

STUDIES OF INHERITANCE AND EVOLUTION
IN ORTHOPTERA. IV¹.

MULTIPLE ALLELOMORPHISM AND INHERITANCE OF
COLOR PATTERNS IN TETTIGIDEA².

BY ALBERT WILLIAM BELLAMY.

(With Plate III.)

INTRODUCTION.

ACCORDING to Bateson each character of an alternative pair is an allelomorphic one. He says ('09, p. 11) "The dissociation of characters from each other in the course of the formation of the germs, we speak of as *segregation*, and the characters which segregate from each other are described as *allelomorphic*, i.e. alternative to each other in the constitution of the gametes."

According to Morgan, allelomorphic characters are characters, the determiners for which have identical loci in homologous chromosomes. Shull ('15, p. 55) speaks of allelomorphism as "A relation between two characters such that the determiners of both do not enter the same gamete, but are separated into sister gametes." If instead of a single pair, a series of several characters exists, each of which behaves towards another as one of an alternative pair, it is said to constitute a system of multiple allelomorphs; the relation of the characters to one another being known as multiple allelomorphism.

Triple systems of allelomorphs have been described in rats, guinea-pigs, rabbits, *Drosophila*, beans, snapdragons, *Lychnis*, *et al.* Quadruple

¹ Studies I, II and III of this series were published by Robert K. Nabours, *Journal of Genetics*, Vols. III. and VII.

² Contribution from the Zoological Laboratory of the Kansas State Agricultural College and Experiment Station, No. 12.

systems are equally well known, having been studied in mice, guinea-pigs, *Drosophila*, and corn. Nabours ('14) published an account of his work with *Paratettix* in which he described what has since been recognized (Dexter, '14) as a system of multiple allelomorphic characters,—the most extensive system yet reported. Nabours showed the existence of eight colour patterns, each allelomorphic to any of the others. Since that time, not only has the behaviour of the eight characters been fully confirmed, but the system has been extended to include in all, at least fourteen patterns and probably several more (Nabours, '17).

MATERIAL AND METHOD.

The material used in this study was collected near Houston, Texas, by Dr Robert K. Nabours and turned over to the writer in October, 1914. I am under deep obligation to him for aid by way of suggestion, encouragement, and criticism.

All the specimens used in the laboratory appear to conform most closely with Hancock's description of *Tettigidea parvipennis pennata* Morse,

Occurrence and distribution: The *Tettigidea* are widely distributed, frequenting the damp surfaces of more or less deeply shaded areas, where mosses, lichens, algae, and decaying vegetation, upon which they feed, are to be found.

Life History. That part of the life cycle from the egg to the adult may be completed in five or six weeks, although mating and deposition of eggs may not occur, at least in the laboratory, for several weeks after the last moult. In one instance, e.g. series (9) of Table I, the first young of the parental generation hatched February 9, 1915. Two females became adult March 9, one of which was mated on March 11, to her father, producing the second generation of young April 22, a little over eleven weeks from the hatching of the first generation to the hatching of the second.

Technique. In the laboratory the grasshoppers are bred in cylindrical screen or glass jars set in pots of moist sandy loam, the surfaces of which are covered with a thin layer of peat. The bottom of a small three-inch pot protrudes about one-half inch above the surface of the soil in the centre of each jar, affording a clean place upon which to

place the food. Some algae also grow upon it. The jars are of two sizes, the mating jars being 8" x 11" and the offspring jars 9" x 15" (cf. Nabours, '14, pp. 143, 144, and Fig. 1).

The grasshoppers are fed on various filamentous algae which grow in abundance during the early spring, throughout the summer, and until late fall, in small streams, live-stock watering troughs, and similar places. In the winter, as well as in the summer, special troughs kept in the greenhouse supply a great deal of the food. If these food sources fail the supply is supplemented with algae and lichens that grow upon flower pots.

Characters under observation. The characters used in this study are the colour markings of the pronota and of the femora of the jumping legs. For present purposes, they may be considered as polyornate "forms" of the species *parvipennis*. For the sake of convenience in reference and recording, the different patterns are represented by capital letters. In instances where these letters are used apparently to indicate a single factor, or gene, it is to be understood that they indicate only the initiative reaction or impulse, or whatever it is, that ultimately results in the character as it appears in the adult animal. The different patterns may then be indicated as follows (see Plate III): *C* = yellowish white striped pronotum. *D* = white lined pronotum (*bilineata*), i.e. two whitish lines extend the full length of the lateral carinae. *E* = slightly fulvo-aeneous plus blackish striped pronotum, i.e. the whole pronotum has an ill-defined blackish stripe on a pallid or slightly fulvo-aeneous background. *F* = narrow banded femora; this is subject to considerable variation, and in some individuals the pattern approaches a circle in outline, while in others it may appear as a white line. *H* (present only in connection with and in addition to some one or two of the other patterns) = light brownish-red pronotum and femora of the jumping legs. *M* = melanic, i.e. the whole animal is a dirty-brown to almost black individual.

Homozygous individuals, since they receive their determiners for the character in question from two parents, are indicated by doubling the letter representing that pattern and heterozygotes are indicated by a combination of the letters corresponding to the patterns represented in their constitution.

EXPERIMENTS.

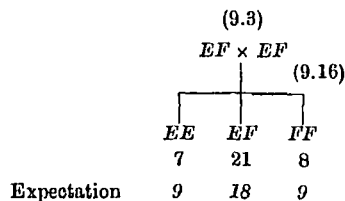
Analysis of the original material. One male of the appearance of *DF* (see plate), one male of the appearance of *CF*, three females of the appearance of *MM*, and one female of the appearance of *EEH*, constituted the original material. They were mated as follows:

- (3) *CF* × *MM*,
 (5) *DF*¹ × *MM*,
 (13) *DF*¹ × *MM*,
 (9) *DF*¹ × *EEH*.

These and the subsequent matings are shown in the table of matings which shows how all of the analyses were carried out.

It may be said that many of the matings were made, not so much in accordance with a previously arranged schedule, but because they represented the only available material. No doubt many of the analyses could have been carried out to better advantage, especially if one could have counted on having the right male and female adult at the *same time*, and if the contingency of the death of a valuable specimen did not have to be reckoned with.

Explanation of Table I. This table gives the entire pedigree. The matings are arranged in serial order reading in columns down the page and from left to right. The number in parentheses immediately above the horizontal line is the mating number; the number in parentheses above the mating is the mating from which the parents came. Take for example:



This is mating number (9.16), the parents coming from (9.3). The actual numbers are 7 : 21 : 8 and the expectations 9 : 18 : 9 respectively.

The original male *DF* was used in (5), (9), (9.1), and (13) and is indicated thus: **DF*.

¹ Same male.

TABLE I.

	<p>Nature</p> <p>$CF \times MM$ (3)</p> <pre> +-----+ CM FM 78 79 </pre>		<p>(3.8)</p> <p>$CC \times CC$ (3.10)</p> <pre> CC 29 </pre>
Expect.	<p>78.5 78.5</p>	Expect.	<p>29</p>
	<p>(3)</p> <p>$CM \times CM$ (3.4)</p> <pre> +-----+ CC CM MM 67 18 </pre>		<p>(3.10)</p> <p>$CC \times CC$ (3.11)</p> <pre> CC 10 </pre>
Expect.	<p>63.75 21.25</p>	Expect.	<p>10</p>
	<p>(3)</p> <p>$FM \times FM$ (3.5)</p> <pre> +-----+ FF FM MM 68 26 </pre>		<p>Nature</p> <p>$*DF \times MM$ (5)</p> <pre> +-----+ DM FM 39 50 </pre>
Expect.	<p>70.5 23.5</p>	Expect.	<p>44.5 44.5</p>
	<p>(3)</p> <p>$CM \times CM$ (3.6)</p> <pre> +-----+ CC CM MM 82 18 </pre>		<p>(5)</p> <p>$DM \times DM$ (5.2)</p> <pre> +-----+ DD DM MM 63 27 </pre>
Expect.	<p>75 25</p>	Expect.	<p>67.5 22.5</p>
	<p>(3)</p> <p>$FM \times FM$ (3.7)</p> <pre> +-----+ FF FM FM 110 57 </pre>		<p>(5)</p> <p>$FM \times DM$ (5.3)</p> <pre> +-----+ DF DM FM MM 7 14 15 14 </pre>
Expect.	<p>125.25 41.75</p>	Expect.	<p>12.5 12.5 12.5 12.5</p>
	<p>(3.6)</p> <p>$CC \times CC$ (3.8)</p> <pre> CC 9 </pre>		<p>(5)</p> <p>$FM \times FM$ (5.5)</p> <pre> +-----+ FF FM MM 30 12 </pre>
Expect.	<p>9</p>	Expect.	<p>31.5 10.5</p>

TABLE I (continued).

<p>(9.4) DE × DE (9.8)</p> <table border="0"> <tr> <td>DD</td> <td>DE</td> <td>EE</td> </tr> <tr> <td>28</td> <td>61</td> <td>26</td> </tr> </table> <p>Expect. 28·7 57·5 28·7</p>	DD	DE	EE	28	61	26	<p>(9.4) (9.3) EE × FF (9.12)</p> <table border="0"> <tr> <td>EF</td> </tr> <tr> <td>4</td> </tr> </table> <p>Expect. 4</p>	EF	4																					
DD	DE	EE																												
28	61	26																												
EF																														
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<p>(9.4) (9.1) DF × DD (9.9)</p> <table border="0"> <tr> <td>DD</td> <td>DF</td> </tr> <tr> <td>8</td> <td>13</td> </tr> </table> <p>Expect. 10·5 10·5</p>	DD	DF	8	13	<p>(9.3) (9.1) FF × DFH (9.15)</p> <table border="0"> <tr> <td>DF</td> <td>FF</td> <td>DFH</td> <td>FFH</td> </tr> <tr> <td>18</td> <td>17</td> <td>19</td> <td>11</td> </tr> </table> <p>Expect. 16·2 16·2 16·2 16·2</p>	DF	FF	DFH	FFH	18	17	19	11																	
DD	DF																													
8	13																													
DF	FF	DFH	FFH																											
18	17	19	11																											
<p>(9.4) DF × DF (9.11)</p> <table border="0"> <tr> <td>DD</td> <td>DF</td> <td>FF</td> </tr> <tr> <td>25</td> <td>39</td> <td>14</td> </tr> </table> <p>Expect. 19·5 39 19·5</p>	DD	DF	FF	25	39	14	<p>(9.3) EF × EF (9.16)</p> <table border="0"> <tr> <td>EE</td> <td>EF</td> <td>FF</td> </tr> <tr> <td>7</td> <td>21</td> <td>8</td> </tr> </table> <p>Expect. 9 18 9</p>	EE	EF	FF	7	21	8																	
DD	DF	FF																												
25	39	14																												
EE	EF	FF																												
7	21	8																												
<p>(9.5) DFH × DFH (9.18)</p> <table border="0"> <tr> <td>DD</td> <td>DF</td> <td>FF</td> <td>DDH</td> <td>DHDH</td> <td>DFH</td> <td>DHFH</td> <td>FFH</td> <td>FHFH</td> </tr> <tr> <td>1</td> <td>4</td> <td>1</td> <td colspan="2">6</td> <td colspan="2">10</td> <td colspan="2">3</td> </tr> <tr> <td>1·56</td> <td>3·12</td> <td>1·56</td> <td colspan="2">4·7</td> <td colspan="2">9·4</td> <td colspan="2">4·7</td> </tr> </table> <p>Expect. 1·56 3·12 1·56 4·7 9·4 4·7</p>	DD	DF	FF	DDH	DHDH	DFH	DHFH	FFH	FHFH	1	4	1	6		10		3		1·56	3·12	1·56	4·7		9·4		4·7		<p>(9.3) EE × EE (9.17)</p> <table border="0"> <tr> <td>EE</td> </tr> <tr> <td>2</td> </tr> </table> <p>Expect. 2</p>	EE	2
DD	DF	FF	DDH	DHDH	DFH	DHFH	FFH	FHFH																						
1	4	1	6		10		3																							
1·56	3·12	1·56	4·7		9·4		4·7																							
EE																														
2																														
<p>(9.4) EE × EE (9.21)</p> <table border="0"> <tr> <td>EE</td> </tr> <tr> <td>5</td> </tr> </table> <p>Expect. 5</p>	EE	5	<p>(9.3) (9.5) FF × EFH (9.24)</p> <table border="0"> <tr> <td>EF</td> <td>FF</td> <td>EFH</td> <td>FFH</td> </tr> <tr> <td>9</td> <td>8</td> <td>3</td> <td>10</td> </tr> </table> <p>Expect. 7·5 7·5 7·5 7·5</p>	EF	FF	EFH	FFH	9	8	3	10																			
EE																														
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EF	FF	EFH	FFH																											
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<p>(9.4) EF × EF (9.22)</p> <table border="0"> <tr> <td>EE</td> <td>EF</td> <td>FF</td> </tr> <tr> <td>9</td> <td>43</td> <td>16</td> </tr> </table> <p>Expect. 16·7 33·5 16·7</p>	EE	EF	FF	9	43	16																								
EE	EF	FF																												
9	43	16																												

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TABLE I (continued).

(9.5)
 $DEH \times DEH$ (9.25)

	DD	DE	EE	DDH	$DHDH$	DEH	$DHEH$	EEH	$EHEH$
	2	1	1	1		3		1	
Expect.	0.56	1	0.56	1.69		3.37		1.69	

(9.5) (9.1)
 $EEH \times DDH$ (9.26)

	DE	DEH	$DHEH$
	9	22	10
Expect.	10.25	20.5	10.25

(9.3) (9.1)
 $FF \times EFH$ (9.29)

	EF	FF	EFH	FFH
	10	16	24	20
Expect.	17.5	17.5	17.5	17.5

(9.3) (9.2)
 $FF \times DEH$ (9.27)

	DF	EF	DFH	EFH
	6	18	18	8
Expect.	12.5	12.5	12.5	12.5

(9.3) (9.8)
 $FF \times DEH$ (9.30)

	DF	EF	DFH	EFH
	9	16	33	6
Expect.	16	16	16	16

(9.5) (9.1)
 $EF \times DD$ (9.28)

	DE	DF
	6	5
Expect.	5.5	5.5

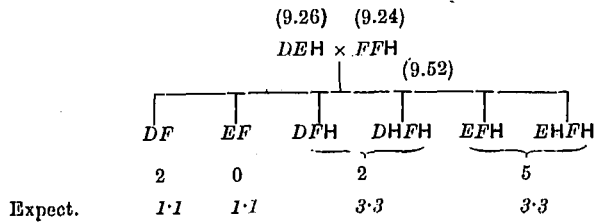
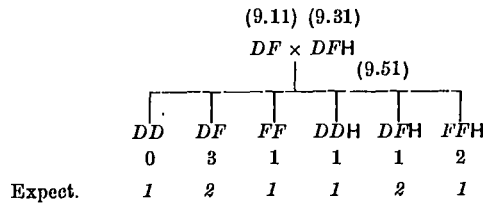
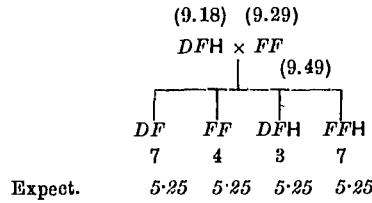
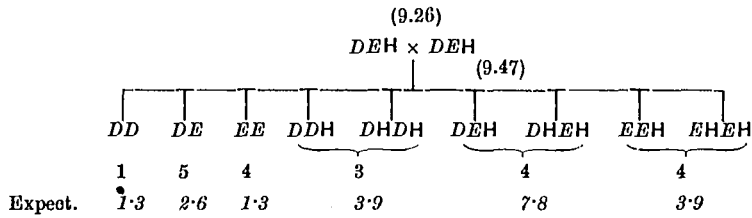
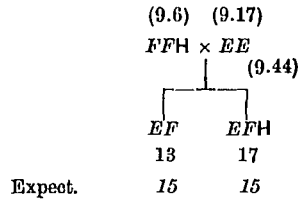
(9.11) (9.18)
 $DD \times FFH$ (9.31)

	DF	DFH
	0	2
Expect.	1	1

(9.8) (9.47)
 $DE \times DEH$ (9.37)

	DD	DE	EE	DDH	DEH	EEH
	3	8	4	2	12	5
Expect.	4.25	8.5	4.25	4.25	8.5	4.25

TABLE I (continued).



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TABLE I (continued).

	(9.6) (9.15) $EFH \times FF$ (9.53)		(3) (13) $CM \times FM$ (18)	
	EF FF EFH FFH		CF CM FM MM	
	0 4 2 3		11 17 13 8	
Expect.	1.75 1.75 1.75 1.75		12.2 12.2 12.2 12.2	
	Nature $*DF \times MM$ (13)		Nature $MMH \times MMH$ (19)	
	DM FM		MM MMH MHH	
	47 45		7 11	
Expect.	46 46		4.5 13.5	
	(13) $DM \times FM$ (13.1)		(19) $MMH \times MMH$ (19.1)	
	DF DM FM MM		MM MMH MHH	
	9 8 10 15		2 7	
Expect.	10.5 10.5 10.5 10.5		2.25 6.75	
	(13) $DF \times DM$ (13.2)		(3) (5) $FM \times FM$ (17)	
	DD DM DF FM		FF FM MM	
	16 8 8		32 11	
Expect.	16 8 8		32.25 10.75	
	(3.6) (5.2) $CM \times DM$ (22)		(3.6) (9.1) $CM \times EFH$ (24)	
	CD CM DM MM		CE CF EM FM CEH CFH EMH FMH	
	18 18 18 15		9 5 5 10 11 7 7 6	
Expect.	17.2 17.2 17.2 17.2		7.5 7.5 7.5 7.5 7.5 7.5 7.5 7.5	

TABLE I (continued).

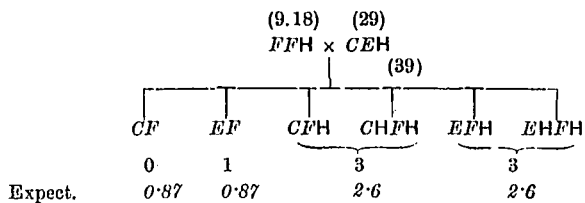
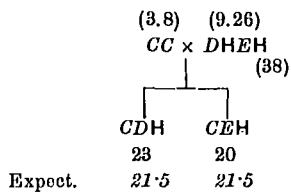
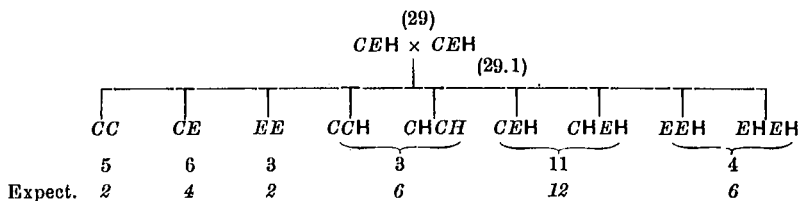
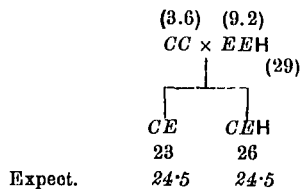
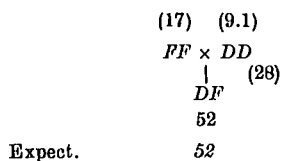
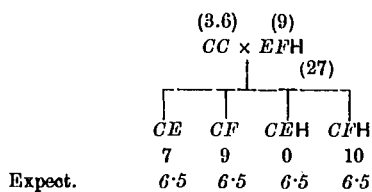
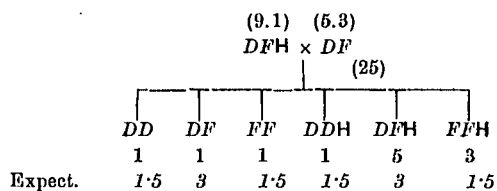


TABLE I (continued).

	(19) (9.17) MMH × EE (40)		(22) (28) CD × DF (44)
	EM EMH		CD CF DD DF
	1 5		5 5 4 5
Expect.	3 3	Expect.	4.75 4.75 4.75 4.75
	(3.8) (5.6) CC × MM (41)		(44) CD × CD (44.3)
	CM		CC CD DD
	29		8 16 9
Expect.	29	Expect.	8.25 16.5 8.25
	(3.8) (38) CC × CDH (42)		(9.49) (29.1) DFH × CC (56)
	CC CD CCH CDH		CD CF CDH CFH
	4 2 4 4		5 5 3 5
Expect.	3.5 3.5 3.5 3.5	Expect.	4.5 4.5 4.5 4.5
	(3.8) (9.47) CC × EHEH (43)		
	CEH		
	90		
Expect.	90		

Table II. Combination of matings (3.5), (3.7), (17), and (5.5).

	FM × FM
	FF FM MM
	240 106
Expect.	259.5 86.5

Table III. Combination of matings (3.6) and (3.4).

	CM × CM
	CC CM MM
	149 36
Expect.	138.75 46.25

A combination of the results given in Tables II and III gives for the first two classes 389 and for the third class, composed entirely of *MM*, 142; the expectations being 398.25 and 132.75 respectively.

Table IV. Combination of the results of the matings giving a "3:1" ratio, viz. (3.4), (3.5), (3.6), (3.7), (5.2), (5.5), and (17). The apparent dominance and recessiveness of certain of these patterns will be mentioned in another connection.

	<u>I</u>	<u>II</u>	III
	552		169
Expect.	540.75		180.25

Table V. Combination of matings giving a "1:2:1" ratio directly.

	<i>DD</i>	<i>DF</i>	<i>FF</i>	
	2	5	3	(5.7)
	25	39	14	(9.11)
	<i>DD</i>	<i>DE</i>	<i>DF</i>	
	28	61	26	(9.8)
	<i>EE</i>	<i>EF</i>	<i>FF</i>	
	35	81	42	(9.3)
	7	21	8	(9.16)
	9	43	15	(9.22)
	<i>CC</i>	<i>CD</i>	<i>DD</i>	
	8	16	9	(44.3)
Totals	114	266	117	
Expect.	124.25	248.5	124.25	

In Tables I, II, III, and IV, the results have been tabulated as though *C*, *D*, and *F* were each "dominant" or epistatic, and *M* "recessive" or hypostatic. This was due, in part, to the fact that when these records were made the writer lacked experience and familiarity with the material, which, because of the great similarity in the case of *CC* and *CM*, of the homozygous and heterozygous forms, made it seem desirable to record the two classes together; and in part due to the fact that *CC* and *CM* are not readily distinguishable until about a week after the last moult, and even then there are a few individuals which cannot readily be distinguished. In the case of *FF* and *FM*, the pattern *FF* is so small that it would be difficult to distinguish between *FF* and *FM*, even though the hybrids were exactly intermediate between them. The case is rare, if it ever occurs, where some detectable difference does not occur between a homozygous form and the hybrid.

The behaviour of H. An examination of Table I shows that the female *EEH* in (9) gave two sorts of gametes, viz. *E* and *EH*; that the female *DEH* in (9.1) gave four sorts of gametes, *D*, *E*, *DH*, *EH*, and that all the

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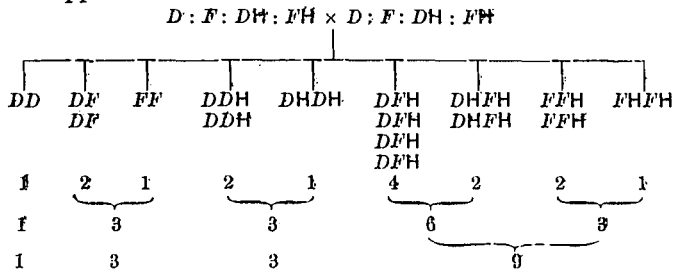
possible combinations with the two gametes of the male give eight classes of young. However, (9.2), $DEH \times DE$, produced six classes of young, which meets the expectation, because when all the possible combinations have been made the classes DE and DEH will each have occurred twice. Homozygotes, or heterozygotes containing H , are better analyzed by mating with homozygous individuals as has been done in (9.15) and (9.27), $FF \times DFH$, and a number of others.

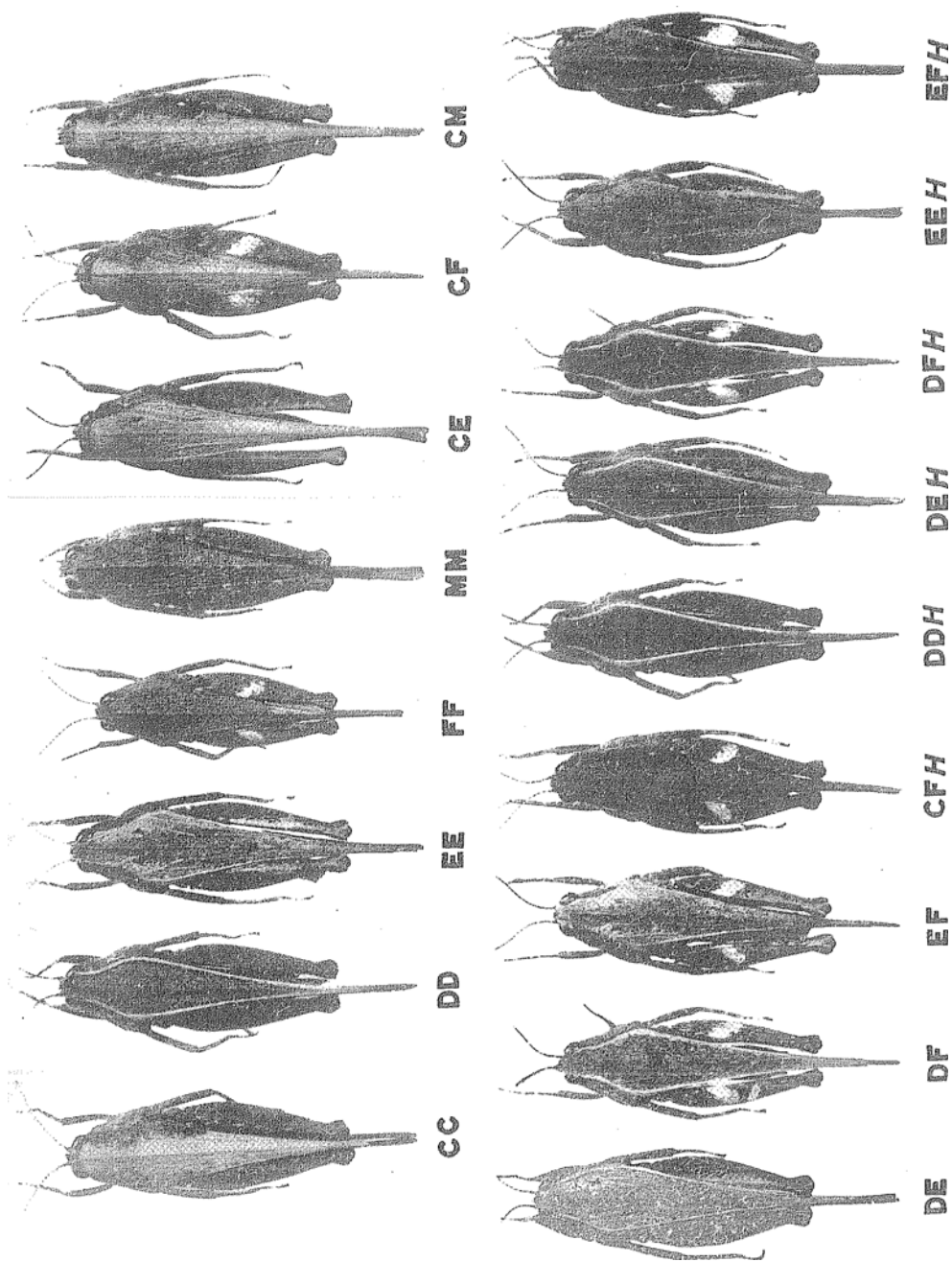
The mating (9.18), $DFH \times DFH$, is of interest because among the nine possible combinations of gametes we should obtain three combinations in which H occurs twice, viz. $DHDH$, $DHFH$, and $FHFH$; i.e. these individuals should have a double dose of H . In the sense that when inbred, all of the gametes will receive the factor (or factors) for H , they will be homozygous for it. It is interesting to note in this connection that a number of individuals appear in such matings as this which have the reddish pigmentation in an appreciably more intense condition than other individuals containing H in the same culture or other cultures. That such individuals may have a double dose of H is shown by matings (38), $CC \times DHEH$, and (43), $CC \times EHEH$; (38) producing CDH 23 and CEH 20; and (43) producing CEH 90.

Homozygotic individuals with a single dose of H , as regards the characters in question, always give two sorts of gametes, while heterozygotic individuals with a single dose of H always give four sorts of gametes. Homozygotic individuals with a double dose of H always give one sort of gametes, while heterozygotic individuals with a double dose of H always give two sorts of gametes.

It is seen that while the zygotic constitution of, e.g., DFH is either $D:FH$ or $F:DH$, its gametic formula is always $D:F:DH:FH$.

All the possible combinations of such a mating as has just been described may be obtained in the usual manner from the "16-square" as for an organism differing in two "independent" characters, or they may be derived in the following manner and the ratios be made somewhat more apparent:





This ratio of 4:2:2:2:2:1:1:1:1, or, when the single and double doses of **H** are counted in the same class as was done for (9.18) and others, of 6:3:3:2:1:1, is actually a 9:3:3:1 ratio; or better, as has been emphasized by Nabours ('17), the 9:3:3:1 ratio is actually a 4:2:2:2:2:1:1:1:1 ratio.

DISCUSSION.

The chief purpose of this paper has been to record the inheritance behaviour of several colour patterns in *Tettigidea* which constitute a system of "multiple allelomorphs"; and of another pigmental characteristic (**H**) "*which exists in connection with and in addition to the other patterns.*"

The theory of multiple allelomorphism as set forth by the Morgan school, postulates that the determiners for all the characters of a given system of multiple allelomorphs shall have identical loci in a pair of homologous chromosomes. There may be as many sets or groups of characters as there are chromosomes in the matured gametes. It is stated that the same results may be explained equally well by assuming that there is complete linkage, i.e. that the determiners lie so close together in the chromosomes that crossing over never takes place, and that the end results would be the same in either case.

If one wishes to interpret these results in the light of this hypothesis, it may be assumed that the "determiners" for the characters *C, D, E, F*, and *M* have identical loci in a single pair of homologous chromosomes. In the case of **H** it need only be assumed that its determiner is borne by some other chromosome. **H** is not sex linked and is apparently, as stated by Nabours for his \odot in *Parutettia*, allelomorphic only to its absence.

This report is based upon 3,219 recorded individuals.

EXPLANATION OF PLATE III.

Five "forms" of *Tettigidea parvipennis* are represented in the first five figures on the Plate, viz. *CC, DD, EE, FF*, and *MM*. The six figures, *CE, CF, CM, DE, DF, EF*, represent hybrids between certain of the preceding forms. The remaining six figures show the result of the addition of the factor **H**. For fuller explanation see text, p. 57.

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