THE GENETIC EVIDENCE OF A MULTIPLE (TRIPLE) ALLELO- MORPH SYSTEM IN BRUCHUS AND ITS RELATION TO SEX-LIMITED INHERITANCE¹

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INTRODUCTION

This paper concerns the origin and genetic behavior of four different body colors, which have manifested themselves in my cultures of the so-called "four-spotted cowpea-weevil," *Bruchus quadrimaculatus*, Fabr. The inheritance of these colors involves both allelomorphism and sex-limited inheritance. These colors, red, black, white, and tan, are more apparent

¹ Contribution from the Zoölogical Laboratory of the UNIVERSITY OF OKLAHOMA. The experiments, however, were carried on at WESTERN RESERVE UNIVERSITY and, in part, at the BIOLOGICAL LABORATORY, Cold Spring Harbor, Long Island.

in the females, and less conspicuous in the males, because the latter usually have tan elytra. The males, however, carry the color factors, although they are not manifested to such a marked degree somatically. Experiments prove that these four color types compose a multiple allelomorph system, and that they also form an epistatic series. The order of dominance is red, black, white and tan.

During a search for insects which might be favorable for genetic studies, the possibilities of the Bruchidae were considered because several species were known to breed readily in stored seed and to produce several generations each year. The first experiments with these insects involved a culture of *Bruchus obtectus*, Say., the "common bean-weevil," but these were given up because it was too difficult to distinguish the sexes. It was difficult to obtain living cultures of the so-called "cowpea-weevil," *Bruchus chinensis*, Linn., but it was comparatively easy to procure living *Bruchus quadrimaculatus*, Fabr.

Several reasons may be given why these beetles are adapted for a study in genetics. It is not necessary to etherize them because they letisimulate when poured out of a culture bottle. Likewise, they breed rapidly and may produce a generation within twenty-five days if the temperature is maintained at 30°C, and the relative humidity at about 80 percent. Lastly, these weevils will breed on any species of cowpea, and bottles of any size may be used as containers.

LIFE HISTORY AND DISTRIBUTION

The adults deposit their eggs on the surface of the cowpea. A few days after oviposition the young larva emerges through an opening which it makes in the under side of the egg; it then burrows into the seed, where it feeds until it reaches the pupa stage. It requires about two weeks for the white, legless larva to attain full growth. At the end of about twenty days from time of egg-deposit the pupa state is reached, and this lasts about five days. At first the pupae are white, but after a few days they change to a light tan color. The adult insect emerges through a circular opening which it makes with its jaws. Usually within one day after emergence, the beetles mate and the females lay their eggs.

Since its introduction, this insect has become widely distributed throughout the United States, Mexico, Brazil, the West Indies, and other warm countries. CHITTENDEN (1898) believes that it is probable that this insect, with its preferred food plant, the cowpea, was introduced from the orient. The weevil is found wherever its food plant grows. It will also breed in stored seed if the proper environmental conditions are furnished.

METHODS OF THE EXPERIMENT

The Whippoorwill variety of the cowpea was used for food because it can be obtained at almost any seed store. This seed was put in flasks plugged with cotton and sterilized in an autoclave, to make certain the destruction of any eggs or larvae or adults which might contaminate the experiment. The seeds were then put into bottles which had been boiled for more than twenty minutes, after which they were plugged with cotton, preparatory to their use as breeding chambers. It was found that this species is subject to the attack of the mite, *Pediculoides ventricosus*, New., which destroys larvae and adults, but this parasite is easily controlled by the sterilization of the food and bottles. One pair of beetles was placed in each container and left until the young emerged. An oven regulated by a thermostat was used to maintain the desired temperature and great care was exercised to keep the proper humidity. The humidity when in excess, affects injuriously both cowpeas and weevils, while if the air is too dry the adults may die, or the eggs, larvae or pupae may be destroyed. A relative humidity of 80 percent proved the most satisfactory. Fresh cowpeas are absolutely essential. The stock cultures were carried on by placing ten females and ten males in a bottle. Virgin females may be obtained by opening infested seed or by using females that have emerged within twelve hours. It is a simple matter to distinguish males from females because of the remarkable sexual dimorphism exhibited in this species.

ORIGIN OF TYPES AND MUTANTS

The insects used were received from the TEXAS AGRICULTURAL EXPERIMENT STATION. They were permitted to interbreed for several generations, to determine their genetic potentialities. The body color of this wild stock in both males and females was tan. In the fourth generation a red female was observed; in the sixth generation a black female was discovered; and a white female appeared in the ninth generation. Other cultures of *Bruchus* from different parts of the United States have been examined for these types. Professor Z. P. METCALF of the NORTH CAROLINA AGRICULTURAL EXPERIMENT STATION sent stock which already contained several red females and black females, but the tan or wild type greatly predominated. No white mutant originated during more than twenty-three generations. The North Carolina red type and black type were isolated and were found to have the same genetic behavior as the reds and blacks which had apparently appeared as mutants in the wild stock that came from Texas. Dur-

ing the summer of 1918, Adzuki beans which were badly infested with this weevil were obtained through the kindness of Dr. A. F. BLAKESLEE, but his stock, when examined, was all tan, and no evidence of any mutant was found during thirteen generations. Infested cowpeas which had been purchased at a seed store in New York City, contained, among several hundred individuals, two black females.

DESCRIPTION OF SPECIES: THE ORIGIN OF THE FOUR COLOR FACTORS

The family Bruchidae comprises three genera of insects: *Spermophagus*, *Caryoborus*, and *Bruchus*. HORN'S (1873) description of *Bruchus quadrimaculatus*, Fabr. follows:

"Elongate oval, moderately shining. Beneath equally clothed with whitish pubescence. Elytra ferruginous or pale brown with large lateral spot and apex broadly black. Head dark brown or black, densely punctured, front sub-carinate. Antennae as long as head and thorax, serrate in both sexes, four basal joints pale rufous, outer joints dark and nearly black. Thorax trapezoidal, broader at base than long, sides distinctly arcuate, base trisinate, basal lobe emarginate and clothed with whitish hairs; color variable from ferruginous to black, coarsely punctured, subgranulate and feebly shining, sparsely clothed with cinereous hair. Scutellum with median impressed line and clothed with whitish hair. Elytra broader at base than thorax and longer than wide, sides feebly arcuate, humeri moderately prominent; striae punctured, intervals flat, densely punctulate; color ferruginous with large lateral spot and apex black, clothed with whitish and cinereous pubescence. Pygidium nearly black with medium line of whitish pubescence. Body beneath piceous, densely punctulate and sparsely but evenly clothed with cinereous hairs; abdomen pale brown. Anterior and middle legs pale rufous, hind legs pale brown. Hind femora armed with an acute tooth on the inner side and a broad triangular tooth on the outer side. Length 3-4.5 mm."

No specific mention has been made in the literature indicating the existence of different types in this species, yet CHITTENDEN (1898) in describing this insect states that the ground color is black, with black, gray, and white pubescence, and WADE (1919) writes that there is an exceedingly wide range of color, which varies from a dark or almost black, to brown or reddish brown.

DESCRIPTION OF TYPES

The tan type or wild form

The tan female has two black spots near the base of the elytra, similar to those in the red and the white types. The entire body is tan with the usual white-hair distribution. The pronotum and head are black, but the antennae are tan. In size it is smaller than the black mutants but larger

than the reds and whites. The male is likewise tan except for the pronotum, head, and eyes, which are black. He has no spots on his elytra. Short white hairs cover the dorsal and ventral sides. The male and female correspond in color to RIDGEWAY'S "testaceous." In crosses with either red, black or white, tan is recessive. The formula is *rr*, which represents male and female of the wild type.

The red type or mutant

The first appearance of the red type occurred in the fourth generation, where it was discovered in the wild stock which had been bred in large numbers. In this type the females are red and the males vary from light red to tan. It required several generations before a type which bred true was segregated. This was accomplished by mating the first red female with a male of the wild stock, although it was doubtful whether this female was a virgin. The F_1 from this cross produced fifty-three red females and fifty-seven males which varied from light red to tan. This indicated that red was dominant to tan in the females. Ten males and ten females of this F_1 generation were inbred. They produced 138 red females, 57 tan females and 221 tan males in the F_2 generation. This further indicated that red is dominant to tan for the females. The next procedure was to obtain fifty virgin females and to mate them separately with F_2 males. Each pair was placed in a separate bottle. Only two pairs bred true to the red type. Since the other cultures produced both red and tan females, they were discarded.

The entire body of the red female is red except for the head and eyes, which are black. Her elytra are also red either with or without markings. Her color resembles RIDGEWAY'S "Hessian brown," but our common hazelnut approximates the color more closely. The elytra of the male and his entire body are of a red-tan color, except that his head and pronotum are black. It is evident that the sex-limited traits are least conspicuous for this type than for any other.

This red mutant was discovered first and since it belongs to a multiple allelomorph series, it seems advisable to use *RR*, as the formula for this type in both sexes. The red type is dominant to either the black, the white or the tan types, and it can be the allelomorph of any other color factor.

The black type or mutant

When the black female, which was first discovered in the sixth generation of the wild or tan stock, was mated with a tan male of the wild stock, the offspring consisted of 27 black females and 29 tan males. These F_1 indi-

viduals produced 153 black females, 61 tan females and 201 tan males. The result indicates that black is dominant to tan in the females. After many attempts, a homozygous strain for the black type was isolated. It has been bred true for more than forty generations. The black female differs from the tan female by being pure black in color and larger. The male of the black type differs from that of the tan male by being gray underneath and by having a black body. Tan predominates in the elytra of the male of the black type, and is similar to the tan of the wild type. Consequently, there is marked sexual dimorphism in the black type. It is advisable to use R^bR^b to indicate this mutant for both sexes, because it was the second mutant discovered in the multiple allelomorph series. The results will prove that black is dominant to either white, or tan, but recessive to red.

The white type or mutant

The white female made her appearance in the ninth generation of inbred wild stock. This white female was mated with a tan male of the pure tan stock. Four white females and seven tan males were procured. In the F_2 generation these produced 15 white females, 8 tan females, and 32 tan males. This indicated that white is dominant to tan in the females. Several F_2 pairs were mated, using virgin females, and after several cultures one of the pairs bred true for white. This stock has been bred homozygously for about thirty generations.

The female of the white type is covered with white pubescence, except for the head, pronotum and antennae, which are black. Her elytra may manifest two or more black spots. The male is gray in color except for his elytra which are of a light tan color. White is dominant to tan, but recessive to red or black. The formula used is R^wR^w . It is a third member of the multiple allelomorph series.

With reference to size differences, the females are usually larger than the males in all four of the types. The adults vary in length from 3 to 5 mm. The black mutants are the largest and the white ones the smallest. The red mutant is larger than the tan or wild type, and both fall between the black and the white types.

THE FORMULAE

The formulae used in this paper are adapted to meet the experimental results obtained. Since no geneticist has developed formulae to account for the modifications necessitated by the sex-limited traits involved, the formulae used by MORGAN and BRIDGES (1913) are adapted here. The proposed formulae are as follows:

	<i>Females</i>	<i>Males</i>
Red type	RR (red elytra and body)	RR (reddish tan elytra and body)
Black type	R^bR^b (black elytra and body)	R^bR^b (tan elytra, dark gray body)
White type	R^wR^w (white elytra and body)	R^wR^w (light tan elytra, gray body)
Tan or wild type	rr (tan elytra and body)	rr (tan elytra and body)

THE EXPERIMENTAL RESULTS

Introduction

In the tests and tables which follow all the males are classified as tan, because the elytra of the male usually resembles the tan of the wild type. But the body colors do show differences. Males of the red type usually manifest a red tinge; the black ones, too, show some black pubescence, and the white males are gray in color.

The first six tests (tables 1 to 12) deal with crosses involving these four factors. They prove that any color factor may pair with any other of this series as an allelomorph. The results from these six tests should prove that the dominant females, the recessive females, and the (tan) males in every instance, approximate a 3:1:4 phenotypic ratio in the F_2 generation. The tests 7 to 13 give the results obtained from various back-crosses. They prove that the color factors are carried by the males as well as by the females. The data to further prove that these factors form a multiple allelomorph system are given in tests 13 to 26.

The heredity of red, black, white and tan types involving one pair of factors

Conclusions from mass cultures (tests 1-6; tables 1-12)

The first six tests show that, when any two factors for the four body colors are brought together in pairs, Mendelian segregation takes place, and further, the order of dominance is red, black, white and tan. When two individuals, each carrying a different color factor, are crossed, their F_2 offspring approximate a 3:1:4 phenotype ratio.

TABLE 1

Test 1 $P_1 = \text{red } \varnothing (RR) \times \text{tan } \sigma^1 (R^bR^b) \text{ of the black type.}$ $F_1 = \text{red } \varnothing (RR^b) \times \text{tan } \sigma^1 (RR^b).$ $F_2 = 3 \text{ red } \varnothing (RR, RR^b, RR^b) : 1 \text{ black } \varnothing (R^bR^b) : 4 \text{ tan } \sigma^1 (RR, RR^b, RR^b, R^bR^b).$

PEDIGREE NUMBER	F ₁		F ₂		
	♀ red	♂ tan	♀ red	♀ black	♂ tan
1 (2) ²	34	35	70	19	74
2	82	77	109	35	129
3 (2)	26	28	56	18	88
28 (2)	22	23	155	51	216
40 (3)	33	51	289	96	351
42 (3)	50	52	299	99	320
43	24	19	133	45	183
50 (5)	47	86	310	106	391
58 (5)	87	88	418	140	599
62	32	35	240	47	267
95 (3)	2	3	13	6	17
152	44	55	532	176	771
153	40	27	366	130	460
154	39	48	532	178	683
193	27	29	176	40	254
194	38	34	231	69	326
256	20	22	657	215	881
257	16	15	286	93	364
269	13	14	336	111	339
308	71	76	551	183	761
309 (2)	44	4	51	21	70
311 (2)	61	54	495	173	748
321 (2)	20	25	390	183	525
322	18	23	307	101	407
Totals.....	850	923	6992	2335	9224
Calculated.....	887	887	6957	2319	9276

² The number in parentheses indicates the number of each sex used in the mass culture. Cultures not thus marked are from single pairs.

TABLE 2

Test 1 P_1 = black ♀ (R^bR^b) × tan ♂ of the red type (RR); F_1 and F_2 as in table 1.

PEDIGREE NUMBER	F_1			F_2	
	♀ red	♂ tan	♀ red	♀ black	♂ tan
27 (2)	33	29	151	49	149
41	19	21	144	56	174
51 (5)	40	40	393	127	504
59 (5)	49	46	217	76	305
63 (6)	44	42	242	80	345
96 (3)	21	24	80	30	82
111	29	26	132	44	199
131 (5)	105	115	461	154	685
149	22	20	165	58	246
187	12	11	49	17	68
251	13	12	163	67	249
252	21	25	506	171	706
255	27	28	328	125	428
306 (2)	68	73	429	163	546
307 (2)	57	60	570	198	662
312 (2)	76	57	546	160	636
314	24	37	186	61	208
315	21	15	227	68	293
317	25	28	314	69	324
318	15	17	659	139	772
Totals.....	721	726	5863	1912	7581
Calculated.....	724	724	5758	1920	7678

TABLE 3

Test 2 $P_1 = \text{red } \varphi (RR) \times \text{tan } \sigma^7 \text{ of the tan type } (rr).$ $F_1 = \text{red } \varphi (Rr) \times \text{tan } \sigma^7 (Rr).$ $F_2 = 3 \text{ red } \varphi (RR, Rr, Rr) : 1 \text{ tan } \varphi (rr) : 4 \text{ tan } \sigma^7 (RR, Rr, Rr, rr).$

PEDIGREE NUMBER	F ₁		F ₂		
	♀ red	♂ tan	♀ red	♀ tan	♂ tan
5	53	57	138	61	221
19	13	18	114	39	185
52	37	35	191	69	251
56 (5)	49	44	220	85	311
86 (4)	20	22	58	21	68
102	15	14	57	23	99
104	30	33	153	98	254
144	34	31	386	110	519
145	32	32	330	112	482
146	26	45	126	48	199
147	31	32	231	78	338
210	22	19	58	22	83
214	1	6	6	1	7
216	24	25	141	36	201
330	27	26	324	134	482
331	15	18	215	73	316
350	25	22	595	119	721
352	22	29	290	90	381
Totals.....	476	508	3633	1218	5118
Calculated.....	492	492	3738	1246	4984

TABLE 4

Test 2 $P_1 = \text{tan } \varphi (rr) \times \text{tan } \sigma^7 \text{ of the red type } (RR); F_1 \text{ and } F_2 \text{ as in table 3.}$

PEDIGREE NUMBER	F ₁		F ₂		
	♀ red	♂ tan	♀ red	♀ tan	♂ tan
4	24	25	181	60	243
30	12	12	64	16	83
65 (5)	38	39	179	58	260
140	11	14	144	49	215
141	15	20	178	47	244
209	18	19	124	42	123
326	11	14	70	19	97
327	16	28	234	54	258
329	16	21	408	134	562
355	25	23	350	113	502
Totals.....	186	215	1932	592	2587
Calculated.....	201	201	1917	639	2556

TABLE 5

Test 3

 $P_1 = \text{black } \varnothing (R^b R^b) \times \text{tan } \sigma^7 (rr) \text{ of the tan type.}$ $F_1 = \text{black } \varnothing (R^b r) \times \text{tan } \sigma^7 (R^b r).$ $F_2 = 3 \text{ black } \varnothing (R^b R^b, R^b r, R^b r):1 \text{ tan } \varnothing (rr):4 \text{ tan } \sigma^7 (R^b R^b, R^b r, R^b r, rr).$

PEDIGREE NUMBER	F ₁		F ₂		
	♀ black	♂ tan	♀ black	♀ tan	♂ tan
6	27	29	153	57	201
11	4	12	33	12	49
35 (4)	22	22	178	60	272
36 (4)	24	21	78	24	153
38 (4)	53	57	230	63	274
46 (5)	48	38	175	60	244
48 (4)	12	6	42	22	63
54 (5)	48	51	164	44	176
60 (5)	52	50	244	96	325
66 (5)	87	86	436	195	668
105	31	31	104	51	151
134	19	36	243	81	308
136	20	22	278	94	330
211	18	18	68	29	93
213 (2)	49	48	176	60	191
310	20	30	285	100	339
313	21	19	237	77	275
323	16	18	222	71	326
325	11	12	240	86	353
Totals	582	606	3586	1282	4791
Calculated	594	594	3622	1207	4830

TABLE 6

Test 3

 $P_1 = \text{tan } \varnothing (rr) \times \text{tan } \sigma^7 (R^b R^b) \text{ of the black type; } F_1 \text{ and } F_2 \text{ as in table 5.}$

PEDIGREE NUMBER	F ₁		F ₂		
	♀ black	♂ tan	♀ black	♀ tan	♂ tan
37 (3)	48	62	181	65	239
47 (3)	21	25	69	23	94
49 (3)	14	21	23	8	21
55 (5)	10	19	31	9	45
57 (5)	68	71	230	98	341
61 (5)	15	13	52	18	84
67 (4)	39	39	97	31	138
97 (3)	20	17	102	37	113
132	33	25	272	82	230
137	27	26	91	20	126
223	13	14	274	61	328
224	3	4	86	4	81
225	18	19	122	41	200
Totals	329	355	1632	497	2040
Calculated	342	342	1563	521	2085

TABLE 7

Test 4

P_1 = red ♀ (RR) $\times$ tan ♂ (R^wR^w) of the white type.

F_1 = red ♀ (RR^w) $\times$ tan ♂ (RR^w).

F_2 = 3 red ♀ (RR, RR^w, RR^w):1 white ♀ (R^wR^w):4 tan ♂ (RR, RR^w, RR^w, R^wR^w).

PEDIGREE NUMBER	F ₁		F ₂		
	♀ red	♂ tan	♀ red	♀ white	♂ tan
7	10	10	47	12	61
83	11	12	63	30	95
87 (2)	24	18	129	64	195
89 (3)	37	33	220	74	301
100	13	18	37	14	54
156	25	26	276	92	383
157	26	23	233	81	311
158	30	32	118	37	163
159	2	4	37	14	52
160	23	27	77	23	106
161	32	39	301	114	416
162	28	26	80	28	108
231	15	14	94	33	147
232	32	33	455	152	603
234	35	31	319	146	472
235	30	32	199	77	370
348	47	40	686	262	980
Totals.....	420	418	3371	1253	4817
Calculated.....	419	419	3540	1180	4720

TABLE 8

Test 4

P_1 = white ♀ (R^wR^w) $\times$ tan ♂ (RR) of the red type; F_1 and F_2 as in table 7.

PEDIGREE NUMBER	F ₁		F ₂		
	♀ red	♂ tan	♀ red	♀ white	♂ tan
70 (2)	23	26	69	22	92
163	11	9	70	24	88
164	20	13	132	62	311
166	27	19	283	85	323
171	2	1	3	1	7
172	20	34	94	22	161
178	34	21	135	47	190
201	2	2	8	3	14
203	10	11	31	12	60
229	3	2	42	16	51
303	8	15	56	15	49
Totals.....	160	153	923	309	1346
Calculated.....	156	156	967	322	1289

TABLE 9

Test 5

P₁ = black ♀ (*R^bR^b*) × tan ♂ (*R^wR^w*) of the white type.
F₁ = black ♀ (*R^bR^w*) × tan ♂ (*R^bR^w*).
F₂ = 3 black ♀ (*R^bR^b*, *R^bR^w*, *R^bR^w*):1 white ♀ (*R^wR^w*):4 tan ♂ (*R^bR^b*, *R^bR^w*, *R^bR^w*, *R^wR^w*).

PEDIGREE NUMBER	F ₁		F ₂		
	♀ black	♂ tan	♀ black	♀ white	♂ tan
74 (5)	43	42	118	31	79
90 (3)	23	17	66	27	82
91 (3)	62	54	187	57	228
92 (3)	22	34	128	42	171
173	33	32	122	40	180
177	29	30	12	2	15
186	17	21	117	33	141
199	15	6	207	36	208
249	25	16	308	135	427
Totals.....	292	272	1413	502	1766
Calculated.....	282	282	1227	409	1636

TABLE 10

Test 5

P₁ = white ♀ (*R^wR^w*) × tan ♂ (*R^bR^b*) of the black type; F₁ and F₂ as in table 9.

PEDIGREE CULTURE	F ₁		F ₂		
	♀ black	♂ tan	♀ black	♀ white	♂ tan
72 (2)	25	27	45	8	52
73 (4)	17	18	5	1	4
93 (3)	14	16	50	17	46
94 (3)	36	39	47	23	48
246	11	16	127	37	105
247	3	1	25	13	44
284	9	10	122	45	168
289	15	10	56	17	78
339	11	17	89	35	115
Totals.....	141	154	566	196	660
Calculated.....	147	147	574	158	732

TABLE 11

Test 6 P_1 = white ♀ (R^wR^w) × tan ♂ (rr) of the tan type. F_1 = white ♀ (R^{wr}) × tan ♂ (R^{wr}). F_2 = 3 white ♀ (R^wR^w, R^{wr}, R^{wr}):1 tan ♀ (rr):4 tan ♂ ($R^wR^w, R^{wr}, R^{wr}, rr$).

PEDIGREE NUMBER	F_1		F_2		
	♀ white	♂ tan	♀ white	♀ tan	♂ tan
22	3	3	21	16	21
75 (3)	20	24	124	28	155
76 (4)	20	19	111	49	175
218	13	8	55	20	86
270	5	6	13	4	19
271	1	12	91	20	133
274	19	17	179	52	273
Totals	81	89	594	189	862
Calculated	85	85	618	206	824

TABLE 12

Test 6 P_1 = tan ♀ (rr) × tan ♂ (R^wR^w) of the tan type; F_1 and F_2 as in table 11.

PEDIGREE NUMBER	F_1		F_2		
	♀ white	♂ tan	♀ white	♀ tan	♂ tan
78 (4)	34	31	48	22	60
81 (4)	17	12	35	11	34
206	22	28	83	20	125
Totals	73	71	166	53	219
Calculated	72	72	165	55	220

Back-cross tests and the heredity of the four body colors

Conclusions from back-cross tests (tests 7 to 13; tables 13 to 19)

These crosses show that any two of the four color factors may stand in relation of allelomorphs to each other. The results also demonstrate that the order of dominance, as previously given, is red, black, white, and tan. Polymorphism and sex-limited inheritance are also manifested. The following tests give further proof.

TABLE 13

Test 7: Red, heterozygous for red and white, by homozygous red. P_1 = red ♀ (RR^w) × tan ♂ (RR) of the red type: five pairs mated. F_1 = red ♀ (RR, RR^w , totals 148): tan ♂ (RR, RR^w , totals 121).

Reciprocal cross

 P_1 = red ♀ (RR) × tan ♂ (RR^w) of a red-white combination: five pairs mated. F_1 = red ♀ (RR, RR^w ; totals 166): tan ♂ (RR, RR^w ; totals 163).

TABLE 14

Test 8: Red, heterozygous for red and white, by homozygous white. P_1 = red ♀ (RR) × tan ♂ (R^wR^w) of the white type. F_1 = 1 red ♀ (RR^w):1 white ♀ (R^wR^w):2 tan ♂ (RR^w, R^wR^w).

CULTURE NUMBER	RED ♀ (RR^w)	WHITE ♀ (R^wR^w)	TAN ♂ (RR^w, R^wR^w)
1046	16	19	44
1054	2	6	5
1055	9	6	15
1056	5	9	5
1057	18	11	49
Totals.....	50	51	111
Calculated.....	53	53	106

Reciprocal cross

 P_1 = white ♀ (R^wR^w) × tan ♂ (RR^w) of a red-white combination. F_1 = Same as above.

CULTURE NUMBER	RED ♀ (RR^w)	WHITE ♀ (R^wR^w)	TAN ♂ (RR^w, R^wR^w)
2031	13	15	29
2036	26	22	44
2037	5	4	21
15611	6	11	14
15612	3	1	5
16170	9	8	11
Totals.....	62	61	124
Calculated.....	62	62	124

TABLE 15

Test 9: Red, heterozygous for red and black, by homozygous black.

P₁ = red ♀ (RR^b) × tan ♂ (R^bR^b) of the black type.
F₁ = 1 red ♀ (RR^b):1 black ♀ (R^bR^b):2 tan ♂ (RR^b, R^bR^b).

CULTURE NUMBER	RED ♀ (RR ^b)	BLACK ♀ (R ^b R ^b)	TAN ♂ (RR ^b , R ^b R ^b)
1012	29	31	26
1013	16	21	42
1014	12	24	53
1029	30	22	25
1030	19	26	45
1031	18	19	39
1032	3	1	1
1047	12	18	25
1048	20	10	28
1521	7	5	15
1536	20	21	42
1577	22	28	25
Totals.....	208	226	368
Calculated.....	201	201	402

Reciprocal cross

P₁ = black ♀ (R^bR^b) × tan ♂ (RR^b) of a red-black combination.
F₁ = Same as above.

CULTURE NUMBER	RED ♀ (RR ^b)	BLACK ♀ (R ^b R ^b)	TAN ♂ (RR ^b , R ^b R ^b)
1311	2	3	1
1004	10	8	41
1008	14	16	26
1026	44	42	106
1027	23	13	49
1028	19	18	35
1029	22	21	39
Totals.....	134	121	297
Calculated.....	138	138	276

TABLE 16

Test 10: Black, heterozygous for black and tan, by homozygous tan.

P_1 = black ♀ ($R^b r$) × tan ♂ (rr) of the tan type.

F_1 = 1 black ♀ ($R^b R$): 1 tan ♀ (rr): 2 tan ♂ ($R^b r, rr$).

CULTURE NUMBER	BLACK ♀ ($R^b r$)	TAN ♀ (rr)	TAN ♂ ($R^b r, rr$)
1023	13	18	47
1362	33	31	64
1377	29	22	43
1379	13	17	32
Totals.....	88	88	186
Calculated.....	90	90	180

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ ($R^b r$) of a black-tan combination.

F_1 = Same as above.

CULTURE NUMBER	BLACK ♀ ($R^b r$)	TAN ♀ (rr)	TAN ♂ ($R^b r, rr$)
1345	3	8	17
1347	2	5	14
1365	5	1	2
1367	7	4	9
13611	9	11	21
13614	6	4	11
Totals.....	32	33	64
Calculated.....	32	32	64

TABLE 17

Test 11: Black, heterozygous for black and white, by homozygous white.

P_1 = black ♀ ($R^b R^w$) × tan ♂ ($R^w R^w$) of the white type.

F_1 = 1 black ♀ ($R^b R^w$): 1 white ♀ ($R^w R^w$): 2 tan ♂ ($R^b R^w, R^w R^w$).

CULTURE NUMBER	BLACK ♀ ($R^b R^w$)	WHITE ♀ ($R^w R^w$)	TAN ♂ ($R^b R^w, R^w R^w$)
1041	14	12	30
1042	12	10	19
1043	16	22	36
1044	18	16	33
1045	12	13	35
Totals.....	72	73	153
Calculated.....	74	74	148

Reciprocal cross

P_1 = white ♀ ($R^w R^w$) × tan ♂ ($R^b R^w$) of a black-white combination.

F_1 = Same as above.

CULTURE NUMBER	BLACK ♀ ($R^b R^w$)	WHITE ♀ ($R^w R^w$)	TAN ♂ ($R^b R^w, R^w R^w$)
1993	5	6	12
2005	17	18	33
2006	22	19	39
2007	24	27	52
2008	19	20	38
Totals.....	87	90	174
Calculated.....	88	88	176

TABLE 18

Test 12: White, heterozygous for white and tan, by homozygous tan.

P_1 = white ♀ (R^{wr}) × tan ♂ (rr) of the tan type.

F_1 = 1 white ♀ (R^{wr}): 1 tan ♀ (rr): 2 tan ♂ (R^{wr}, rr).

CULTURE NUMBER	WHITE ♀ (R^{wr})	TAN ♀ (rr)	TAN ♂ (R^{wr}, rr)
1058	15	15	29
1060	10	11	23
2016	19	20	40
2017	8	9	18
2018	13	12	24
Totals.....	65	67	134
Calculated.....	67	67	134

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ (R^{wr}) of a white-tan combination.

F_1 = Same as above.

CULTURE NUMBER	WHITE ♀ (R^{wr})	TAN ♀ (rr)	TAN ♂ (R^{wr}, rr)
1034	3	4	6
1036	6	13	19
2019	10	6	19
2020	16	17	34
1049	12	11	22
Totals.....	47	51	100
Calculated.....	50	50	100

TABLE 19

Test 13: Red, heterozygous for red and tan, by homozygous tan.

P_1 = red ♀ (Rr) × tan ♂ (rr) of the tan type.

F_1 = 1 red ♀ (Rr): 1 tan ♀ (rr): 2 tan ♂ (Rr, rr).

CULTURE NUMBER	RED ♀ (Rr)	TAN ♀ (rr)	TAN ♂ (Rr, rr)
2031	15	16	32
2032	19	18	35
2033	10	9	20
2034	17	19	36
2035	20	21	42
Totals.....	81	83	165
Calculated.....	82	82	164

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ (Rr) of a red-tan combination.

F_1 = Same as above.

CULTURE NUMBER	RED ♀ (Rr)	TAN ♀ (rr)	TAN ♂ (Rr, rr)
2036	21	20	42
2037	18	19	37
2038	14	12	25
2039	12	13	24
2040	16	16	31
Totals.....	81	80	159
Calculated.....	80	80	160

The genetic behavior of hybrid crosses involving three factors in relation to a multiple allelomorph series

Conclusions based on the preceding crosses involving three color factors (tests 13 to 24; tables 20 to 30)

When a Bruchid which is heterozygous for any two color factors, is mated with a homozygous individual carrying a third color factor, the progeny will approximate a 1:1 ratio or a 1:1:2 ratio. These ratios are, of course, typical sex-limited ones.

This group of tests furnishes proof that the four color factors form a system of multiple allelomorphs, for it is evident that only two of these factors can exist at any one time in any one individual, and since the elytra colors are sex-limited, they are not manifested in the males.

TABLE 20

Test 14: White, heterozygous for white and tan, by homozygous red.

P_1 = white ♀ ($R^w r$) × tan ♂ (RR) of the red type; two pairs mated.

F_1 = 1 red ♀ (RR^w, Rr ; totals 32):1 tan ♂ (RR^w, Rr ; totals 31).

Reciprocal cross

P_1 = red ♀ (RR) × tan ♂ ($R^w r$) of a white-tan combination; five pairs mated.

F_1 = 1 red ♀ (RR^w, Rr ; totals 93):1 tan ♂ (RR^w, Rr ; totals 68).

TABLE 21

Test 15: Black, heterozygous for black and white, by homozygous tan.

P_1 = black ♀ ($R^b R^w$) × tan ♂ (rr) of the tan type; six pairs mated.

F_1 = 1 black ♀ ($R^b r$; totals 75):1 white ♀ ($R^w r$; totals 96):2 tan ♂ ($R^b r, R^w r$; totals 184).

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ ($R^b R^w$) of a black-white combination; seven pairs mated.

F_1 = 1 black ♀ ($R^b r$; totals 50):1 white ♀ ($R^w r$; totals 50):2 tan ♂ ($R^b r, R^w r$; totals 74).

TABLE 22

Test 16: Black, heterozygous for black and tan, by homozygous white.

P_1 = black ♀ ($R^b r$) × tan ♂ ($R^w R^w$) of the white type; six pairs mated.

F_1 = 1 black ♀ ($R^b R^w$; totals 122):1 white ♀ ($R^w r$; totals 121):2 tan ♂ ($R^b R^w, R^w r$; totals 248).

Reciprocal cross

P_1 = white ♀ ($R^w R^w$) × tan ♂ ($R^b r$) of a black-tan combination; two pairs mated.

F_1 = 1 black ♀ ($R^b R^w$; totals 36):1 white ♀ ($R^w r$; totals 40):2 tan ♂ ($R^b R^w, R^w r$; totals 79).

TABLE 23

Test 17: Red, heterozygous for red and white, by homozygous tan.

P_1 = red ♀ (RR^w) × tan ♂ (rr) of the tan type; seven pairs mated.

F_1 = 1 red ♀ (Rr ; totals 144):1 white ♀ ($R^w r$; totals 137):2 tan ♂ ($Rr, R^w r$; totals 268).

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ (RR^w) of a red-white combination; five pairs mated.

F_1 = 1 red ♀ (Rr ; totals 78):1 white ♀ ($R^w r$; totals 70):2 tan ♂ ($Rr, R^w r$; totals 184).

TABLE 24

Test 18: Red, heterozygous for red and white, by homozygous black. P_1 = red ♀ (RR^w) × tan ♂ (R^bR^b) of the black type; six pairs mated. F_1 = 1 red ♀ (RR^b ; totals 104):1 black ♀ (R^bR^w ; totals 90):2 tan ♂ (RR^b , R^bR^w ; totals 197).

Reciprocal cross

 P_1 = black ♀ (R^bR^b) × tan ♂ (RR^w) of a red-white combination; four pairs mated. F_1 = 1 red ♀ (RR^b ; totals 53):1 black ♀ (R^bR^w ; totals 51):2 tan ♂ (RR^b , R^bR^w ; totals 121).

TABLE 25

Test 19: Red, heterozygous for red and black, by homozygous tan. P_1 = red ♀ (RR^b) × tan ♂ (rr) of the tan type; six pairs mated. F_1 = 1 red ♀ (Rr ; totals 97):1 black ♀ (R^br ; totals 79):2 tan ♂ (Rr , R^br ; totals 194).

Reciprocal cross

 P_1 = tan ♀ (rr) × tan ♂ (RR^b) of a red-black combination; three pairs mated. F_1 = 1 red ♀ (Rr ; totals 34):1 black ♀ (R^br ; totals 22):2 tan ♂ (Rr , R^br ; totals 48).

TABLE 26

Test 20: Red, heterozygous for red and black, by homozygous white. P_1 = red ♀ (RR^b) × tan ♂ (R^wR^w) of the white type; four pairs mated. F_1 = 1 red ♀ (RR^w ; totals 39):1 black ♀ (R^bR^w ; totals 33):2 tan ♂ (RR^w , R^bR^w ; totals 76).

Reciprocal cross

 P_1 = white ♀ (R^wR^w) × tan ♂ (RR^b) of a red-black combination; four pairs mated. F_1 = 1 red ♀ (RR^w ; totals 36):1 black ♀ (R^bR^w ; totals 36):2 tan ♂ (RR^w , R^bR^w ; totals 69).

TABLE 27

Test 21: Black, heterozygous for black and tan, by homozygous red. P_1 = black ♀ (R^br) × tan ♂ (RR) of the red type; five pairs mated. F_1 = 1 red ♀ (RR^b , Rr ; totals 204):1 tan ♂ (RR^b , Rr ; totals 192).

Reciprocal cross

 P_1 = red ♀ (RR) × tan ♂ (R^br) of a black-tan combination; four pairs mated. F_1 = 1 red ♀ (RR^b , Rr ; totals 166):1 tan ♂ (RR^b , Rr ; totals 200).

TABLE 28

Test 22: Black, heterozygous for black and white, by homozygous red. P_1 = black ♀ (R^bR^w) × tan ♂ (RR) of the red type; six pairs mated. F_1 = red ♀ (RR^b , RR^w ; totals 217):tan ♂ (RR^b , RR^w ; totals 227).

Reciprocal cross

 P_1 = red ♀ (RR) × tan ♂ (R^bR^w) of a black-white combination; three pairs mated. F_1 = 1 red ♀ (RR^b , RR^w ; totals 50):1 tan ♂ (RR^b , RR^w ; totals 36).

TABLE 29

Test 23: White, heterozygous for white and tan, by homozygous black. P_1 = white ♀ (R^wr) × tan ♂ (R^bR^b) of the black type; two pairs mated. F_1 = 1 black ♀ (R^bR^w , R^br ; totals 51):1 tan ♂ (R^bR^w , R^br ; totals 40).

Reciprocal cross

 P_1 = black ♀ (R^bR^b) × tan ♂ (R^wr) of a white-tan combination; seven pairs mated. F_1 = 1 black ♀ (R^bR^w , R^br ; totals 155):1 tan ♂ (R^bR^w , R^br ; totals 142).

TABLE 30

Test 24: Red, heterozygous for red and tan, by homozygous black. P_1 = black ♀ (R^bR^b) × tan ♂ (Rr) of a red-tan combination; four pairs mated. F_1 = 1 red ♀ (RR^b ; totals 56):1 black ♀ (R^br ; totals 61):2 tan ♂ (RR^b , R^br ; totals 123).*Further proof of a multiple allelomorph series by the genetic behavior of two hybrid crosses*

Conclusions based on hybrid crosses involving four factors for body color (tests 25 to 36; tables 31 to 42)

It is again evident from these tests that only two of the factors for body color can exist at any one time in any individual. This is a proof of a multiple allelomorph system. The reciprocal crosses prove that the males carry the same combinations as the females, although they are not conspicuous in their phenotypes. The ratios derived from this group of tests are 1:1:2, 2:1:1:4, and 3:1:4; these ratios give evidence of sex-limitation.

TABLE 31

Test 25: Red, heterozygous for red and black, by white, heterozygous for white and tan. P_1 = red ♀ (RR^b) × tan ♂ (R^wr); eleven pairs mated. F_1 = 1 red ♀ (RR^w , Rr ; totals 190):1 black ♀ (R^bR^w , R^br ; totals 196):2 tan ♂ (RR^w , Rr , R^bR^w , R^br ; totals 311).

Reciprocal cross

 P_1 = white ♀ (R^wr) × tan ♂ (RR^b); nine pairs mated. F_1 = 1 red ♀ (RR^w , Rr ; totals 167):1 black ♀ (R^bR^w , R^br ; totals 119):2 tan ♂ (RR^w , Rr , R^bR^w , R^br ; totals 375).

TABLE 32

Test 26: Red, heterozygous for red and black, by black, heterozygous for black and white. P_1 = red ♀ (RR^b) × tan ♂ (R^bR^w); six pairs mated. F_1 = 1 red ♀ (RR^b , RR^w ; totals 88):1 black ♀ (R^bR^b , R^bR^w ; totals 86):2 tan ♂ (RR^b , RR^w , R^bR^b , R^bR^w ; totals 148).

Reciprocal cross

 P_1 = black ♀ (R^bR^w) × tan ♂ (RR^b); five pairs mated. F_1 = 1 red ♀ (RR^b , RR^w ; totals 95):1 black ♀ (R^bR^b , R^bR^w ; totals 91):2 tan ♂ (RR^b , RR^w , R^bR^b , R^bR^w ; totals 179).

TABLE 33

Test 27: Red, heterozygous for red and black, by black, heterozygous for black and tan. P_1 = red ♀ (RR^b) × tan ♂ (R^br); nine pairs mated. F_1 = 1 red ♀ (RR^b , Rr ; totals 185):1 black ♀ (R^bR^b , R^br ; totals 182):2 tan ♂ (RR^b , Rr , R^bR^b , R^br ; totals 346).

Reciprocal cross

 P_1 = black ♀ (R^br) × tan ♂ (RR^b); nine pairs mated. F_1 = 1 red ♀ (RR^b , Rr ; totals 176):1 black ♀ (R^bR^b , R^br ; totals 174):2 tan ♂ (RR^b , Rr , R^bR^b , R^br ; totals 383).

TABLE 34

Test 28: White, heterozygous for white and tan, by red, heterozygous for red and white.

P_1 = white ♀ ($R^w r$) × tan ♂ (RR^w); two pairs mated.

F_1 = 1 red ♀ (RR^w, Rr ; totals 24):1 white ♀ ($R^w R^w, R^w r$; totals 30):2 tan ♂ ($RR^w, Rr, R^w R^w, R^w r$; totals 89).

TABLE 35

Test 29: Red, heterozygous for red and tan, by black, heterozygous for black and tan.

P_1 = red ♀ (Rr) × tan ♂ ($R^b r$); twelve pairs mated.

F_1 = 2 red ♀ (RR^b, Rr ; totals 161):1 black ♀ ($R^b r$; totals 83):1 tan ♀ (rr ; totals 89):4 tan ♂ ($RR^b, Rr, R^b r, rr$; totals 345).

Reciprocal cross

P_1 = black ♀ ($R^b r$) × tan ♂ (Rr); six pairs mated.

F_1 = 2 red ♀ (RR^b, Rr ; totals 151):1 black ♀ ($R^b r$; totals 49):1 tan ♀ (rr ; totals 61):4 tan ♂ ($RR^b, Rr, R^b r, rr$; totals 249).

TABLE 36

Test 30: Red, heterozygous for red and white, by black, heterozygous for black and tan.

P_1 = red ♀ (RR^w) × tan ♂ ($R^b r$); eleven pairs mated.

F_1 = 2 red ♀ (RR^b, Rr ; totals 179):1 black ♀ ($R^b R^w$; totals 59):1 white ♀ ($R^w r$; totals 78):4 tan ♂ ($RR^b, Rr, R^b R^w, R^w r$; totals 320).

Reciprocal cross

P_1 = black ♀ ($R^b r$) × tan ♂ (RR^w); nine pairs mated.

F_1 = 2 red ♀ (RR^b, Rr ; totals 154):1 black ♀ ($R^b R^w$; totals 62):1 white ♀ ($R^w r$; totals 67):4 tan ♂ ($RR^b, Rr, R^b R^w, R^w r$; totals 307).

TABLE 37

Test 31: Black, heterozygous for black and white, by red, heterozygous for red and white.

P_1 = black ♀ ($R^b R^w$) × tan ♂ (RR^w); seven pairs mated.

F_1 = 2 red ♀ (RR^b, RR^w ; totals 74):1 black ♀ ($R^b R^w$; totals 40):1 white ♀ ($R^w R^w$; totals 39):4 tan ♂ ($RR^b, RR^w, R^b R^w, R^w R^w$; totals 198).

Reciprocal cross

P_1 = red ♀ (RR^w) × tan ♂ ($R^b R^w$); seven pairs mated.

F_1 = 2 red ♀ (RR^b, RR^w ; totals 95):1 black ♀ ($R^b R^w$; totals 53):1 white ♀ ($R^w R^w$; totals 48):4 tan ♂ ($RR^b, RR^w, R^b R^w, R^w R^w$; totals 236).

TABLE 38

Test 32: Black, heterozygous for black and tan, by white, heterozygous for white and tan.

P_1 = black ♀ ($R^b r$) × tan ♂ ($R^w r$); eight pairs mated.

F_1 = 2 black ♀ ($R^b R^w, R^b r$; totals 127):1 white ♀ ($R^w r$; totals 51):1 tan ♀ (rr ; totals 52):4 tan ♂ ($R^b R^w, R^b r, R^w r, rr$; totals 245).

Reciprocal cross

P_1 = white ♀ ($R^w r$) × tan ♂ ($R^b r$); five pairs mated.

F_1 = 2 black ♀ ($R^b R^w, R^b r$; totals 52):1 white ♀ ($R^w r$; totals 26):1 tan ♀ (rr ; totals 31):4 tan ♂ ($R^b R^w, R^b r, R^w r, rr$; totals 147).

TABLE 39

Test 33: Red, heterozygous for red and tan, by black, heterozygous for black and white.

P_1 = red ♀ (Rr) × tan ♂ (R^bR^w); fourteen pairs mated.

F_1 = 2 red ♀ (RR^b, RR^w ; totals 159):1 black ♀ (R^br ; totals 79):1 white ♀ (R^wr ; totals 68):4 tan ♂ (RR^b, RR^w, R^br, R^wr ; totals 287).

Reciprocal cross

P_1 = black ♀ (R^bR^w) × tan ♂ (Rr); one pair mated.

F_1 = 2 red ♀ (RR^b, RR^w ; totals 21):1 black ♀ (R^br ; totals 9):1 white ♀ (R^wr ; totals 11):4 tan ♂ (RR^b, RR^w, R^br, R^wr ; totals 47).

TABLE 40

Test 34: White, heterozygous for white and tan, by red, heterozygous for red and tan.

P_1 = white ♀ (R^wr) × tan ♂ (Rr); one pair mated.

F_1 = 2 red ♀ (RR^w, Rr ; totals 13):1 white ♀ (R^wr ; totals 6):1 tan ♀ (rr ; totals 5):4 tan ♂ (RR^w, Rr, R^wr, rr ; totals 19).

TABLE 41

Test 35: Red, heterozygous for red and white, by red, heterozygous for red and tan.

P_1 = red ♀ (RR^w) × tan ♂ (Rr); seven pairs.

F_1 = 3 red ♀ (RR, RR^w, Rr ; totals 160):1 white ♀ (R^wr ; totals 54):4 tan ♂ (RR, RR^w, Rr, R^wr ; totals 214).

Reciprocal cross

P_1 = red ♀ (Rr) × tan (RR^w); one pair mated.

F_1 = 3 red ♀ (RR, RR^w, Rr ; totals 5):1 white ♀ (R^wr ; totals 2):4 tan ♂ (RR, RR^w, Rr, R^wr ; totals 11).

TABLE 42

Test 36: Red, heterozygous for red and tan, by red, heterozygous for red and black.

P_1 = red ♀ (Rr) × tan ♂ (RR^b); seven pairs mated.

F_1 = 3 red ♀ (RR, RR^b, Rr ; totals 167):1 black ♀ (R^br ; totals 44):4 tan ♂ (RR, RR^b, Rr, R^br ; totals 234).

Reciprocal cross

P_1 = red ♀ (RR^b) × tan ♂ (Rr); one pair mated.

F_1 = 3 red ♀ (RR, RR^b, Rr ; totals 36):1 black ♀ (R^br ; totals 16):4 tan ♂ (RR, RR^b, Rr, R^br ; totals 54).

DISCUSSION

The following arguments, taken from MORGAN, STURTEVANT, MULLER and BRIDGES (1915) are in favor of a multiple allelomorph series:

1. That multiple allelomorphs seem to affect the same character. This is true for *Bruchus*, since the four body colors (red, black, white and tan) affect the entire color pattern.

2. That an individual may contain only two of the genes of the allelomorph series. These may be the same gene or different members of the allelomorph series. This behavior is manifested in *Bruchus*.

3. When any two mutant types of an allelomorphous series are crossed they give a type in the F_1 that is like the dominant parent or intermediate, because neither brings in the normal allelomorph of the other; consequently the wild type is not reconstituted. This relationship holds for the red, black and white mutant types of *Bruchus*.

4. There is no crossing over between the members of a multiple allelomorphous series since such genes occupy the same locus. No crossing over takes place between the four body colors of *Bruchus*.

In all these four respects the mutants of *Bruchus* fulfill the requirements of a multiple allelomorphous series.

In view of the observation that color dominance appears in the order of red, black, white and tan, it occurred to the writer that it might be interesting to note the correlation, if any, of this color dominance with such physiological traits as vigor, number of progeny, size and the like. As far as can be ascertained, the eggs of these four types are exactly similar in size and color. In the mature beetles, it was discovered that the blacks have the greatest number of progeny, and are most vigorous; the reds follow next in number of offspring and vigor; the tans (or wild type) are next in order, while the white ones rank fourth, because of a seeming lack of vigor and reproductive power. The types in order of size, are black, tan, red and white. There is, further, a marked variation as regards color in these types; for the whites may approach the blacks and the reds may verge on the whites as well as on the tans. Great care is therefore necessary to avoid chance errors in classification.

The sexual dimorphism found in *Bruchus* is similar to one discovered in *Drosophila*. The following quotation from MORGAN (1916) is pertinent:

"A mutant appeared in which the eye color of the female was different from that of the male. The eye color of the female is a dark eosin color, that of the male yellowish eosin. From the beginning this difference was as marked as it is today. Breeding experiments show that eosin eye color differs from the red color of the eye of the wild fly by a single mutant factor. Here, then, at a single step a type appeared that was sexually dimorphic."

It is evident that the color types in *Bruchus* manifest a similar behavior.

Another interpretation could be put on this sexual dimorphism in *Bruchus*, which could be made to account for this sex-limitation in color. FOOT and STROBELL (1913) discovered a sex-limited trait in two species of Hemiptera. In one species both sexes were without a spot, while the males in the second species carried a spot. In regard to this MORGAN (1919) states that the results are explicable on the assumption that a single dominant factor, not sex-linked, causes the spot in the males, but the

presence of the gene in the female produces no effect; consequently, the effect is sex-limited and its expression is determined by the rest of the hereditary complex in male or female. This interpretation would likewise account for the results obtained in *Bruchus*. In this connection, another quotation from MORGAN and his associates (MORGAN, STURTEVANT, MULLER and BRIDGES 1915) is noteworthy:

"Thus while the accessory sexual organs, as well as the secondary sexual characters, may be modified by special differentiators that are not present in the sex chromosomes; yet the sex factor also produces an effect on their development which is different according to whether the sex factor exists in single or double amount."

The results obtained in *Bruchus* are very similar to the sex-limited inheritance found in Ayrshire cattle as interpreted by WENTWORTH (1916). It is of interest in this connection to quote the author:

"Two general types of inheritance as related to sex exist, aside from the ordinary secondary sex characters. Sex-linked inheritance depends on the great mass of hereditary factors that have been shown to be linked in transmission to the sex-determining factors; while sex-limited factors follow the simple Mendelian scheme of inheritance, but show a reversal of dominance in the two sexes."

The nearest genetic evidence related to this problem is found in the observations on the Java butterfly (*Papilio memnon*, L.) by JACOBSON. These results were discussed in detail by DE MEIJERE (1910), who applied Mendelian principles to these experiments.

To quote MORGAN (1914):

"DE MEIJERE accounts for the results of matings in this species, recorded by JACOBSON, on the assumption of three factors, one for each type of female. The three factors are treated as allelomorphs, and therefore only two of them can be present in any individual, and since they are allelomorphs they pass into different gametes. The order of dominance is Achates, Agenor, Laomedon. The male carries the same factors, but they are not effective in him."

The genetic behavior in *Bruchus* is somewhat similar to that obtained for *Papilio*, except that in the former four factors are involved and in the latter only three.

CONCLUSIONS

1. This paper presents the genetic basis of the inheritance of four body and elytra colors in *Bruchus quadrimaculatus*, Fabr.
2. The results prove for *Bruchus* that any color factor can be an allelomorph with any other factor for body color. The order of dominance is red, black, white, and tan.

3. The four factors (R , R^b , R^w , and r) for the four body colors (red, black, white and tan) constitute a multiple allelomorph system.
4. Sexual dimorphism is exhibited in this species.
5. The life-history studies indicate that this weevil is favorable for genetic researches.

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