MOSAIC DOMINANCE IN THE INHERITANCE OF COLOR PATTERNS IN THE LADY-BIRD BEETLE, HARMONIA AXYRIDIS*,[1]

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INTRODUCTION

HARMONIA AXYRIDIS Pallas is a species of the coleopterous family Coccinellidae. Its distribution extends from southern Siberia (Altai Mountains) to Manchuria, Korea, Japan, and China. The color patterns on the elytra, and also on the pronotum, of this species are extraordinarily variable, so much so that some of the color patterns have been described by the old school of taxonomic entomologists as belonging not only to several species but also in fact to different genera. No less than two hundred different color forms are known from different localities (HEMMELMANN, in MADER 1932, TAN and LI 1932). As shown by DOBZHANSKY (1924) and by TAN and LI (1932), each of these color forms is found in only a part of the geographic distribution area of the species, and the population of each geographic region can be described in terms of the relative frequencies of the color patterns found in it.

In the entomological literature, the color variants of *Harmonia axyridis* have been given Latin names, subject to the taxonomic priority rules. The above quoted HEMMELMANN carried this to the extreme by giving a separate name to each variant. He is responsible for the great majority of a total of 105 names listed by KORSCHEFSKY (1932). This is, of course, a superfluous and unscientific procedure. The writer found it most convenient to classify the entire variety of color patterns in fifteen classes represented in figure 61. The genetic analysis of the color patterns was started by TAN and LI (1932, 1934), who found these patterns to be inherited in a simple Mendelian way. TAN and LI first assumed several loci to account for their inheritance, but HOSHINO (1940) and TAN (1942 and unpublished data) concluded that a series of multiple alleles of a single autosomal locus accounts for all the data available.

TAN (1942) pointed out an interesting phenomenon of "mosaicism" in the expression of the color pattern in individuals heterozygous for different alleles. The essence of this phenomenon is as follows. When two color patterns in homozygotes differ in that one shows a black pigmentation on the part of the elytron which is not black in the other, the heterozygote always has this part black. If each of two color patterns in homozygotes has black areas that are not black in the other, the heterozygote develops black pigmentation on

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any part of the elytron which is black in either homozygote. In other words, the heterozygotes form black pigment on any part of the elytron which is pigmented in the respective homozygotes. The present article reports further data bearing on this phenomenon of "mosaic dominance."

MATERIAL AND METHOD

The color patterns of *Harmonia axyridis* can be divided in two groups. One group, to which the name *succinea* will be applied, has yellow elytra or yellow with black spots. The position of the black spots is quite constant (fig. 10), but their number varies from zero to a maximum of 19 (on both elytra together). The odd spot lies at the scutellar angle and is shared by both elytra. The size of the spots varies, and some of them may fuse together into black bands. TAN and LI (1932) found that the variations in the number and size of the black spots on the yellow background in the form *succinea* are in part determined by the length of the pupal period. A prolongation of pupal development owing to low temperatures brings more and larger spots, while acceleration of the development leads toward reduction of the spotting. The other group of color patterns has a black background of the elytra with a varying number and form of yellow or orange spots (fig. 13–23). These patterns are *conspicua*-1 (fig. 13), *conspicua*-2 (fig. 14), *transversifascia*-3 (fig. 15), *transversifascia*-1 (fig. 16), *equicolor* (fig. 17), *spectabilis*-1 (fig. 18), *spectabilis*-2 (fig. 19), *intermedia* (fig. 20), *aulica*-2 (fig. 21), *aulica*-1 (fig. 22), and *tripunctata* (fig. 23).

The initial material used in our crosses was collected in the vicinity of the town of Meitan, province of Kweichow, southwestern China. The most common color variants in this locality are *succinea* (fig. 1–11), *conspicua*-1, and *spectabilis*-1. Less frequently occurring types are *aulica* and *transversifascia*. As indicated above, the name "*succinea*" is used to include all forms with yellow background of the elytra, regardless of the number of spots.

The following experimental procedure was adopted. Any type of color pattern the inheritance of which was to be studied was first of all outcrossed to a homozygous *succinea* line. Since all color patterns have pigmented parts of the elytra which are light in *succinea*, the heterozygous forms are invariably distinguishable from *succinea*. Among the offspring, those which were heterozygous for *succinea* and another allele were selected for further experiments. Consequently, with 12 alleles, a series of 11 different types of heterozygotes with *succinea* was established. These different types of heterozygotes were then intercrossed for the purpose of obtaining heterozygotes for different specific alleles in each combination.

The experiments were carried on in the summer months of 1943 and 1944. The technique was essentially the same as had been previously described (TAN 1933). For each type of mating, a pair of reciprocal crosses involving one female and one male were originally planned. In feeding the young larvae, special caution was taken to avoid contamination by wild larvae not infrequently found among the aphids. This is especially important in the crosses between the dominant heterozygotes and *succinea* ($S^aS^b \times ss$), where the

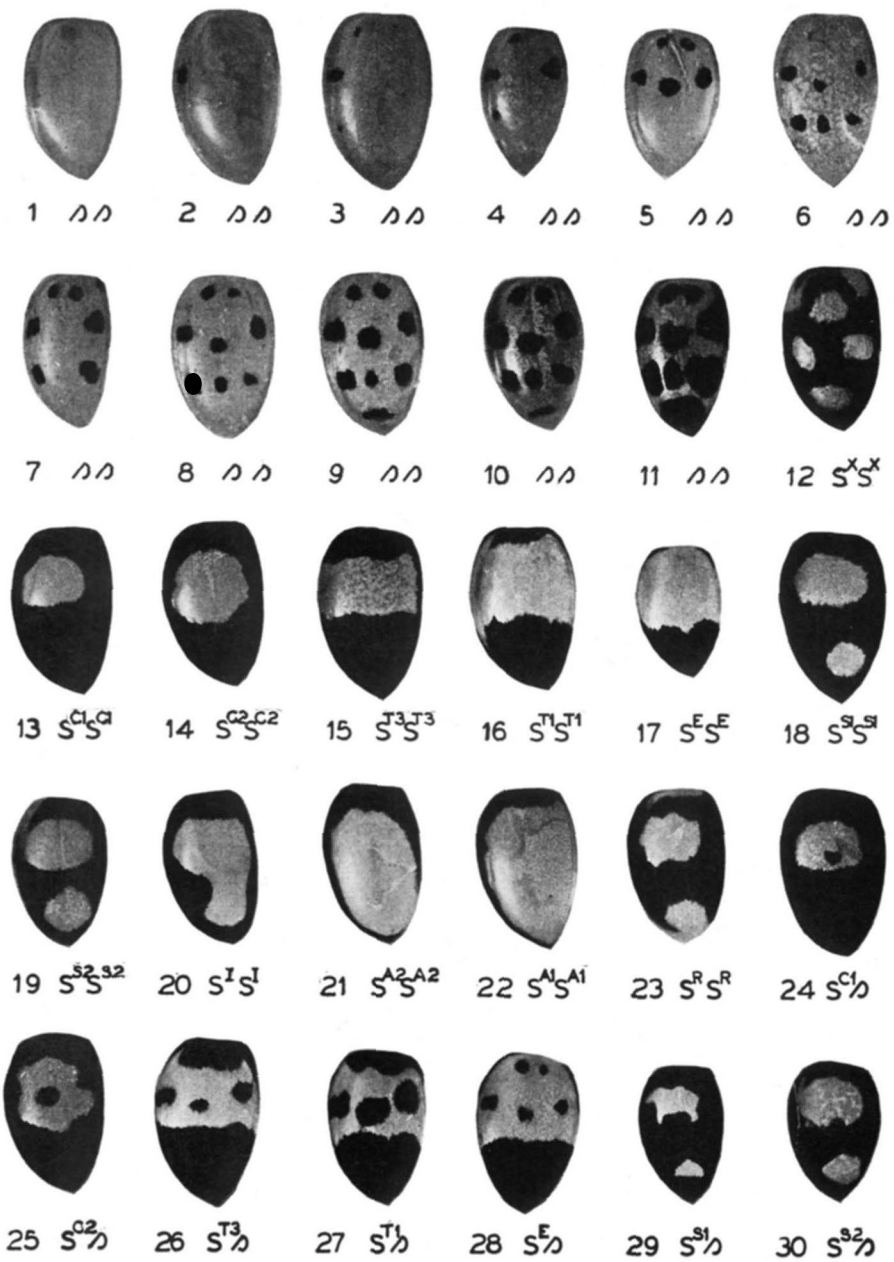

PLATE I, FIGURES 1–30. See reverse for description.

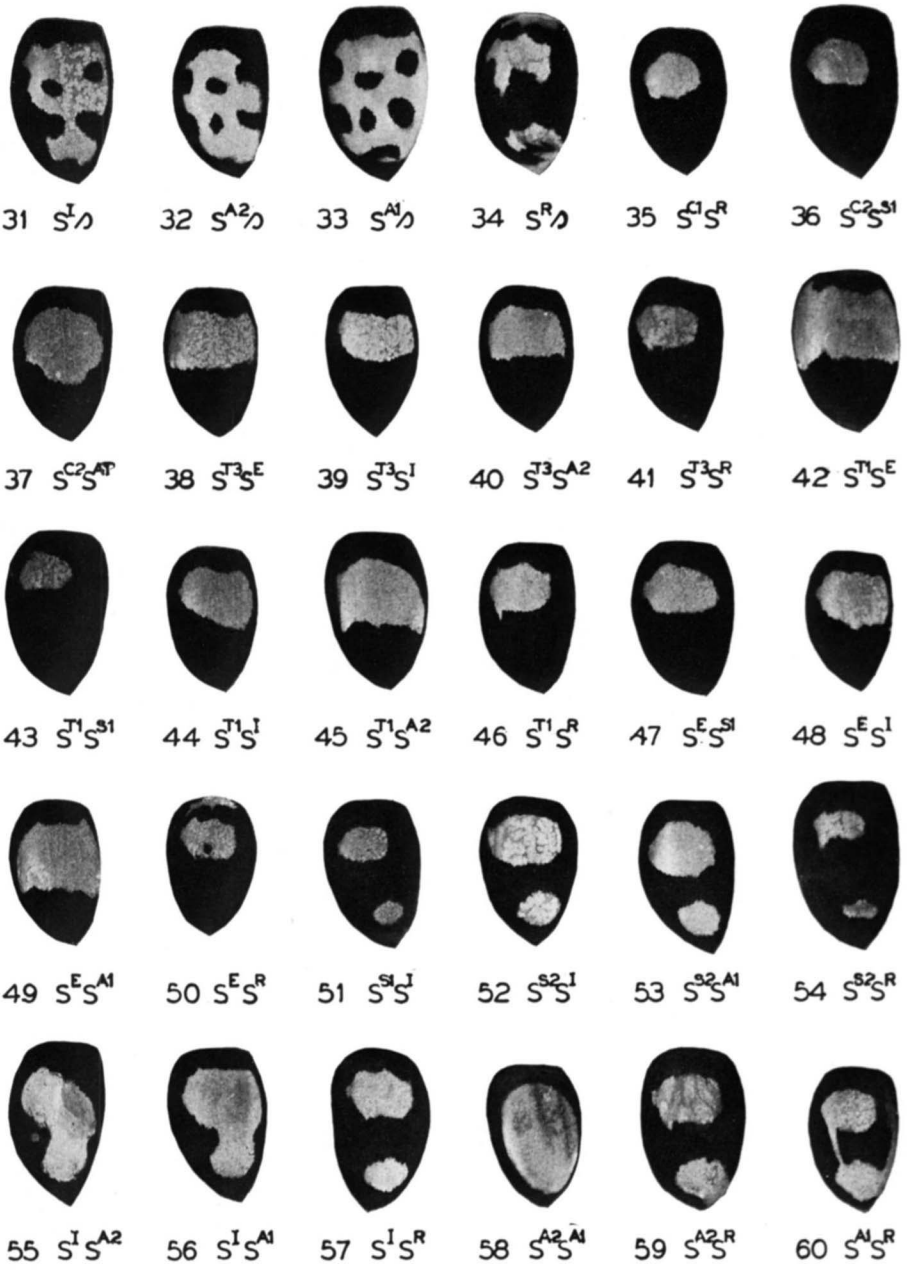

PLATE 1 and 2.—Figures 1–60: Pictures of left elytra of *Harmonia axyridis* showing the color patterns of various homozygotes and heterozygotes for 12 different alleles. The allelic symbols are: *s* for *succinea*, S^{X} for *axyridis*, S^{C1} for *conspicua*-1, S^{C2} for *conspicua*-2, S^{T3} for *transversifascia*-3, S^{T1} for *transversifascia*-1, S^{E} for *equicolor*, S^{S1} for *spectabilis*-1, S^{S2} for *spectabilis*-2, S^{I} for *intermedia*, S^{A2} for *aulica*-2, S^{A1} for *aulica*-1, and S^{R} for *tripunctata*.

presence or the absence of *succinea* in the progeny is crucial in determining the allelic behavior of these genes. Because of the frequent trouble with the aphid supply and the labor demanded in individual handling (since the larvae are carnivorous), many crosses gave finally few or even no adult offspring. This accounts for the discrepancy or the entire absence of the data in a number of cases.

All pictures were taken from the pinned material of single representative specimen for each kind brought over from China. These specimens were actually obtained from the crosses. Each picture represents only the left elytron, which was carefully detached from the beetle with the aid of a pair of fine forceps. The photographic reprints were slightly retouched in the black colored area so as to eliminate the artificial effect of light on the shining surface.

EXPERIMENTAL RESULTS AND OBSERVATIONS

Individuals heterozygous for each of the 11 types with *succinea* were obtained following the matings of the respective types to *succinea*. The genetic constitutions of these heterozygotes are: $S^{C1}s$, $S^{C2}s$, $S^{T3}s$, $S^{T1}s$, $S^{E}s$, $S^{S1}s$, $S^{S2}s$, $S^{I}s$, $S^{A2}s$, $S^{A1}s$, $S^{R}s$.

The elytral color patterns of the heterozygotes for *succinea* (*s*) and the other alleles show what could be described as a recessiveness of *succinea*, if it were not for a peculiar feature which can be denoted as presence of "indents" (see fig. 29, 30, and 34) or of small black dots within the yellow area (see fig. 26 and 28) or of both (fig. 25, 27, 31, 32, and 33). It should be recalled that the elytra of *succinea* are either yellow without spots or yellow with various numbers, up to 19, of black spots varying in size but occupying perfectly definite positions. Now, the heterozygotes between *succinea* and the other alleles invariably show black pigment on the parts of the elytra which are darkly pigmented in the homozygotes for the alleles other than *succinea*. Moreover, these heterozygotes may or may not show the "indents" or the characteristic black spots corresponding in locations to those of the spots which may or may not be present in homozygous *succinea*. Thus, heterozygotes for *conspicua*-1 and succinea ($S^{C1}s$) may either resemble *conspicua*-1 homozygotes (fig. 13) or they may be as shown in figure 24. *Conspicua*-2/*succinea* heterozygotes ($S^{C2}s$) may be as shown in figure 14 or in figure 25. *Transversifascia*-3/*succinea* ($S^{T3}s$) may be as shown in figure 15 or in figure 26. Similar comparisons can be made between figures 16 and 27, 17 and 28, 18 and 29, 19 and 30, 20 and 31, 21 and 32, 22 and 33, and 23 and 34.

It is easy to account for the origin of these variations in the forms heterozygous for *succinea*. The black spots of *succinea* appear in the heterozygotes in their proper positions, provided the developmental conditions for each spot are such as to permit their appearance. Otherwise, the spots fail to appear and the *succinea* characteristics seem completely recessive. The recessiveness is, consequently, a spurious one in this case. This interpretation has been checked by crossing individuals collected in nature and showing "indents" or spots with *succinea* from the laboratory. The individuals proved to be heterozygotes

for *succinea* and the other alleles. TAN and LI (1932) have recorded individuals with "indents" or characteristic spots in natural populations.

The results of the intercrosses of the different types of *succinea* heterozygotes are presented in tables 1 and 2 for the "inclusive" and "overlapping" types of heterozygous combinations, respectively. By inclusive type, we mean that the heterozygotes are composed of two such alleles that the black pigmented area of the pattern characteristic of one allele in homozygous condition is entirely included within that characteristic of the other allele in homozygous condition. In this case, the color pattern of the heterozygotes cannot be distinguished from that of the type of homozygote which has the more extensive black pigmented area. For example, the color pattern of the heterozygote between *transversifascia*-1 and *equicolor* ($S^{T1}S^{E}$) as shown in figure 42 is similar to that of the *transversifascia*-1 homozygotes (fig. 16). In the case of overlapping combinations, the two alleles differ so that the distribution of the black pigment characteristic of one in homozygous condition overlaps the distribution of that characteristic of the other in homozygous condition. Hence, mosaicism prevails, and the color pattern of the heterozygotes can always be distinguished from that of either parental homozygous types. The expression of the color pattern in the overlapping heterozygotes constitutes the main proof for the phenomenon of mosaic dominance.

Denoting one allele other than *succinea* as S^{a}, and another allele as S^{b}, a cross between two such *succinea* heterozygotes ($S^{a}s \times S^{b}s$) will produce $\frac{1}{4}$ so called "dominant" heterozygotes ($S^{a}S^{b}$), $\frac{1}{4}$ one parental type of *succinea* heterozygote ($S^{a}s$), $\frac{1}{4}$ the other parental type of succinea heterozygote ($S^{b}s$), and $\frac{1}{4}$ homozygous *succinea* (ss). In these tables, the two specific "dominant" alleles concerned (S^{a} and S^{b}) in each type of cross are indicated in the second column from the left. S^{a} is being referred to the allele, whose symbol is placed to the left in the column and S^{b} to the other allele whose symbol is placed to the right. In table 1, No. 1, S^{a} and S^{b} refer to the alleles S^{C1} and S^{T1} respectively, and the four classes of progeny $S^{a}S^{b}$, $S^{a}s$, $S^{b}s$, and ss are consequently represented by $S^{C1}S^{T1}$, $S^{C1}s$, $S^{T1}s$, and ss, respectively. For each cross, the genotypes of both female and male parent are given separately under the heading "parental types," and their respective origin from particular pedigree cross number is shown in parentheses. In the case quoted above (table 1, No. 1), for instance, the genotype of the female parent is $S^{C1}s$, which came from cross No. 503, while the genotype of the male parent is sS^{T1}, which came from cross No. 103. The two allelic symbols of each genotype are so represented that the one from the maternal side is placed to the left and the one from the paternal side to the right. The genotype written as $S^{C1}s$ means that the allele S^{C1} came from the grandmother and the allele s from the grandfather; the one written as sS^{T1} means that the allele s came from the grandmother and the allele S^{T1} from the grandfather. This system of reference is adopted in each of the four tables in this report. When the results of the reciprocal crosses are available, they are separately presented under one specific combination to show whether there are any differences among the reciprocal crosses. For example, in table 1, No. 7, the results for the combination $S^{T3}S^{E}$ were obtained

from two reciprocal crosses No. 143 and No. 145. If the results for one direction of mating were obtained from two separate crosses, the number of these crosses are given side by side. In table 2, No. 5, for instance, the results of the cross between $S^{T3}s$ as a female parent and sS^{R} as a male parent were obtained from two separate crosses Nos. 137 and 144.

As pointed out above, in the case of the inclusive type of heterozygous combinations, the effect on the pattern produced by one allele is covered up by that produced by the other. A distinction of "hypostatic" allele for the former

TABLE 1

Results of the intercrosses between different types of succinea heterozygotes ($S^{a}s \times S^{b}s$) for inclusive combinations.

NO.	ALLELES CONCERNED $S^{a}S^{b}$	CROSS NO.	PARENTAL TYPES (PEDIGREE NO.) ♀	♂	PROGENY CLASSES $S^{a}S^{b}+S^{a}s$	$S^{b}s$	ss	TOTAL
1	$S^{C1}S^{T1}$	180	$S^{C1}s$(503)	sS^{T1}(103)	11	4	6	21
2	$S^{C1}S^{E}$	204	$S^{C1}s$(177)	sS^{E}(124)	12	9	11	32
3	$S^{C1}S^{I}$	177	$S^{C1}s$(503)	sS^{I}(104)	15	7	5	27
4	$S^{C1}S^{R}$	228	$S^{C1}s$(180)	sS^{R}(133)	6	4	2	12
5	$S^{C2}S^{E}$	124	$S^{C2}s$(110)	sS^{E}(124)	14	9	8	31
6	$S^{T3}S^{T1}$	227	sS^{T1}(120)	sS^{T3}(122)	7	2	6	15
7	$S^{T3}S^{E}$	143	$S^{T3}s$(104)	sS^{E}(102)	(12	(9	(7	
		145	sS^{E}(102)	$S^{T3}s$(104)	17)	9)	12)	66
8	$S^{T1}S^{E}$	152	sS^{T1}(103)	sS^{E}(102)	25	12	10	47
9	$S^{I}S^{A1}$	123	$S^{A1}s$(501)	sS^{I}(104)	(15	(9	(6	
		147	$S^{I}s$(103)	$S^{A1}s$(111)	43)	24)	30)	127
10	$S^{A2}S^{A1}$	199	sS^{A2}(155)	$S^{A1}s$(123)	20	7	7	34
				Total	197	105	110	412

and "epistatic" allele for the latter is here suggested for the convenience of description. Throughout table 1, S^{a} is used in every combination to stand for the "epistatic" allele and S^{b} for the "hypostatic" allele. Since *succinea* heterozygotes for the epistatic allele ($S^{a}s$) that do not show the characteristic *succinea* effect of "indents" or spots are indistinguishable from the homozygotes for the epistatic allele ($S^{a}S^{a}$), to which the inclusive heterozygotes ($S^{a}S^{b}$) bear similarity, the class $S^{a}S^{b}$ cannot be distinguished with certainty from the class $S^{a}s$. Hence in table 1, these two classes are classified together including those $S^{a}s$ that do show the "*succinea* effect." The expected ratio should be 2 ($S^{a}S^{b}+S^{a}s$):1 $S^{b}s$:1 ss instead of 1 $S^{a}S^{b}$:1 $S^{a}s$:1 $S^{b}s$:1 ss. As the data for a number of such inclusive combinations including $S^{C1}S^{C2}$, $S^{C1}S^{S1}$, $S^{C1}S^{A2}$, $S^{C1}S^{A1}$, $S^{C2}S^{A2}$, $S^{C2}S^{A1}$, $S^{S1}S^{I}$, $S^{S1}S^{A2}$, and $S^{S1}S^{A1}$ had been previously obtained (TAN 1942), only the new combinations were experimentally tested. Data are available here for the following: $S^{C1}S^{T1}$, $S^{C1}S^{E}$, $S^{C1}S^{I}$, $S^{C1}S^{R}$, $S^{C2}S^{E}$, $S^{T3}S^{T1}$, $S^{T3}S^{E}$, $S^{T1}S^{E}$, $S^{I}S^{A1}$ and $S^{A2}S^{A1}$. As shown in table 1, the observed

TABLE 2

Results of the intercrosses between different types of succinea heterozygotes ($S^as \times S^bs$) for overlapping combinations.

NO.	ALLELES CONCERNED S^aS^b	CROSS NO.	PARENTAL TYPES (PEDIGREE NO.) ♀	♂	PROGENY CLASSES S^aS^b	S^as	S^bs	ss	TOTAL
1	$S^{T3}S^{S2}$	159	$S^{T3}s$(104)	sS^{S2}(105)	7	8	4	7	26
2	$S^{T3}S^{I}$	104	$S^{T3}s$(wild)	$S^{I}s$(wild)	(28 25)	(18 19)	(19 23)	(27 16)	
		115	sS^{I}(104)	$S^{T3}s$(104)					175
3	$S^{T3}S^{A2}$	161	$S^{A2}s$(102)	$S^{T3}s$(104)	2	3	—	—	5
4	$S^{T3}S^{A1}$	120	$S^{T3}s$(104)	$S^{A1}s$(105)	(27 4)	(23 8)	(29 8)	(24 13)	
		146	$S^{A1}s$(111)	$S^{T3}s$(104)					136
5	$S^{T3}S^{R}$	117	sS^{R}(101)	$S^{T3}s$(104)	(17 15)	(11 9)	(20 13)	(21 17)	
		137, 144	$S^{T3}s$(104)	sS^{R}(101)					123
6	$S^{T1}S^{S1}$	1005	$S^{T1}S^{T1}$(223)	$S^{S1}s$(wild)	164	175	—	2	341
7	$S^{T1}S^{I}$	103	$S^{I}s$(wild)	$S^{T1}s$(wild)	(8 1)	(21 —)	(20 1)	(21 1)	
		163	sS^{T1}(103)	$S^{I}s$(103)					73
8	$S^{T1}S^{A2}$	155	sS^{T1}(103)	$S^{A2}s$(102)	(23 2)	(24 12)	(25 4)	(24 5)	
		156	$S^{A2}s$(102)	$S^{T1}s$(103)					119
9	$S^{T1}S^{A1}$	168	$S^{A1}s$(111)	$S^{T1}s$(103)	16	15	12	10	53
10	$S^{T1}S^{R}$	154	sS^{R}(101)	sS^{T1}(103)	10	8	19	18	55
11	$S^{E}S^{S1}$	1006	$S^{E}s$(253)	$S^{S1}s$(wild)	(22 7)	(27 8)	(20 5)	(21 7)	
		1050A	$S^{S1}s$(1002)	$S^{E}s$(1020)					117
12	$S^{E}S^{I}$	126	sS^{I}(104)	sS^{E}(102)	(11 12)	(3 12)	(5 19)	(6 25)	
		149	sS^{E}(102)	$S^{I}s$(103)					93
13	$S^{E}S^{A2}$	102	$S^{A2}s$(wild)	$S^{E}s$(wild)	16	14	13	12	55
14	$S^{E}S^{A1}$	164	sS^{E}(102)	$S^{A1}s$(105)	11	6	6	11	34
15	$S^{E}S^{R}$	116	sS^{E}(102)	sS^{R}(101)	(22 11)	(9 6)	(29 7)	(20 10)	
		151	sS^{R}(101)	sS^{E}(102)					114
16	$S^{S2}S^{I}$	150	sS^{S2}(105)	$S^{I}s$(104)	13	7	16	18	54
17	$S^{S2}S^{A2}$	233	sS^{A2}(153)	$S^{S2}s$(150)	3	3	1	4	11
18	$S^{S2}S^{A1}$	105	$S^{A1}s$(wild)	$S^{S2}s$(wild)	15	5	9	17	46
19	$S^{S2}S^{R}$	232	$S^{S2}s$(209)	sS^{R}(137)	1	—	2	1	4
20	$S^{I}S^{A2}$	148	$S^{I}s$(103)	$S^{A2}s$(102)	17	15	17	16	65
21	$S^{I}S^{R}$	133	$S^{I}s$(103)	sS^{R}(101)	(7 27)	(8 13)	(9 16)	(6 14)	
		138	sS^{R}(101)	$S^{I}s$(104)					100
22	$S^{A2}S^{R}$	197	$S^{A2}s$(161)	$S^{R}s$(117)	5	—	5	2	12
23	$S^{A1}S^{R}$	166	$S^{A1}s$(111)	sS^{R}(101)	(7 2)	(3 4)	(12 —)	(17 4)	
		187	sS^{R}(133)	sS^{A1}(164)					49
			Total		558	497	388	417	1860
			Minus No. 6		164	175	—	2	341
			Total for 1:1:1:1 ratio		394	322	388	415	1519

ratios agree in most cases with the expected. Of all the possible combinations belonging to the inclusive type, experimental data are now lacking only in two cases, namely, $S^{C1}S^{T3}$ and $S^{C1}S^{S2}$. As illustrative of the nature of the inclusive heterozygotes, one finds the similarity between figure 35 ($S^{C1}S^{R}$) and figure 13 ($S^{C1}S^{C1}$), figure 38 ($S^{T3}S^{E}$) and figure 15 ($S^{T3}S^{T3}$), figure 42 ($S^{T1}S^{E}$) and figure 16 ($S^{T1}S^{T1}$), figure 51 ($S^{S1}S^{I}$) and figure 18 ($S^{S1}S^{S1}$), figure 56 ($S^{I}S^{A1}$) and figure 20 ($S^{I}S^{I}$), and figure 58 ($S^{A2}S^{A1}$) and figure 21 ($S^{A2}S^{A2}$).

The data for the overlapping dominant heterozygotes are shown in table 2. A total of 23 different combinations were recovered. These are: $S^{T3}S^{S2}$, $S^{T3}S^{I}$, $S^{T3}S^{A2}$, $S^{T3}S^{A1}$, $S^{T3}S^{R}$, $S^{T1}S^{S1}$, $S^{T1}S^{I}$, $S^{T1}S^{A2}$, $S^{T1}S^{A1}$, $S^{T1}S^{R}$, $S^{E}S^{S1}$, $S^{E}S^{I}$, $S^{E}S^{A2}$, $S^{E}S^{A1}$, $S^{E}S^{R}$, $S^{S2}S^{I}$, $S^{S2}S^{A2}$, $S^{S2}S^{A1}$, $S^{S2}S^{R}$, $S^{I}S^{A2}$, $S^{I}S^{R}$, $S^{A2}S^{R}$, and $S^{A1}S^{R}$. With one exception, all were obtained from the intercross of *succinea* heterozygotes ($S^{a}s \times S^{b}s$), and the frequencies of the four classes of individuals in the progeny fit to 1 $S^{a}S^{b}$:1 $S^{a}s$:1 $S^{b}s$:1 *ss* ratio in most cases. The observed overlapping heterozygotes, being the class $S^{a}S^{b}$, is represented in approximately 25 percent of the offspring in each type of cross. The exceptional case is shown in table 2, No. 6 representing the combination $S^{T1}S^{S1}$, which was recovered from a cross between a homozygous *transversifascia*-1 ($S^{T1}S^{T1}$) female and a *spectabilis*-1/*succinea* ($S^{S1}s$) male. As expected, this cross gives 164 *transversifascia*-1/*spectabilis*-1 overlapping heterozygotes ($S^{T1}S^{S1}$) and 175 *transversifascia*-1/*succinea* heterozygotes ($S^{T1}s$) which fit very closely to 1:1 ratio. The two *succinea* individuals maybe due to contamination or mutation or other cause. In a few cases such as for the combinations $S^{T3}S^{A2}$, $S^{S2}S^{R}$, and $S^{A2}S^{R}$ as shown in Nos. 3, 19, and 22 in table 2, the heterozygotes were recovered among a few individuals in the progeny. In several other cases, which gave only very few or no offspring, the overlapping heterozygotes were not recovered. Hence the data for combinations $S^{C2}S^{R}$, $S^{C2}S^{I}$, $S^{T3}S^{S1}$, $S^{T1}S^{S2}$, and $S^{S1}S^{R}$ are lacking.

In each of these recovered combinations, the overlapping heterozygotes can invariably be distinguished from the two parental types concerned. Some of these patterns are shown in figures 36, 39–41, 43–50, 52–55, 57, 59, and 60. These pictures cover all the overlapping types of heterozygotes recorded in table 2 with the exception of the combinations $S^{T3}S^{S2}$, $S^{T3}S^{A1}$, $S^{T1}S^{A1}$, $S^{E}S^{A2}$, and $S^{S2}S^{A2}$, for which the pictures are lacking because the elytra of these specimens were damaged beyond recovery.

By comparing the color patterns of each type of overlapping heterozygote with the color patterns of the two corresponding types of homozygotes, one is surprised to note that mosaicism prevails in all cases. As a matter of fact, the specificity of each allele is so remarkably clear cut in the heterozygote's color pattern that the relatively minor differences distinguishing between S^{C1} and S^{C2}, between S^{T1} and S^{T3}, between S^{S1} and S^{S2}, and between S^{A1} and S^{A2} can be clearly demonstrated with respect to a third allele. For example, figure 39 ($S^{T3}S^{I}$) and figure 44 ($S^{T1}S^{I}$) reveal obviously the difference between the effects of the allele S^{T3} and that of the other allele S^{T1}, since each is combined with a common third allele, which is S^{I} in this case. In other words, the difference between the characteristic patterns of any of these varieties, how-

ever little it may be, is a real one, and the autonomy of the individual effect in the developing heterozygote is true to every allele and probably in any allelic combination.

As pointed out in a preceding section, the heterozygotes between any dominant allele and *succinea* may give the characteristic "indents" or spots in the yellow area. That this manifestation is due to the effect of the *succinea* alleles alone is further substantiated by the observations that in any heterozygous combinations between two alleles other than *succinea*, the yellow area is always devoid of such modifications. Among a total of 558 overlapping heterozygotes examined (table 2) only one individual showed a small black spot in the yellow area. This was found in the heterozygote S^ES^R, as shown in figure 50.

Table 3 summarizes the results of the crosses between overlapping heterozygotes and *succinea*. The only inclusive type of heterozygote involved in this series of experiments was $S^{C1}S^{A2}$, which came from a cross between two homozygotes. The results show that in every successful cross, the progeny consists of two classes, S^as and S^bs in an approximately 1:1 ratio. There appeared two *succinea* homozygotes, one in cross No. 122 (table 3, No. 3) between ss ♀ and $S^{T3}S^I$ ♂ and the other cross No. 191 (table 3, No. 17) between S^RS^I ♀ and ss ♂. They were presumably due to the contamination of wild larvae in the process of breeding. Since they were found in only two individuals out of a total of 451 reported in this series of experiments, they can be considered as exceptions. The available evidence suffices to show that the various pattern forms are inherited as multiple alleles and that each of the tested dominant heterozygotes (S^aS^b) is composed of only two specific alleles. The allelic inheritance of various variants of color pattern types of *Harmonia axyridis* can be considered fully proven, especially because of the fact that 11 of the 12 variants are involved in this series of experiments in at least one combination (table 3) and that the relevant data for *conspicua-2*, which is not available in this experiment, was obtained in a previous report (TAN 1942).

The data from the inbreeding of the various overlapping heterozygotes and of one inclusive heterozygote ($S^{C1}S^{A2}$) are presented in table 4. The expected types and the ratio for the progeny classes should be two overlapping heterozygotes same as the parents (S^aS^b) to one type of homozygotes (S^aS^a) and to one the other type of homozygotes (S^bS^b). From each successful cross, the types of offspring obtained agree with this expectation. Hence, various types of dominant homozygotes are recovered. With the exception of $S^{C2}S^{C2}$, every type of dominant homozygote is represented in at least one inbred line. In fact, the pictures illustrating the color patterns of the dominant homozygotes as shown in figures 13 to 23 were taken from these individuals, the only exception being $S^{C2}S^{C2}$ (fig. 14) obtained from the previous experiments. But the numerical data concerned in this series of experiments significantly deviated from the expected 2 (S^aS^b):1 (S^as):1 (S^bs) ratio in many cases. Theoretically, the proportion between heterozygotes and the sum of the two classes of homozygotes should be equal. Actually, most crosses gave more

TABLE 3

Results of the crosses between different types of overlapping heterozygotes and succinea homozygotes ($S^aS^b \times ss$).

NO.	ALLELES CONCERNED S^a S^b	CROSS NO.	PARENTAL TYPES (PEDIGREE NO.) ♀	♂	PROGENY CLASSES S^as	S^bs	ss	TOTAL
1	S^{C1} S^{A2}	1014B	$s\,s$ (1002)	$S^{A2}S^{C1}$ (1003)	(15)	(16)		
		1018A	$S^{A2}S^{C1}$ (1003)	$s\,s$ (1002)	(7)	(6)		44
2	S^{T3} S^{S2}	193	$S^{T3}S^{S2}$ (159)	$s\,s$ (wild)	4	4		8
3	S^{T3} S^{I}	122	$s\,s$ (105)	$S^{T3}S^{I}$ (104)	(33)	(31)	1	
		140	$S^{T3}S^{I}$ (104)	$s\,s$ (104)	(1)	(4)		70
4	S^{T3} S^{A1}	208	$s\,s$ (155)	$S^{A1}S^{T3}$ (146)	4	5		9
5	S^{T3} S^{R}	183	$S^{R}S^{T3}$ (117)	$s\,s$ (117)	(8)	(9)		
		184	$s\,s$ (115)	$S^{R}S^{T3}$ (117)	(9)	(6)		32
6	S^{T1} S^{S1}	1046B	$s\,s$ (1002)	$S^{T1}S^{S1}$ (1005)	7	4		11
7	S^{T1} S^{I}	139	$S^{I}S^{T1}$ (103)	$s\,s$ (101)	26	26		52
8	S^{T1} S^{A2}	221	$S^{T1}S^{A2}$ (155)	$s\,s$ (155)	4	2		6
9	S^{T1} S^{A1}	224	$S^{A1}S^{T1}$ (168)	$s\,s$ (168)	4	5		9
10	S^{E} S^{S1}	1012, 1020	$S^{E}S^{S1}$ (1006)	$s\,s$ (1002)	18	17		35
11	S^{E} S^{I}	185	$S^{I}S^{E}$ (126)	$s\,s$ (126)	8	11		19
12	S^{E} S^{A2}	132	$S^{A2}S^{E}$ (102)	$s\,s$ (102)	(2)	(2)		
		114	$s\,s$ (102)	$S^{A2}S^{E}$ (102)	(14)	(16)		34
13	S^{E} S^{A1}	241, 245	$S^{E}S^{A1}$ (164)	$s\,s$ (126)	3	5		8
14	S^{E} S^{R}	220	$S^{R}S^{E}$ (153)	$s\,s$ (155)	7	11		18
15	S^{S2} S^{A1}	170	$s\,s$ (503)	$S^{A1}S^{S2}$ (105)	8	8		16
16	S^{I} S^{A2}	194	$S^{I}S^{A2}$ (148)	$s\,s$ (138)	(6)	(7)		
		213	$s\,s$ (157)	$S^{I}S^{A2}$ (148)	(2)	(2)		17
17	S^{I} S^{R}	190	$s\,s$ (145)	$S^{R}S^{I}$ (138)	(7)	(5)		
		191	$S^{R}S^{I}$ (138)	$s\,s$ (149)	(25)	(18)	1	56
18	S^{A2} S^{R}	215	$s\,s$ (117)	$S^{R}S^{A2}$ (153)	3	2		5
19	S^{A1} S^{R}	237	$S^{R}S^{A1}$ (166)	$s\,s$ (166)	1	1		2
				Total	226	223	2	451

heterozygotes as compared to homozygotes. Some of the more significant differences are found in the inbreeding lines, $S^{T3}S^{R}$ (table 4, No. 4), $S^{E}S^{A2}$ (No. 11), and $S^{E}S^{I}$ (No. 10). In only two cases, the inbred lines of $S^{T1}S^{A1}$ (No. 8) and of $S^{T1}S^{I}$ (No. 6), the homozygotes outnumber the heterozygotes. The results are significant in showing that there is a differential survival between the homozygotes and the heterozygotes. The total number of heterozygotes is 162 and that of homozygotes is 87. The probable explanation is that some of these alleles are associated with a semi-lethal effect in homozygous condition.

TABLE 4

Results of the inbreeding of the different combinations of overlapping heterozygotes ($S^aS^b \times S^aS^b$).

NO.	ALLELES CONCERNED S^a S^b	CROSS NO.	PARENTAL TYPES (PEDIGREE NO.) ♀ AND ♂	PROGENY CLASSES S^aS^b	S^aS^a	S^bS^b	TOTAL
1*	S^{C1} S^{A2}	1014	$S^{C1}S^{A2}$ (1003)		10	5	15
2	S^{T3} S^{I}	128, 174	$S^{T3}S^{I}$ (104)	13	8	2	23
3	S^{T3} S^{A1}	205, 207	$S^{T3}S^{A1}$ (120)	6	5	1	12
4	S^{T3} S^{R}	200, 201	$S^{R}S^{T3}$ (117)	23	1	2	26
5	S^{T1} S^{S1}	1013A	$S^{T1}S^{S1}$ (1005)	10	3	4	17
6	S^{T1} S^{I}	142	$S^{I}S^{T1}$ (103)	3	6	4	13
7	S^{T1} S^{A2}	230	$S^{A2}S^{T1}$ (155)	—	1	1	2
8	S^{T1} S^{A1}	223, 243	$S^{A1}S^{T1}$ (168)	6	5	4	15
9	S^{T1} S^{R}	235	$S^{R}S^{T1}$ (154)	14	—	4	18
10	S^{E} S^{I}	195, 196	$S^{I}S^{E}$ (126)	21	—	5	26
11	S^{E} S^{A2}	171	$S^{E}S^{A2}$ (102)	19	3	8	30
12	S^{E} S^{R}	206	$S^{E}S^{R}$ (153)	3	2	—	5
13	S^{S2} S^{I}	192	$S^{S2}S^{I}$ (150)	10	5	—	15
14	S^{S2} S^{A1}	175	$S^{S2}S^{A1}$ (105)	5	—	—	5
15	S^{I} S^{R}	181, 186	$S^{I}S^{R}$ (138)	21	6	3	30
16	S^{A2} S^{R}	216	$S^{R}S^{A2}$ (153)	4	—	1	5
17	S^{A1} S^{R}	238	$S^{R}S^{A1}$ (166)	4	2	1	7
		Total for overlapping types:		162	47	40	249

* Inclusive heterozygote, S^aS^b and S^aS^a, cannot be distinguished.

DISCUSSION

Two principal conclusions emerge from the data presented above. First, the inheritance of all the types of color pattern found in our material on *Harmonia axyridis* can be accounted for by assuming 12 alleles of a single autosomal locus. Second, the color patterns to be found in the heterozygotes carrying any two alleles can be predicted on the basis of the rule of mosaic dominance. This rule states that any portion of the elytra which has black pigment in the homozygotes for a given allele will have black pigment also in the heterozygotes in which that allele is present. In other words, if the color patterns in any two different homozygotes are known, the color pattern in the heterozygote can be predicted by superimposition of the patterns of the homozygotes, and leaving unpigmented only those sections of the elytra which have no black pigment in either homozygote. A re-examination of the data of HOSHINO (1940) in the light of the rule of mosaic dominance shows that this rule is applicable also to the heterozygotes carrying the three alleles studied by him but which were not present in our material, since they are rare or absent in the population of that part of China in which our material was collected. It is very probable that the rule of mosaic dominance applies to all the 15 alleles which are known to govern the elytral color pattern in *Harmonia axyridis*.

The precision with which the rule of mosaic dominance holds is remarkable. We have traced the color patterns on the elytra of individuals homozygous for the 15 known alleles on a semi-transparent paper, and superimposed the resulting drawings in all combinations. Making black any part of the elytron which is black in either homozygote, we obtain the 105 "theoretical" patterns shown in the closed squares in figure 61. The pattern in each square shows the condition predicted in the heterozygotes carrying the alleles which, when homozygous, have the patterns represented at the top of the vertical row and at the extreme left of the horizontal row. A total of 55 heterozygotes the color patterns of which have thus been predicted were actually obtained in the experiments reported in this paper or in a previous one (TAN 1942). They are marked in figure 61 by the sign "T." Some of the heterozygotes (about 15) were obtained by HOSHINO (1940) but not in our experiments. They are marked in figure 61 by "H." Heterozygotes which have not been obtained and studied up to now are marked by a question mark in figure 61. These unknown heterozygotes are mostly combinations of the rare alleles studied by us—namely, *conspicua-2* (S^{C2}), *transversifascia-3* (S^{T3}), *transversifascia-1* (S^{T1}), *equicolor* (S^{E}), *spectabilis-2* (S^{S2}), *tripunctata* (S^{R}), and *aulica-2* (S^{A2}), with the alleles *axyridis* (S^{X}), *transversifascia-2* (S^{T2}) and *forficula* (S^{F}) studied by HOSHINO but not present in Chinese populations.

Comparison of the predicted patterns in figure 61 with those shown in figures 24–60 in the present paper or in papers of TAN (1942) and HOSHINO (1940) shows striking coincidence of the predicted and the observed patterns. Especially interesting, of course, are the patterns of the overlapping heterozygotes, which always have the yellow coloration restricted to only those parts of the elytra which are yellow in both corresponding homozygotes. The only variations are those produced by the "*succinea* effect" described above, which concerns the presence or absence of the black spots on the yellow background which may or may not be present in the *succinea* homozygotes. The sole exception from the rule of mosaic dominance found till now is a specimen shown in figure 50 which should have had the color pattern indicated by the sign "!" in figure 61. This specimen, presumed to be a heterozygote for the alleles S^{E} and S^{R}, should not have the black spot inside the yellow area above the middle of the length of the elytron. The presence of this spot is a characteristic of the *succinea* pattern, and the allele *s* was not supposed to be present in the specimen just referred to. The writer owes to PROFESSOR M. M. RHOADES the suggestion that this single exceptional specimen might have been a trisomic, carrying the three alleles S^{E}, S^{R}, and *s*. This appears quite probable, especially because of the fact that this specimen was obtained from a cross between $S^{E}s$ and $S^{R}s$.

On the basis of the knowledge of the inheritance of color patterns of the beetle, a re-examination of the published figures of the pattern types found in nature shows that a number of them represent, in reality, the heterozygotes of one kind or the other. The abridged forms of black varieties carrying small black spots or "indents" in the yellow area are the remarkable examples of

this kind. For this reason, the proposal of HEMMELMANN (*cf.* MADER 1932) to give a separate Latin variety name for each color pattern found in nature appears valueless. It is true that some of the published figures of HEMMELMANN or of TAN and LI (1932) do not fit into either the known homozygous or

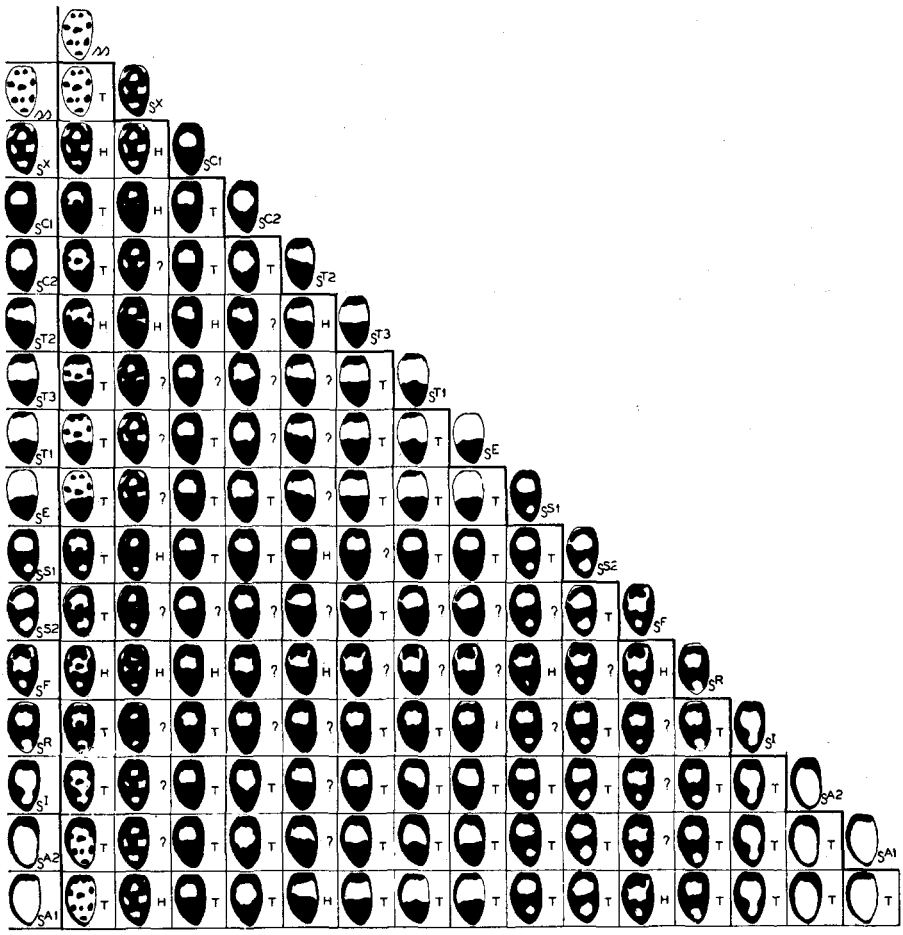

FIGURE 61.—The theoretical color patterns for the different combinations of the 15 known alleles in *Harmonia axyridis*. The symbol *T* marks the ones actually obtained by TAN in this paper or in a previous paper (1942); *H*, obtained by HOSHINO (1940);?, not obtained so far; and !, a single individual in this class showing *succinea* effect.

heterozygous combinations of the 15 alleles. One outstanding case is the pure black form known as variety *corvina* (*cf.* fig. 21 of MADER 1932). This and other cases suggest that there probably exist several more alleles which have not been included in the laboratory experiments so far.

How widespread is the phenomenon of mosaic dominance is difficult to tell. The dominance relationships in *Adalia bipunctata*, another member of the

family Coccinellidae, have been described by LUS (1928, 1932), who has also examined the inheritance of three color patterns in the related species, *Adalia decempunctata*. In neither of these species is the dominance order of the color patterns in accord with the rule of mosaic dominance. Other species of Coccinellidae have not so far been studied in enough detail to give a fair test of the applicability of this rule.

The best analogue of the behavior of the color pattern alleles in *Harmonia axyridis* is that of the scute-achaete alleles in *Drosophila melanogaster* described particularly by SEREBROVSKY and DUBININ (see a review in GOLDSCHMIDT 1938). The mutants at these loci are characterized by the absence of different sets of the bristles present on the body of the wild type fly. The mutants are recessive to the wild type condition, and the compounds heterozygous for any two of the mutant alleles have only those bristles missing which are missing in the homozygotes for both alleles taken separately. This so-called "step-allelomorphism" in the scute-achaete locus of *Drosophila melanogaster* has led to the so-called subgene hypothesis, which postulates that each gene is composed of a series of "subgenes," each subgene being responsible for the presence or absence of a definite bristle or a few definite bristles. The alternative explanation proposed by GOLDSCHMIDT (1931) assumes that each allele acts at a different time, and perhaps with different speed, governing the diffusion processes of some bristle-forming substances originating from some centers of the bristle pattern.

A similar hypothesis would, of course, fit the *Harmonia axyridis* also. One would have to assume that the elytron is a mosaic of many sections the coloration of each of which is determined independently from the others, or else that each allele present in an individual determines a pigment-forming "stream" in the elytron independent from the "stream" produced by the other allele. It is hardly necessary to say that there is no evidence of the existence of the pattern-forming "streams" or centers either in the scute case in *Drosophila melanogaster* or in the elytral pigmentation case of *Harmonia axyridis*. It may be noted, however, that Harmonia offers a very favorable experimental material for studies in this field. When the beetle emerges from the pupa, the entire elytron is yellowish-orange without black markings. The black pigment appears gradually, from the periphery of the elytron to its center. It has been shown by cutting parts of the elytron that some substance or substances pass from the body into the hardening elytron (unpublished data). It will be interesting to investigate further the distribution of this stream of substances in connection with the problem of the development of the black pattern.

Another analogy, possibly a more remote one, to the phenomenon of mosaic dominance in *Harmonia axyridis* is found among genes determining serological characters in the higher vertebrates. Thus, the blood group genes A and a^B in man produce the antigens A and B quite independently from each other. It is, however, rather far-fetched to suppose that each of the 15 alleles of the color pattern in *Harmonia axyridis* produces a separate substance

responsible for the deposition of the black pigment in strictly definite portions of the elytral surface.

Although some of the alleles of the elytral color pattern occur more frequently than others in the natural populations of *Harmonia axyridis*, no allele is sufficiently common throughout the distribution area to be regarded as the "wild type." The absence of a normal or wild type condition is interesting in connection with the absence in this case of the simple dominance-recessive relations usually exhibited between the wild type allele on one hand and mutant alleles on the other. Mutant alleles are presumably unfavorable for the survival of the species in all environments to which the species is normally exposed. The gene action is consequently adjusted to produce an end product which we call "wild type" in as many individuals and under as many circumstances as possible. The fact that all the alleles studied by us in *Harmonia axyridis* occur in natural populations suggests that they are at least tolerated by natural selection. Complete dominance and recessiveness have no biological meaning in such conditions. It does not follow, of course, that the color patterns and the alleles which influence them are adaptively neutral. It is possible that some of them are more favored in certain environments in which the species lives and others in other environments. In this respect the finding of TIMOFEEFF-RESSOVSKY (1940) is of interest—namely, that the dark variants of *Adalia bipunctata* are favored during the summer while the red variants are more favorable for survival during hibernations. Similar effects of natural selection on the incidence of various gene arrangements in different seasons have been established by DOBZHANSKY (1943) in *Drosophila pseudoobscura* and by DUBININ and TINIAKOV (1945) in *Drosophila funebris*. A careful study of the situation in *Harmonia axyridis* from this point of view is a matter for future work.

SUMMARY

The inheritance of elytral color patterns in the lady-bird beetle, *Harmonia axyridis*, has been studied. The material was collected in Meitan of Kweichow province, southwestern part of China. The inheritance of color patterns can be accounted for by assuming 12 alleles of an autosomal locus. The color patterns and the alleles responsible for them are *succinea* (*s*), *conspicua*-1 (S^{C1}), *conspicua*-2 (S^{C2}), *transversifascia*-3 (S^{T3}), *transversifascia*-1 (S^{T1}), *equicolor* (S^{E}), *spectabilis*-1 (S^{S1}), *spectabilis*-2 (S^{S2}), *intermedia* (S^{I}), *aulica*-2 (S^{A2}), *aulica*-1 (S^{A1}), and *tripunctata* (S^{R}).

Succinea homozygotes (*ss*) have yellow elytra with a varying number of black spots (0–19). The number and size of the spots present in homozygous *succinea* depend upon the temperature during the pupal development. All other variants of the elytral color pattern have a black background with yellow or orange spots.

The crosses between *succinea* homozygotes and each of the 11 other variants give rise to heterozygotes in which the *succinea* characters are recessive, except that the characteristic spots of the *succinea* parent may be found on the yellow areas.

Heterozygotes involving alleles other than *succinea* may be classified into two categories—namely, inclusive combinations and overlapping combinations. In the former, which result from combinations of two alleles where the black pigmented area characteristic of one in homozygous condition includes the black pigmented area produced by the other allele in homozygous condition, the pattern of the heterozygotes cannot be distinguished from that of the homozygotes having the more extensive black pigmented area. In the case of overlapping heterozygotes, which are combinations of two alleles where the black pigmented area of the pattern characteristic of one allele in homozygous condition overlaps the characteristic region of distribution of the other allele in homozygous condition, the pattern of the heterozygotes can invariably be distinguished from the patterns of either parental homozygous type.

The expression of the color pattern in the heterozygotes conforms to the rule of mosaic dominance, which states that any portion of the elytra which has black pigment in the homozygote for a given allele will have black pigment also in the heterozygotes in which that allele is present. The only exceptional individual which seems to break this rule shows the mosaic effects of three alleles—namely, S^E, S^R, and *s*. This individual might have been a trisomic.

The rule of mosaic dominance has been found equally applicable to the heterozygotes carrying three alleles which have been studied by HOSHINO (1940)—namely, *axyridis* (S^X), *transversifascia-2* (S^{T2}), and *forficula* (S^F).

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