
2132	*N*	*N*	*N*	*c*	164	1	—	—	23
2134	*N*	*N*	*N*	*N*	103	3	—	—	7
2135	*a*	*N*	*N*	*N*	173	3	—	—	11
2138	*d*	*N*	*a*	*N*	206	2	—	—	23
2139	*N*	*c*	*N*	*c*	220	4	—	—	16
2140	*d*	*N*	*N*	*N*	217	4	—	—	21
2141	*N*	*N*	*a*	*N*	273	4	1	—	16
2143	*a*	*N*	*a*	*N*	260	7	—	1	6
2144	*d*	*N*	*a*	*N*	185	13	—	—	9
2146	*a*	*N*	*a*	*N*	221	2	—	—	33
2147	*a*	*N*	*a*	*N*	236	2	1	—	16
2138*a*	*d*	*N*	*a*	*N*	268	1	—	1	67
2132*a*	*N*	*N*	*N*	*c*	275	—	1	1	34
2134*a*	*N*	*N*	*N*	*N*	260	2	1	—	12
2154	*d*	*N*	*N*	*N*	239	2	3	1	8
2139*a*	*N*	*c*	*N*	*c*	222	2	1	—	10
2144*a*	*d*	*N*	*a*	*N*	190	8	3	1	17
2164	*N*	*N*	*N*	*N*	256	3	—	—	34
2165	*N*	*c*	*N*	*c*	283	8	—	2	71
2166	*N*	*c*	*N*	*c*	238	8	2	—	69
2170	*N*	*c*	*N*	*c*	204	1	—	—	30
2171	*N*	*c*	*N*	*N*	326	3	—	1	52
2172	*N*	*c*	*N*	*c*	362	4	—	2	40
2174	*N*	*c*	*N*	*c*	226	1	1	—	38
2175	*a*	*c*	*N*	*c*	325	20	4	3	18
2176	*N*	*N*	*N*	*N*	251	5	1	—	22

TABLE 14 (Continued)

Culture No.	*P*				*F*$_1$				
	♀		♂		Total	Middle leg			Hind leg
	Middle leg	Hind leg	Middle leg	Hind leg		absent	deformed	reduplicated	abnormal
2177	*a*	*c*	*d*	*N*	266	5	1	2	28
2179	*a*	*N*	*r*	*N*	210	3+1*	2	—	26
2180	*r*	*N*	*r*	*N*	315	21	—	1	24
2182	*N*	*c*	*N*	*c*	341	1	1	—	31
2183	*N*	*N*	*N*	*r*	346	—	1	3	43
2186	*r*	*N*	*r*	*N*	259	1+1*	—	—	28
2189	*N*	*N*	*N*	*N*	357	2	1	—	95
2190	*N*	*c*	*N*	*c*	283	1	2	—	65
2191	*N*	*c*	*N*	*c*	377	—	—	1	74
2192	*N*	*N*	*N*	*N*	262	2	—	2	81
2193	*N*	*c*	*N*	*c*	327	3	—	—	84
2195	*N*	*N*	*N*	*N*	401	7	1	1	81
2196	*N*	*c*	*N*	*c*	328	1	—	2	87
2197	*N*	*c*	*N*	*c*	351	8	—	—	101
2198	*a*	*N*	*a*	*N*	274	8	2	1	9
2206	*a*	*N*	*a*	*N*	223	5	1	—	20
2207	*r*	*N*	*a*	*N*	186	4	—	—	29
2208	*r*	*N*	*r*	*N*	335	10	—	1*	74
2216	*r*	*N*	*N*	*N*	412	10	—	1	34
2217	*a*	*N*	*N*	*c*	352	1	1	—	26
2218	*a*	*N*	*N*	*c*	365	1	—	—	62
2219	*a*	*N*	*N*	*c*	355	1	2	—	51

N—Normal, *a*—absent, *c*—crippled (hind leg), *d*—deformed (middle leg)
* abnormality of fore leg.

middle leg, which connect the reduplication of the leg with the complete absence of the leg.

These instanees of the doubling of the leg remind one of the character "*Reduplicated leg*" worked out by Miss HOGE ('15). *Reduplicated leg*, however, is a sex-linked character and appears in any leg, but predominantly in the fore leg; whereas, the character before us is not sex-linked and appears almost exclusively in the middle leg. Moreover, her cases of reduplication, without any exception, conform well with BATESON's rules, contrary to some cases we have here.

GENERAL DISCUSSION

Crippled is a mutant character striking in various respects. First, it is a highly variable character and its manifestation depends much on external conditions. Several cases similar in this respect are known in *Drosophila*. MORGAN ('15) has found that the character called *Abnormal abdomen* is strongly marked when the larvae were given moist food, but is often suppressed entirely in flies reard with dry food. Miss HOGE ('15) has shown that the character *Reduplicated leg* appears in the highest percentage of flies when they are reared in the 10° C ice-chest; but under warmer condition the character virtually disappears. According to WARREN ('20), the mutant type of spotting on the abdomen of *Drosophila busckii* becomes recessive under high temperature, while under low temperature it becomes dominant. HYDE ('22) lastly, has confirmed that the expression of the mutant character *variable eye*, which he found in *Drosophila hydei*, depends upon environmental conditions. Cultures of this mutant, kept warm and dry, produce forms with the eyes reduced to mere specks; whereas, the cultures kept cool and moist give rise to individuals with full-sized eyes.

Second and more striking than the first, is that the variation of this character falls into two types sharply distinguished from each other, namely, *crip-h* and *crip-m*, both of which are highly variable within each type. Third, these two types change from the one to the other in accordance with the condition of food on which the larvae feed. It may be very interesting if one could identify the factor in the state of food which is responsible for this change.

The question arises as to why the *crip-m* flies were not found in the first part of the experiment, but appeared later in some particular cultures. The only plausible explanation for this seems to be the appearance of a modifying factor. It was, however, impossible for me to locate this factor, owing to the very low percentage of *crip-m* flies which appeared in each culture.

Another striking feature of this character we find in the reduplication of the leg. As mentioned already, this occurs in two different types: 1. when the plane of division falls in the dorso-ventral plane of the leg, the resulting two limbs are formed as mirror images of each other; 2. when, on the other hand, the plane is parallel with the horizontal plane of the leg, two limbs of the same asymmetry are formed one over the other.

Cases of the reduplication of the leg belonging to the former type are not at all rare especially in arthropods, and can be found in the literature rather commonly. But the latter type is quite unique. In all cases of this type it is very likely that the two limbs of the duplex leg have arisen with comparatively little influence on each other. In support of this, assumption it may be pointed out that, in most cases of reduplication of this category, the limb which can be identified as supernumerary, is connected with the ordinary limb at the point of articulation of the segments. Even where the leg is forked in the middle of the segment, the proximal part of the segment is always compound, showing that the real point of division exists probably at this end. The results of experiments performed by HARRISON ('18, '21), DETWILER ('22) and SWETT ('24, '26) on the limb-buds of *Amblystoma* show that two limbs of the same asymmentry may occasionally be produced side by side, when the bud is split into two separate halves and these develop independently with little mutual interaction. Anyway, it seems indispensable, for bringing about this sort of reduplication, to ensure the independent development of each rudiment.

As to the physiological cause of crippledness, nothing can be said, except that it is probably due to disharmony in the development of the parts of the leg. However, it is beyond any conjecture that, under certain conditions of food, the hind leg is affected, while, under different conditions, the middle leg is affected in a way entirely different from the hind leg.

SOME ADDITIONAL REMARKS

Cases of Reduplication of Fore Leg

A few cases of reduplication of the fore leg have been found. None of those individuals passed on the character to the progeny.

The fly shown in Pl. xx, Fig. 2 appeared in Dr. A. H. STURTEVANT'S culture No. 14890, from *echinus crossveinless* and 100 percent crossing-over stock which were not at all related to the present strain. The femurs of the fore legs are fused at the median line of the body. The tibia of the left leg is forked and the distal parts are doubled. The fly was a female. She was crossed with a '*Xple*' male, but no individual with a similar abnormality was found among the progeny.

Pl. xx, fig. 3. The right fore leg of a male fly found in the *black purple cinnabar crip-h* strain. The femur, tibia and first tarsal segment are compound; the second to fifth tarsal segments reduplicated, and the two branches are situated like mirror-images of each other. The progeny of this fly was not obtained.

Pl. xx. fig. 4. A female that appeared in a culture of the backcross of "*Xple*" × *crip-h* by *crip-h*. A supernumerary compound leg is inserted between the ordinary fore legs on the median line of the body. The leg consists of two limbs, right and left, fused into one from the coxa to the tibia. These segments are naturally much thicker than those of the normal leg, but much shorter in length. The tarsal segments are reduplicated; the two branches are situated like mirror-images of each other. The fly was mated with one of her brothers. No individual with an extra leg appeared among the progeny.

Factor reducing Crossing-over Value between the Loci Purple and Cinnabar

CLAUSEN ('24), after a careful study based on the characters *black jaunty purple* and *vestigial*, estimated the crossing-over value between the loci *purple* and *cinnabar* to be approximately 2. 8. In the present experiments, in which *black purple cinnabar* and *crippled* flies were used as material, the average value 1. 6 was obtained for the same; and in a few cultures the value exceeded 2 (Table 15). Thus, it is very likely that there is a factor which reduces the crossing-over value of this region in that strain. The value of the crossing-over between the loci *black* and *purple* was found to be about 5.5, not much different from the standard value 6. o.

Reversion of Factor for Purple

In a culture from the cross between two *black purple cinnabar crip-h*

TABLE 15.

Crossing-over value between *black* and *purple*, and between *purple* and *cinnabar* of *black-purple-crip-h-cinnabar* stain.

Culture No.	*P* ♀	*P* ♂	*Total number of flies*	*Crossing-over value between b and pr.*	*Crossing-over value between pr and cn*
213	/*bprcn*	*bprcn*/*bprcn*	983	4·7	0·9
216	〃	〃	621	7·9	1·1
217	/*bpr*	〃	294	4·1	—
219	/*bprcn*	〃	838	5·7	1·0
222	〃	〃	1157	5·0	1·5
262	*cn*/*bprcn*	〃	404	5·4	—
268	*b*/*bprcn*	〃	326	—	2·1
271	〃	〃	468	—	1·7
189	*bcn*/*pr*	〃	346	7·2	1·4
193	〃	〃	385	6·5	1·8
2199	/*bpr*	〃	375	6·1	—
2200	〃	*bpr*/*bpr*	384	5·0	—
2201	/*bprcn*	*bprcn*/*bprcn*	348	5·7	1·1
2202	〃	〃	445	6·9	3·4
2203	〃	〃	451	6·0	1·3
2204	〃	〃	392	4·8	2·3
2210	〃	〃	424	4·2	1·2
2211	〃	〃	653	3·0	1·4
Average				5·5	1·6

flies appeared a single female with *cinnabar*-colored eyes among the whole brood consisting of 143 flies. With this fly was mated a *purple* fly, and there came out 81 *purple*-eyed flies and 70 *red*-eyed flies in the next generation. Two females of these 70 *reds* were crossed with *black purple cinnabar crip-h* males; and many offspring of various types were obtained as shown in Table 16. These experiments show that one of the *purple* genes carried by the original fly had reverted to normal *red*. Here is little possibility of contamination, because of the following two reasons: First, as the reverted *purple* factor was found to be associated

TABLE 16.

$$\frac{b \text{ reversed } PR\ cn}{b\ pr\ cn} \times \frac{B\ pr\ CN}{B\ pr\ CN}$$

$$F_1 \left(\frac{b \text{ reversed } PR\ cn}{B\ pr\ CN} \right) \times \frac{b\,pr\,cn}{b\,pr\,cn}$$

Culture No.	*Total*	*pr*	*bcn*	*bpr*	*cn*	*b*	*prcn*
89	346	149	167	12	13	1	4
93	385	191	162	10	15	2	5
Totals	731	340	329	22	28	3	9

with the *crip-h* factor, there is no room for suspecting that the former factor had come from some unrelated strain. Second, if any recombination of the factors *black crip-h cinnabar* occurs in some culture of the heterozygous *black purple cinnabar crip-h* strain, this must result from a double crossing-over between the loci *black* and *crip-h*; and such a recombination must be very rare, if it occur at all, owing to the very short distance between the loci.

SUMMARY

(1). *Crippled* is a new mutant character which appears in the leg of *Drosophila melanogaster*.

(2). Two types may be distinguished in the character, namely, *crip-h*, appearing in the hind leg, and *crip-m*, appearing in the middle leg. In the former type some segment or segments of one of the hind

legs is shortened, broadened, straightened, crooked, or twisted. In the latter type one of the middle legs is reduplicated, dwindles, or entirely disappears.

(3). *Crippled* is a recessive character, but it may be concealed in the homozygous state. The cross between homozygous individuals gives under 25.° C usually 10 to 30 per cent *crippled* offspring, most of which are *crip-h* and a few may be *crip-m*.

(4). Higher temperature (29°—30° C) or lower temperature (8°—15°C) produces a higher percentage of *crip-h* individuals.

(5). The percentage of *crip-h* individuals in the same culture is higher in the earlier half of counting than in the later half.

(6). No special type or grade of *crip-h* is inherited.

(7). The leg (right or left) to become *crippled* seems to be determined at random.

(8). The factor for *crip-h* lies in the second chromosome between the loci *purple* and *cinnabar*.

(9). The factor for *Hairless* seems to have a tendency to make some flies *crippled* which would otherwise appear normal.

(10). *Crip-m* flies appear only near the end of the counting, after the food has become old.

(11). The decrease of the percentage of *crip-h* flies and the appearance of *crip-m* flies near the end of counting, seem to be due to the same cause connected with a certain change in the condition of the food.

(12). More than thirty individuals with a reduplicated middle leg have been found, and the rules of reduplication have been formulated on the basis of these examples.

(13). The most important of the rules of reduplication is that, in the reduplicated leg the plane of division coincides with either a vertica (dorso-ventral) or a horizontal (antero-posterior) plane of the leg, and the resulting two limbs are in the former case mirror-images of each other, while in the latter they are of the same asymmetry, and one lies over the other.

(14). The latter type of reduplication of the leg is novel, and probably has never been reported.

(15). The factor for *crip-m* is the same as the factor for *crip-h.*

(16). A few cases of the reduplication of the fore leg have been described.

(17). A factor reducing the crossing-over value between the loci *purple* and *cinnabar* probably exists in the *black-purple-crippled-cinnabar* strain.

(18). A case of the reversion of the factor for *purple* has been reported.

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EXPLANATION OF PLATES XVI—XX

Plate XVI.

Microphotographs of some of the reduplicated legs, × 60.

Fig. 1. Same leg as in Pl. XIX, fig. 1.
Fig. 2. ,, ,, ,, ,, ,, fig. 3.
Fig. 3. ,, ,, ,, ,, ,, fig. 5.
Fig. 4. ,, ,, ,, Pl. XX, fig. 1.
Fig. 5. ,, ,, ,, Pl. XIX, fig. 9.
Fig. 6. ,, ,, ,, Pl. XVIII, fig. 13.
Fig. 7. ,, ,, ,, Pl. XIX, fig. 6.
Fig. 8. ,, ,, ,, Pl. XVIII, fig. 9.
Fig. 9. ,, ,, ,, Pl. XVIII, fig. 14.
Fig. 10. ,, ,, ,, Pl. XIX, fig. 12.
Fig. 11. ,, ,, ,, ,, ,, fig. 11.

All figures in Plates XVII—XX are enlarged 50 times natural size, and were drawn by the aid of ABBE'S apparatus.

Plate XVII.

Abnormalities of hind leg (*crip-h*).

Fig. 1. Right leg; tarsus curved sharply near the joint between third and fourth segment. This is the ancestor of the whole strain of *crippled*.

Fig. 2. Right leg; tibia curved at middle.

Fig. 3. Left leg; tibia curved and slightly twisted; first and second tarsal segments twisted.

Fig. 4. Left leg; all segments from femur to last tarsal segment more or less deformed; femur and first tarsal segment deformed most of all.

Fig. 5. Left leg; tibia straightened; first and second tarsal segments slightly broadened and curved.

Fig. 6. Left leg; tibia curved and slightly twisted; first and second tarsa segments shortened.

Fig. 7. Left leg; whole leg shaped something like a cork-screw; femur much shortened and disfigured; tibia and proximal part of tarsus twisted.

Fig. 8. Left leg; femur inflated, constricted near base; tibia shortened and curved to dorsal side; first two tarsal segments inflated like beads.

Fig. 9. 10. Left leg; somewhat like fig. 8; proximal tarsal segments crooked.

Fig. 11. Right leg; tibia bent towards the dorsal side near distal end.

Fig. 12. Right leg; Whole leg folded up, being curved sharply twice; femur, tibia and first tarsal segment much deformed.

Fig. 13. Right leg; second tarsal segment bent sharply towards dorsal side.

Fig. 14. Left leg; femur somewhat deformed; tibia swollen considerably at distal end: proximal tarsal segments fused into a spoon-shaped body; tarminal claws missing.

Fig. 15. Both legs deformed; right leg with tibia curved, tarsus crooked sharply near middle, with distal end directed anteriorly; left leg cut off at base of femur.

Fig. 16. Right legs; both middle and hind legs crippled; femur broadened and shortened tibia curved dorsally in both legs; first and second tarsal segments of hind leg broadened and flattened.

Fig. 17. Right legs; both middle and hind legs crippled; middle leg lacking tarsal segments except first segment; hind leg with first tarsal segment crooked.

Fig. 18. Left leg; femur crooked; tibia and tarsus gone.

Fig. 19. Left leg; tibia short; tarsus missing.

Fig. 20. Left leg; femur and tibia fused longitudinally into one stump-like mass; tarsus missing.

Figs. 21, 22. Left leg; tibia shortened and deformed; tarsal segments dilated and much deformed.

Fig. 23. Right leg; tibia straightened, twisted at distal end; distal tarsal segments missing.

Fig. 24. Left leg; tibia straightened; distal tarsal segments missing.

Plates XVIII & XIX.

Abnormalities of middle leg (*crip-m*).

The diagram attached to each figure shows the relative situation of the parts reduplicated and the side to which those parts belong; limbs are represented in transverse section, the right limb as having a longer spur on the right side, and the left limb on the left side.

Pl. XVIII, Fig. 1. Left leg; entire leg dwindles and folded up.

Fig. 2. Left leg; all segments from femur to tarsus shortened; tarsus curved to dorsal side, terminal segment gone.

Fig. 3. Right leg; femur, tibia and first tarsal segment shortened and curved; second to fifth tarsal segment gone.

Fig. 4. Right leg; entire leg much reduced in size; third to fifth tarsal segment missing, first and second rudimentary; stump-shaped process near median line of body.

Figs. 5,—17. Explanation may be found in text.

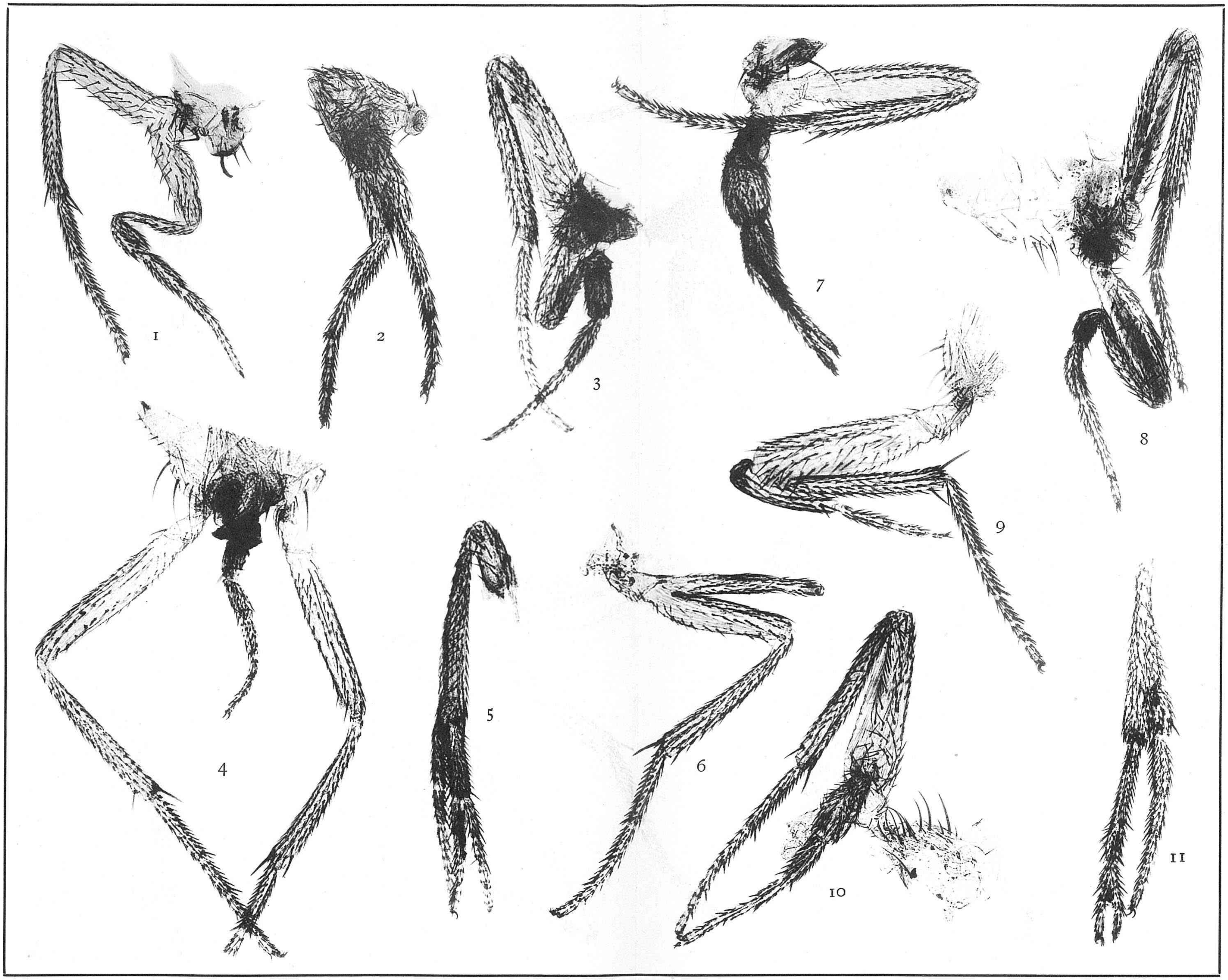
Pl. XIX, figs. 1—12. explanation may be found in text.

Plate XX.

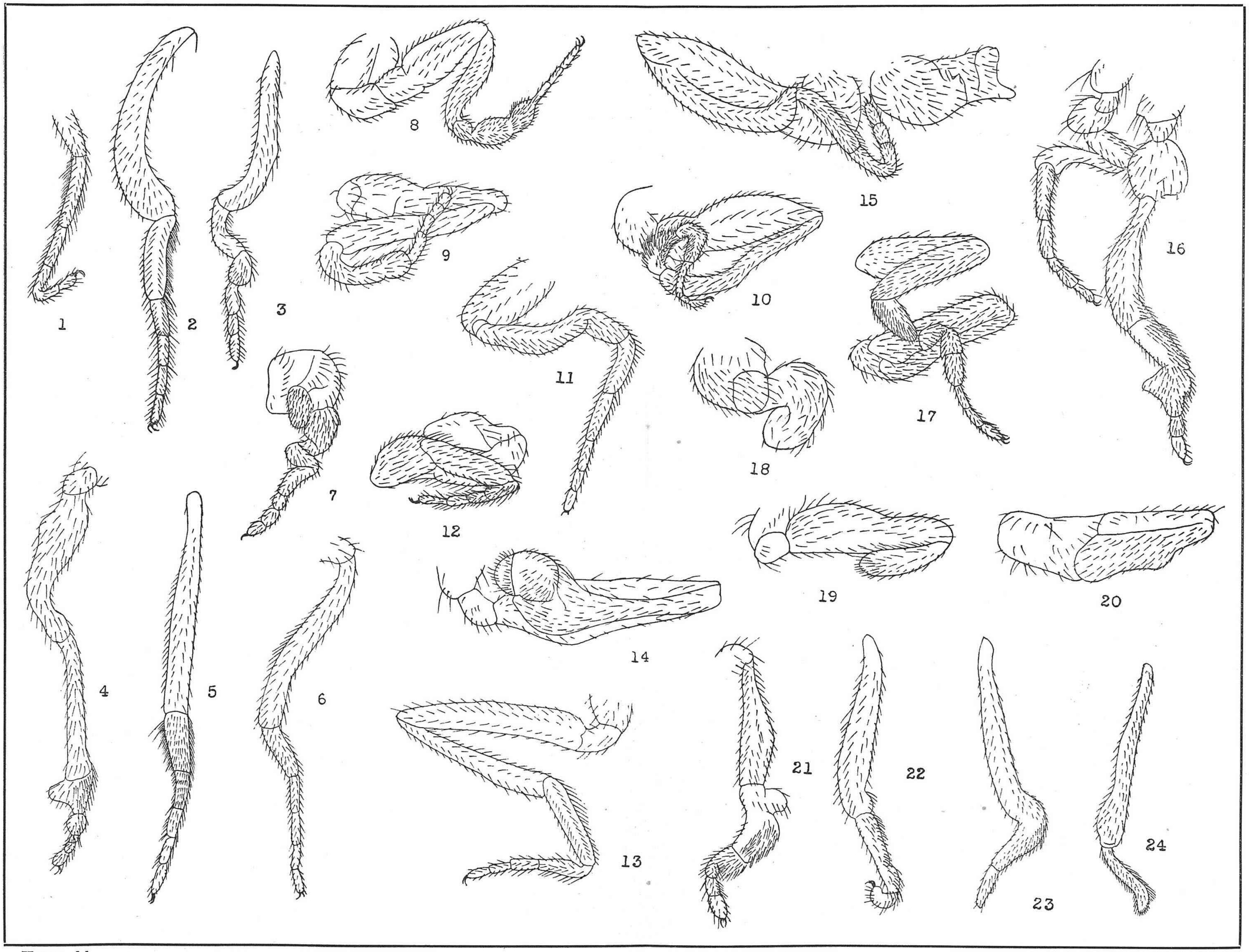
Reduplication of fore or middle leg, etc.

Figs. 1—4. Explanation may be found in text.

Fig. 5. Abnormal fly found in *black purple cinnabar crip-m* strain, with antenna-like process projecting from center of right eye.



Komai & Omi Photo



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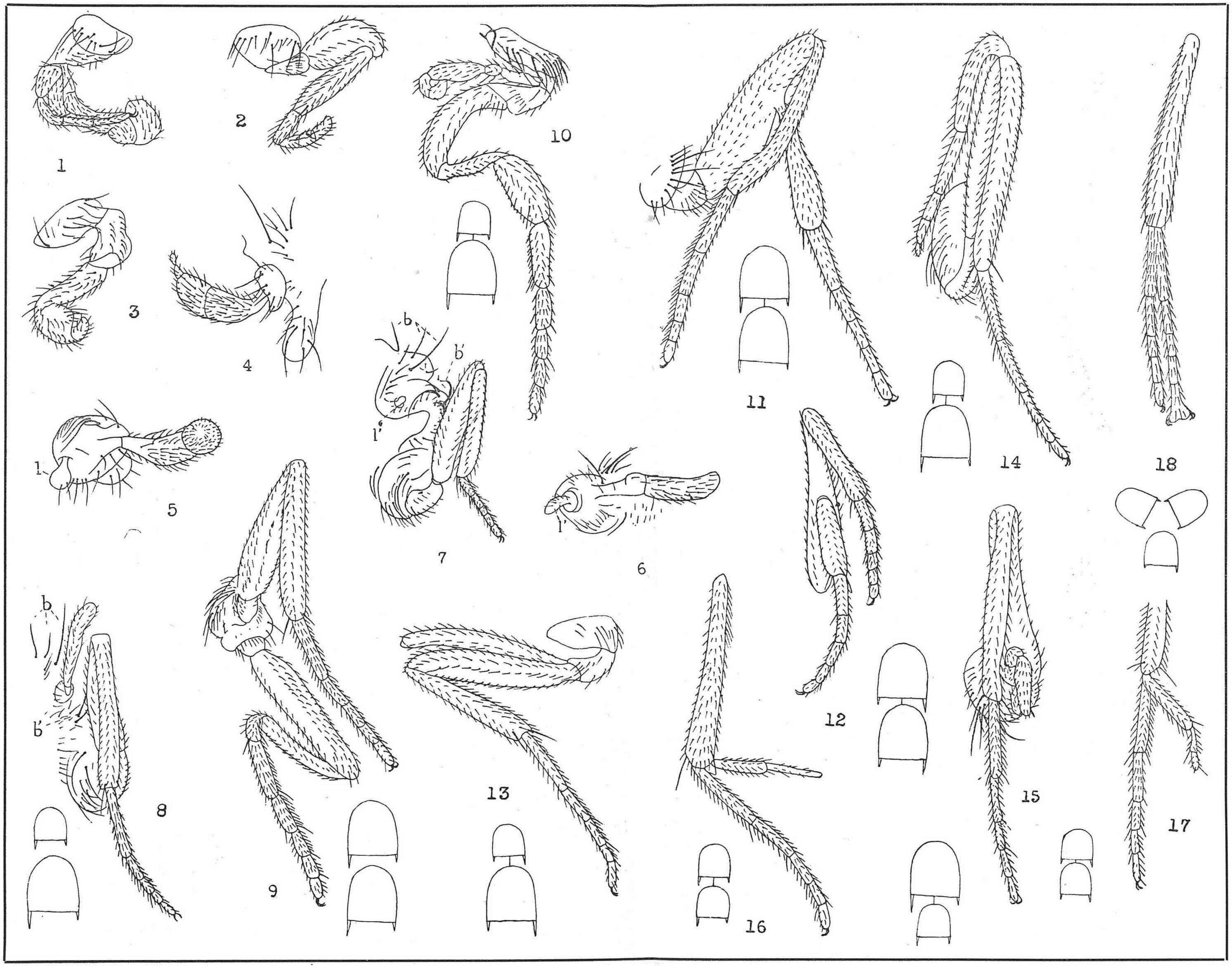

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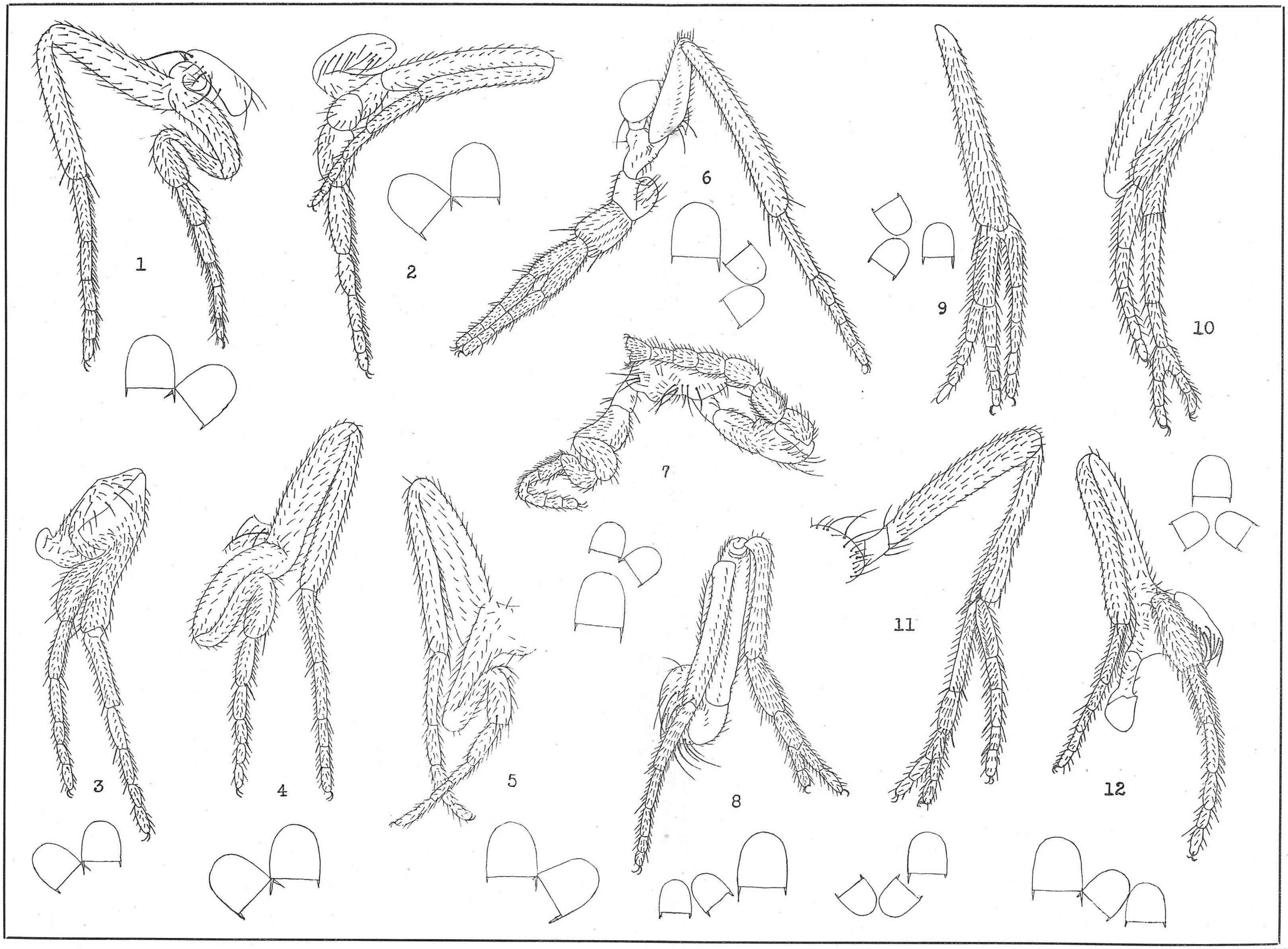

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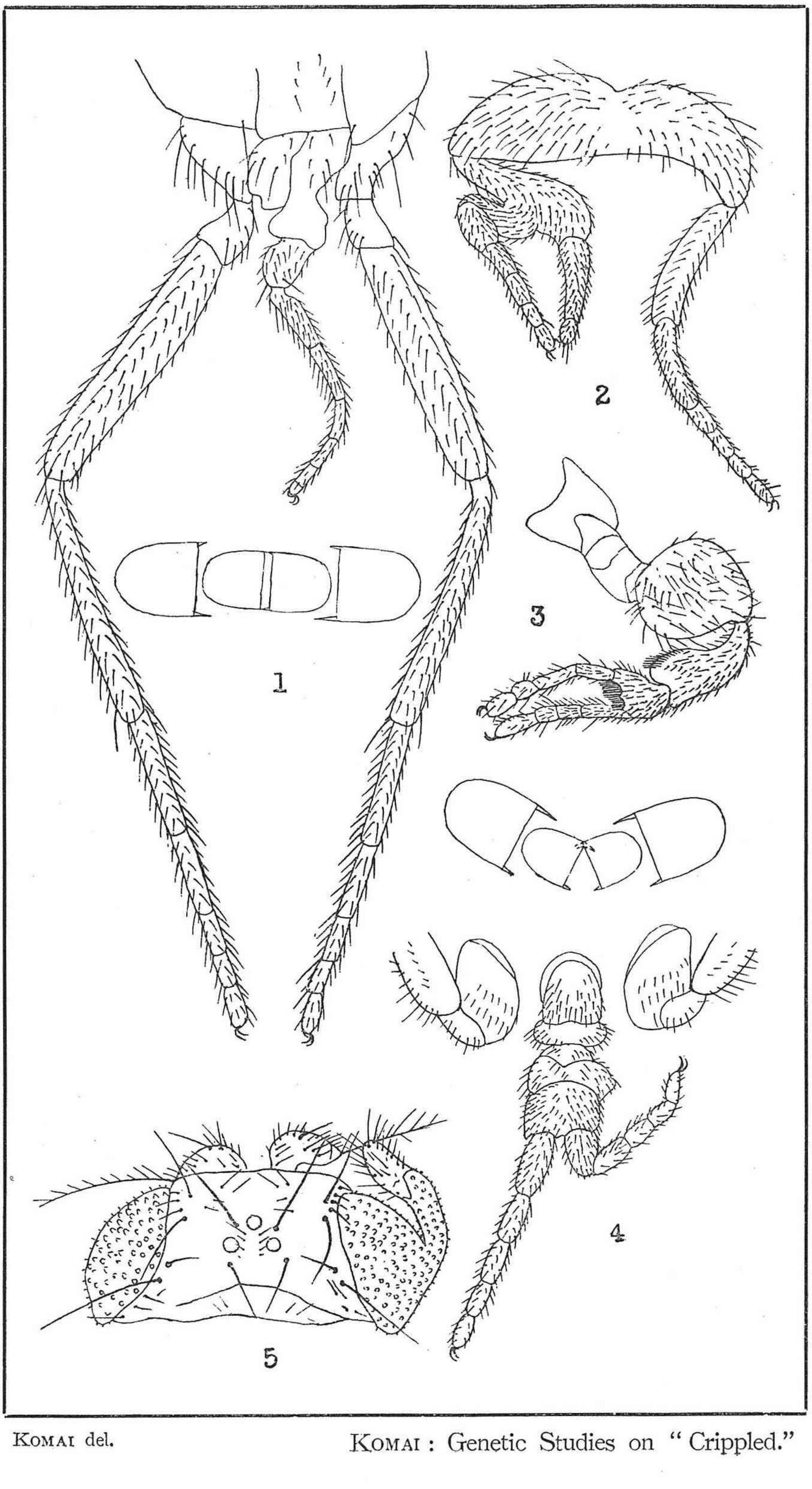

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KOMAI : Genetic Studies on "Crippled."