GENETICAL STUDIES ON THE PATTERN TYPES OF THE LADY-BIRD BEETLE, *HARMONIA AXYRIDIS* PALLAS

By YASUSI HOSINO
Zoological Institute, Kyoto Imperial University

(With Twenty-nine Text-figures)

Introduction

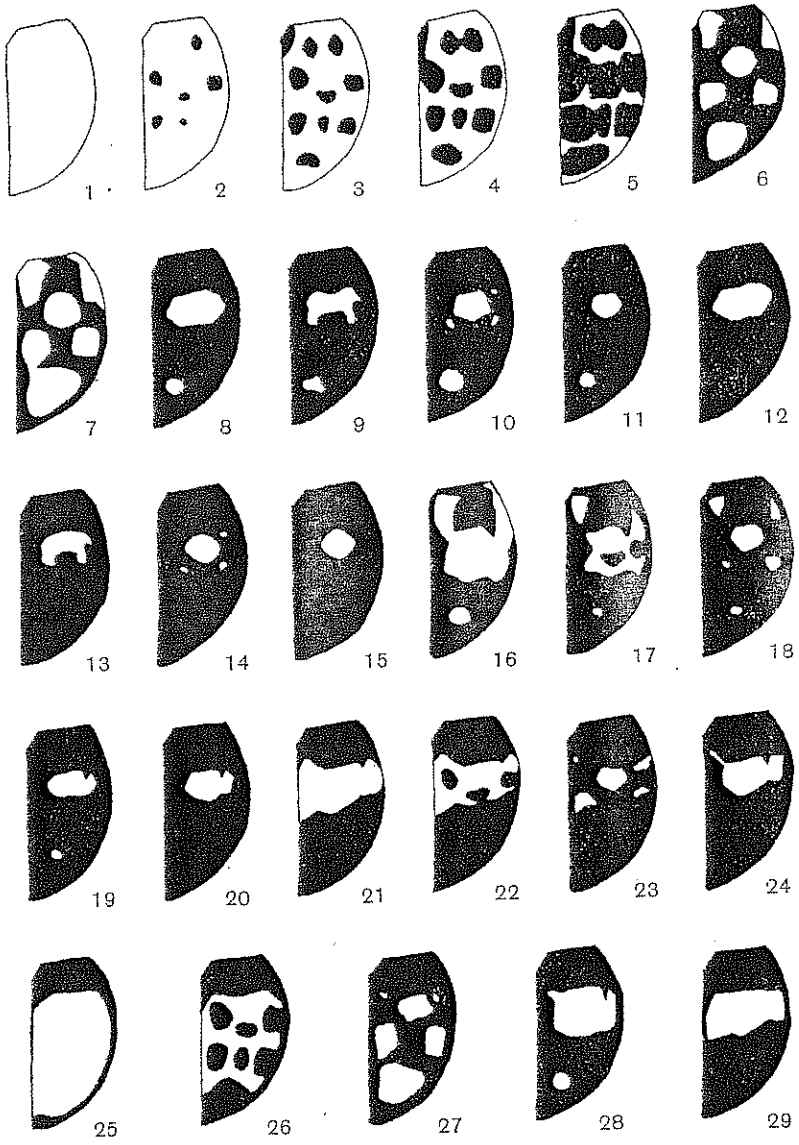
The lady-bird beetle, *Harmonia axyridis* Pallas, is well known for the great variability of its elytral, as well as thoracic, pattern (Figs. 1–29). The ground colour of the elytra may be either orange yellow (Figs. 1–5) or black (Figs. 6–29). In the former case there are commonly nineteen black spots arranged as shown in Fig. 3 (var. *succinea*). The spots are often enlarged to become confluent with one another (Figs. 4, 5), or they diminish in size and the smaller ones disappear (Fig. 2); in the extreme case of the latter tendency the elytra become uniformly orange without any trace of spots (Fig. 1). The size of the spots in this type is apparently correlated with the amount of humidity and the degree of temperature in environment: in hot and dry climate they become smaller, while in cold and humid climate they are enlarged (cf. Dobzhansky, 1924, 1933).

Among the types with the black ground, the one in Figs. 6, 7 has six spots of orange colour on each side (var. *axyridis*). Other common types are the one with two spots on each side (var. *spectabilis*), and that with a single spot (var. *conspicua*). Those shown in Figs. 16, 17, 21, 22 and 25, 26, belong to rarer types.

Tan & Li (1932–3, 1934) have studied the heredity of these commoner types. They found that *succinea* is recessive to any other type, while *aulica*, *spectabilis* and *conspicua* are due to dominant genes independent of one another.

I have been working on the same problem since 1932. The results have confirmed Tan & Li's findings partly, but are at variance with them in an important point, namely, that the genes of all the types undoubtedly form multiple allelomorphic series, instead of being independent of one another. Though the genes for *axyridis*, *spectabilis* and *conspicua* are largely dominant to the gene for *succinea*, yet the heterozygotes can be distinguished from homozygotes by slight but distinctive features.

This paper deals with the facts which seem to be fairly firmly established by the data so far obtained. They include the heredity of all the



Figs. 1–29

1–5, *succinea* (pp); 6, *axyridis* ($P^{A}P^{A}$, $P^{A}p$); 7, *axyridis* ($P^{A}p$); 8, *spectabilis* ($P^{S}P^{S}$, $P^{S}P^{Au}$, $P^{S}p$); 9, *spectabilis* ($P^{S}p$); 10, 11, heterozygote of *spectabilis* and *axyridis* ($P^{S}P^{A}$); 12, *conspicua* ($P^{C}P^{C}$, $P^{C}P^{S}$, $P^{C}P^{T}$, $P^{C}P^{Au}$, $P^{T}P^{S}$, $P^{C}p$); 13, *conspicua* ($P^{C}p$); 14, 15, heterozygote of *conspicua* and *axyridis* ($P^{C}P^{A}$); 16, *forficula* ($P^{F}P^{F}$, $P^{F}p$); 17, *forficula* ($P^{F}p$); 18, heterozygote of *axyridis* and *forficula* ($P^{A}P^{F}$); 19, heterozygote of *spectabilis* and *forficula* ($P^{S}P^{F}$); 20, heterozygote of *conspicua* and *forficula* ($P^{C}P^{F}$); 21, *transversifascia* ($P^{T}P^{T}$, $P^{T}p$); 22, *transversifascia* ($P^{T}p$); 23, heterozygote of *transversifascia* and *axyridis* ($P^{T}P^{A}$); 24, heterozygote of *transversifascia* and *forficula* ($P^{T}P^{F}$); 25, *aulica* ($P^{Au}P^{Au}$, $P^{Au}p$); 26, *aulica* ($P^{Au}p$); 27, heterozygote of *axyridis* and *aulica* ($P^{A}P^{Au}$); 28, heterozygote of *forficula* and *aulica* ($P^{F}P^{Au}$); 29, heterozygote of *transversifascia* and *aulica* ($P^{T}P^{Au}$).

patterns dealt with in Tan & Li's paper, besides three types which were not treated by them. Further data will be reserved for later papers.

The material was derived from individuals collected in the field in the vicinity of Tokyo. The larvae were reared in glass tubes or in Petri dishes. Various kinds of aphids obtained from the field served as food. Certain kinds of aphids are unsuitable for the purpose, apparently being poisonous to the larvae.

EXPERIMENTAL DATA

Succinea

When *succinea* is bred *inter se*, the progeny is all *succinea*, with no other type (Table I). This shows that all *succinea* individuals are homozygous for the gene.

TABLE I

Succinea × *succinea*

Cross no.	Parents	Progeny *succinea* ♀	♂	Total
1	pp pp	65	47	112

Axyridis

The mating *axyridis* × *axyridis* sometimes gives only *axyridis* in F_1 (Table II, no. 2), but at other times it throws *succinea* also in a nearly 3 : 1 ratio (no. 3). The backcross yields *axyridis* and *succinea* in approximately equal frequency (no. 4). Among the individuals of *axyridis*, the heterozygotes often can be distinguished from the homozygotes in that the spots are confluent with one another (Fig. 7). However, the heterozygote may show the same appearance as the homozygote (Fig. 6).

Consequently, it is clear that *axyridis* behaves as a simple dominant to *succinea*. $\mathbf{P^A}$ will be used as the symbol for *axyridis* and **p** that for *succinea*.

TABLE II

Nos. 2, 3, axyridis × axyridis; *no.* 4, axyridis × succinea

Cross no.	Parents		Progeny *axyridis* ♀	♂	Total	*succinea* ♀	♂	Total	Total
2	$\mathbf{P^AP^A}$	$\mathbf{P^AP^A}$	19	14	33	—	—	—	—
3	$\mathbf{P^Ap}$	$\mathbf{P^Ap}$	28	25	53	11	8	19	72
Ratio (cross 3)					2·944			1·056	4·000
4	$\mathbf{P^Ap}$	pp	18	13	31	16	9	25	56
Ratio (cross 4)					1·107			0·893	2·000

Spectabilis

Spectabilis × *spectabilis* gives exclusively *spectabilis* in some cultures (Table III, no. 5), while in others it gives *spectabilis* and *succinea* in a ratio approximately 3 : 1 (no. 6). Among the individuals of *spectabilis*, the heterozygotes often can be distinguished from the homozygotes in that the anterior spot has a concavity on both the postero-lateral and posterior sides (Fig. 9). The concavity, however, is missing in some cases, and the heterozygote may show the same appearance as the homozygote

TABLE III

Spectabilis × *spectabilis*

			Progeny					
			spectabilis			*succinea*		
Cross no.	Parents		♀	♂	Total	♀	♂	Total	Total
5	$P^{S}P^{S}$	$P^{S}P^{S}$	63	50	113	—	—	—	—
6	$P^{S}p$	$P^{S}p$	82	72	154	29	27	56	210
Ratio (cross 6)					2·933			1·065	4·000

TABLE IV

Nos. 7, 8, spectabilis × axyridis; *no.* 9, *heterozygote of* spectabilis *and* axyridis × *heterozygote of* spectabilis *and* axyridis

			Progeny								
			spectabilis			Heterozygote of *spectabilis* and *axyridis*			*axyridis*			
Cross no.	Parents		♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
7	$P^{S}P^{S}$	$P^{A}P^{A}$	—	—	—	8	13	21	—	—	—	—
8	$P^{S}p$	$P^{A}P^{A}$	—	—	—	18	13	31	13	21	34	65
Ratio (cross 8)								0·954			1·046	2·000
9	$P^{S}P^{A}$	$P^{S}P^{A}$	8	8	16	23	20	43	16	10	26	85
Ratio (cross 9)					0·753			2·024			1·223	4·000

(Fig. 8). These experiments show that *spectabilis* is a simple dominant to *succinea*.

The heterozygote of *spectabilis* and *axyridis* also resembles *spectabilis*, but can be distinguished from the homozygous *spectabilis* in that the anterior spot is smaller than that of the latter and often provided with accessory specks, one on each of its antero-lateral, postero-lateral and postero-median corners (Figs. 10, 11). From the mating, a homozygous *spectabilis* with a homozygous *axyridis*, are given only individuals like Figs. 10, 11 (Table IV, no. 4). But if a heterozygous *spectabilis* is used, about half of the F_1 individuals are *axyridis* (no. 8). The heterozygotes

inter se throw *spectabilis*, heterozygotes and *axyridis* in an approximately 1 : 2 : 1 ratio (no. 9). These findings show clearly that the genes for *spectabilis*, *axyridis* and *succinea* are in a multiple allelomorphic series. P^S will be used for *spectabilis*.

Conspicua

Conspicua behaves very much like *spectabilis* when mated to *succinea* or to *axyridis*. The heterozygote of *conspicua* and *succinea* has a spot similar to the anterior spot of the heterozygote of *spectabilis* and *succinea* (Figs. 12, 13). The heterozygote of *conspicua* and *axyridis* also has a spot much resembling the anterior spot of the heterozygote of *spectabilis* and *axyridis* (Figs. 14, 15).

TABLE V

Nos. 10, 12, conspicua × succinea; *no.* 11, conspicua × conspicua

Cross no.	Parents		Progeny: *conspicua* ♀	*conspicua* ♂	*conspicua* Total	*succinea* ♀	*succinea* ♂	*succinea* Total	Total
10	P^cP^c	pp	40	21	61	—	—	—	—
11	P^cp	P^cp	49	31	80	15	11	26	106
Ratio (cross 11)					3·019			0·981	4·000
12	P^cp	pp	3	1	4	2	1	3	7
Ratio (cross 12)					1·143			0·857	2·000

The cross, homozygous *conspicua* × *succinea*, gives only individuals like Figs. 12, 13 (Table V, no. 10); in F_2 *succinea* appears forming about one-quarter of the whole population (no. 11). The backcross gives the two types in a nearly 1 : 1 ratio (no. 12). It is thus clear that *conspicua* is a simple dominant to *succinea* like other types.

Heterozygotes of *conspicua* and *axyridis* mated together throw *conspicua*, heterozygotes and *axyridis* in an approximately 1 : 2 : 1 ratio (Table VI, no. 13). *Conspicua* mated with the heterozygote gave in an experiment 2 *conspicua* : 1 heterozygote of *conspicua* and *axyridis* : 1 *axyridis* (no. 14). Another experiment, where a heterozygote of *conspicua* and *axyridis* was crossed with *succinea*, produced *conspicua* and *axyridis* in about the same number (no. 15).

A homozygous *conspicua* mated to a homozygous *spectabilis* gives *conspicua* alone in F_1 (Table VII, no. 16), and *conspicua* and *spectabilis* in a 3 : 1 ratio in F_2 (no. 17). F_1 backcrossed gives *conspicua* and *spectabilis* in a 1 : 1 ratio (no. 18).

It is evident then that *conspicua* is another gene belonging to the same allelomorphic series as all the genes already mentioned, and largely dominant to any of these. P^C will be used for this gene.

TABLE VI

No. 13, *heterozygote of* conspicua *and* axyridis × *heterozygote of* conspicua *and* axyridis; *no.* 14, conspicua × *heterozygote of* conspicua *and* axyridis; *no.* 15, *heterozygote of* conspicua *and* axyridis × succinea

			Progeny								
			conspicua			Heterozygote of *conspicua* and *axyridis*			*axyridis*			
Cross no.	Parents		♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
13	P^CP^A	P^CP^A	1	2	3	5	3	8	2	1	3	14
Ratio (cross 13)					0·857			2·286			0·857	4·000
14	P^Cp	P^CP^A	11	11	22	5	5	10	2	8	10	42
Ratio (cross 14)					2·096			0·952			0·952	4·000
15	P^CP^A	pp	1	7	8	—	—	—	9	3	12	20
Ratio (cross 15)					0·800						1·200	2·000

TABLE VII

Nos. 16, 18, conspicua × spectabilis; *no.* 17, conspicua × conspicua

			Progeny						
			conspicua			*spectabilis*			
Cross no.	Parents		♀	♂	Total	♀	♂	Total	Total
16	P^CP^C	P^SP^S	52	47	99	—	—	—	—
17	P^CP^S	P^CP^S	83	91	174	27	27	54	228
Ratio (cross 17)					3·053			0·947	4·000
18	P^CP^S	P^SP^S	57	55	112	48	54	102	214
Ratio (cross 18)					1·047			0·953	2·000

Forficula[1]

This is one of the rarer pattern types occasionally seen among the specimens collected in the field. The pattern resembles that of *axyridis*, but differs from it in that the anterior five spots are confluent in the manner shown in Figs. 16, 17 and the posterior-most spot is smaller than in *axyridis*. The heterozygote of *forficula* and *succinea* often can be distinguished from the homozygotes in that the anterior spot has a black speck in it (Fig. 17). However, the speck is missing in some cases and the heterozygotes may show the same appearance as the homozygotes (Fig. 16). An individual of this type gave in a cross with *succinea*, *forficula*

[1] Name given by Prof. T. Komai.

alone (Table VIII, no. 19), which produced in the next generation *forficula* and *succinea* approximately in a 3 : 1 ratio (no. 20). The backcross gave these types nearly in the same frequency (no. 21).

A heterozygote of *axyridis* and *succinea* mated to a heterozygote of *forficula* and *succinea* threw four different types, *axyridis*, heterozygote of *axyridis* and *forficula*, *forficula* and *succinea*, in nearly equal frequency (Table IX, no. 22). The backcross of the heterozygote with *succinea* gave

TABLE VIII

Nos. 19, 21, forficula × succinea; *no.* 20, forficula × forficula

		Progeny					
		forficula			*succinea*		
Cross no.	Parents	♀	♂	Total	♀	♂	Total	Total
19	P^FP^F pp	9	15	24	—	—	—	—
20	P^Fp P^Fp	17	5	22	3	7	10	32
Ratio (cross 20)				2·750			1·250	4·000
21	P^Fp pp	26	25	51	34	29	63	114
Ratio (cross 21)				0·895			1·105	2·000

TABLE IX

No. 22, axyridis × forficula; *no.* 23, *heterozygote of* axyridis *and* forficula × succinea

		Progeny											
		axyridis			Heterozygote of *axyridis* and *forficula*			*forficula*			*succinea*			
Cross no.	Parents	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
22	P^Ap P^Fp	6	7	13	9	7	16	8	4	12	10	3	13	54
Ratio (cross 22)				1·963			1·185			0·889			0·963	4·000
23	P^AP^F pp	11	6	17	—	—	—	10	5	15	—	—	—	32
Ratio (cross 23)				1·062						0·938				2·000

axyridis and *forficula* in nearly the same number (no. 23). The heterozygote of *axyridis* and *forficula* resembles *axyridis*, but can be distinguished from it in that the intero-median spot is smaller than the other spots (Fig. 18). Likewise the heterozygote of *forficula* and *spectabilis* or *conspicua* can be told by the peculiar shape of the anterior spot which has an indentation at the antero-lateral corner (Figs. 19, 20).

A crossing experiment between *spectabilis* and *forficula* gave *spectabilis*, heterozygote of *spectabilis* and *forficula*, *forficula* and *succinea* in nearly

equal frequency (Table X, no. 24). Another experiment yielded from the same combination, heterozygote of *spectabilis* and *forficula* and *forficula* in 1 : 1 ratio (no. 25). The heterozygotes together threw *spectabilis*, heterozygote of *spectabilis* and *forficula* and *forficula* in an approximately 1 : 2 : 1 ratio (no. 26).

TABLE X

Nos. 24, 25, spectabilis × forficula; *no.* 26, *heterozygote of* spectabilis *and* forficula × *heterozygote of* spectabilis *and* forficula

		Progeny												
		spectabilis			Heterozygote of *spectabilis* and *forficula*			*forficula*			*succinea*			
Cross no.	Parents	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
24	$P^{S}p$ $P^{F}p$	2	3	5	1	2	3	2	1	3	1	3	4	15
Ratio (cross 24)				1·333			0·800			0·800			1·067	4·000
25	$P^{S}p$ $P^{F}P^{F}$	—	—	—	5	8	13	5	7	12	—	—	—	25
Ratio (cross 25)							1·040			0·960				2·000
26	$P^{S}P^{F}$ $P^{S}P^{F}$	3	11	14	11	22	33	8	8	16	—	—	—	63
Ratio (cross 26)				0·889			2·095			1·016				4·000

TABLE XI

No. 27, conspicua × fortificula; *no.* 28, *heterozygote of* conspicua *and* fortificula × succinea

		Progeny												
		conspicua			Heterozygote of *conspicua* and *forficula*			*forficula*			*succinea*			
Cross no.	Parents	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
27	$P^{C}p$ $P^{F}p$	7	5	12	13	3	16	11	7	18	7	6	13	59
Ratio (cross 27)				0·814			1·085			1·220			0·881	4·000
28	$P^{C}P^{F}$ pp	12	16	28	—	—	—	14	10	24	—	—	—	52
Ratio (cross 28)				1·077						0·923				2·000

The F_1 of a cross between *conspicua* and *forficula* consisted of 1 *conspicua* : 1 heterozygote of *conspicua* and *forficula* : 1 *forficula* : 1 *succinea* (Table XI, no. 27). This shows that the parents had both been heterozygotes of *succinea*. A heterozygote of *conspicua* and *forficula* backcrossed to *succinea* produced *conspicua* and *forficula* in about the same number (no. 28).

All these experiments show clearly that *forficula* belongs to the same allelomorphic series as that of all the other genes. P^{F} may be used as the symbol for it.

Transversifascia

Transversifascia is another rare type with a pattern as in Figs. 21, 22. Among the individuals of *transversifascia*, the heterozygote of *transversifascia* and *succinea* can be distinguished from the homozygote in that the spot has one or three black specks in it (Fig. 22). However, these specks are often missing, when the heterozygote cannot be distinguished from the homozygote (Fig. 21). The heterozygote of *transversifascia* and *axyridis* and that of *transversifascia* and *forficula* are shown in Figs. 23 and 24 respectively.

In an experiment *transversifascia* × *transversifascia*, *succinea* was segregated, forming about one-quarter of the population (Table XII, no. 29). *Transversifascia* × *succinea* produced both types in 1 : 1 ratio (no. 30).

TABLE XII

No. 29, transversifascia × transversifascia; *no.* 30, transversifascia × succinea

			Progeny					
			transversifascia			*succinea*		
Cross no.	Parents		♀	♂	Total	♀	♂	Total	Total
29	$P^T p$	$P^T p$	13	15	28	4	3	7	35
Ratio (cross 29)					3·200			0·800	4·000
30	$P^T p$	pp	14	13	27	13	14	27	54
Ratio (cross 30)					1·000			1·000	2·000

It is thus evident that *transversifascia* is also a simple dominant to *succinea*.

The cross *transversifascia* × *axyridis* produced in an experiment *transversifascia*, heterozygote of *transversifascia* and *axyridis*, *axyridis* and *succinea* in an approximately 1 : 1 : 1 : 1 ratio (Table XIII, no. 31), and in another, heterozygote and *axyridis* in a nearly 1 : 1 ratio (no. 32). The heterozygote backcrossed to *succinea* gave *transversifascia* and *axyridis* in 1 : 1 ratio (no. 33).

Transversifascia mated with *spectabilis* gave *conspicua*, *transversifascia*, *spectabilis* and *succinea* in an approximately 1 : 1 : 1 : 1 ratio (Table XIV, no. 34). One of the F_1 *conspicua* was mated to *succinea*, and threw only *transversifascia* and *spectabilis* in about the same numbers (no. 35). This result shows that the heterozygote of *transversifascia* and *spectabilis* cannot be distinguished from *conspicua* in its phenotype.

From a cross *conspicua* × *transversifascia*, *conspicua*, *transversifascia* and *succinea* were produced in an approximately 2 : 1 : 1 ratio (Table XV, no. 36). This suggests that the heterozygote of *conspicua* and *trans-*

versifascia is phenotypically identical with *conspicua*. This suggestion is confirmed by another experiment in which one of the *conspicua* from no. 36 mated to *succinea* threw *conspicua* and *transversifascia* in a nearly 1 : 1 ratio (no. 37).

TABLE XIII

Nos. 31, 32, transversifascia × axyridis; *no.* 33, *heterozygote of* transversifascia *and* axyridis × succinea

			Progeny										
			transversifascia			Heterozygote of *transversifascia* and *axyridis*			*axyridis*			*succinea*			
Cross no.	Parents		♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
31	$P^{T}p$	$P^{A}p$	1	4	5	1	5	6	3	1	4	4	—	4	19
Ratio (cross 31)					1·053			1·263			0·842			0·842	4·000
32	$P^{T}p$	$P^{A}P^{A}$	—	—	—	5	7	12	4	10	14	—	—	—	26
Ratio (cross 32)								0·923			1·077				2·000
33	$P^{T}P^{A}$	pp	6	—	6	—	—	—	4	2	6	—	—	—	12
Ratio (cross 33)					1·000						1·000				2·000

TABLE XIV

No. 34, transversifascia × spectabilis; *no.* 35, conspicua × succinea

			Progeny										
			conspicua			*transversifascia*			*spectabilis*			*succinea*			
Cross no.	Parents		♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
34	$P^{T}p$	$P^{S}p$	13	7	20	13	12	25	8	11	19	9	12	21	85
Ratio (cross 34)					0·941			1·177			0·895			0·987	4·000
35	$P^{T}P^{S}$	pp	—	—	—	1	4	5	2	5	7	—	—	—	12
Ratio (cross 35)								0·833			1·167				2·000

TABLE XV

No. 36, conspicua × transversifascia; *no.* 37, conspicua × succinea

			Progeny									
			conspicua			*transversifascia*			*succinea*			
Cross no.	Parents		♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
36	$P^{C}p$	$P^{T}p$	4	5	9	3	2	5	2	2	4	18
Ratio (cross 36)					2·000			1·111			0·889	4·000
37	$P^{C}P^{T}$	pp	3	13	16	8	5	13	—	—	—	29
Ratio (cross 37)					1·103			0·897				2·000

A cross between *transversifascia* and *forficula* gave *transversifascia*, heterozygote of *transversifascia* and *forficula*, *forficula* and *succinea* in an approximately 1 : 1 : 1 : 1 ratio (Table XVI, no. 38). The heterozygote

mated to *succinea* seggregated *transversifascia* and *forficula* in about a 1 : 1 ratio (no. 39).

These experiments show clearly that *transversifascia* is another allelomorph of all the genes stated. P^T may be used as the symbol for the gene.

This is another rare pattern type shown in Figs. 25, 26. The heterozygote of *aulica* and *succinea* often can be distinguished from the homozygote in that the spot encloses black specks (Fig. 26). But these specks are missing in some cases, when the heterozygote cannot be distinguished from the homozygote (Fig. 25). The heterozygote of *axyridis* and *aulica* resembles *axyridis*, but can be distinguished from it by the anterior two spots being very small or entirely absent (Fig. 27). The heterozygote of

TABLE XVI

No. 38, transversifascia × forficula; *no.* 39, *heterozygote of* transversifascia *and* forficula × succinea

Cross no.	Parents	Progeny: *transversifascia* ♀	♂	Total	Heterozygote of *transversifascia* and *forficula* ♀	♂	Total	*forficula* ♀	♂	Total	*succinea* ♀	♂	Total	Total
38	P^Tp P^Fp	6	2	8	6	1	7	4	3	7	5	2	7	29
Ratio (cross 38)				1·102			0·966			0·966			0·966	4·000
39	P^TP^F pp	12	8	20	—	—	—	16	10	26	—	—	—	46
Ratio (cross 39)				0·870						1·130				2·000

Aulica

forficula and *aulica* and that of *transversifascia* and *aulica* are shown in Figs. 28 and 29 respectively. A heterozygote of *conspicua* and *axyridis* mated to a heterozygote of *aulica* and *succinea* threw three different types, *conspicua*, *axyridis* and heterozygote of *axyridis* and *aulica*, in an approximately 2 : 1 : 1 ratio (Table XVII, no. 40). The heterozygote of *axyridis* and *aulica* mated with *succinea* gave *axyridis* and *aulica* in 1 : 1 ratio (no. 41).

A cross of *spectabilis* with the heterozygote of *axyridis* and *aulica* gave *spectabilis*, heterozygote of *spectabilis* and *axyridis*, *axyridis* and *aulica* in a nearly 1 : 1 : 1 : 1 ratio, showing that the original *spectabliis* had been a heterozygote of *spectabilis* and *aulica* (Table XVIII, no. 42).

A mating between *forficula* and *aulica* gave *forficula*, the heterozygote of *forficula* and *aulica*, *aulica* and *succinea* in nearly equal frequency (Table XIX, no. 43).

The cross *transversifascia* × *aulica* produced *transversifascia*, *aulica* and *succinea* in an approximately 2 : 1 : 1 ratio (Table XX, no. 44). The heterozygote of *transversifascia* and *aulica* crossed with *succinea* produced *transversifascia* and *aulica* in an approximately 1 : 1 ratio (no. 45).

TABLE XVII

No. 40, *heterozygote of* conspicua *and* axyridis × aulica; *no.* 41, *heterozygote of* axyridis *and* aulica × succinea

		Progeny												
		conspicua			*axyridis*			Heterozygote of *axyridis* and *aulica*			*aulica*			
Cross no.	Parents	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Total
40	$P^{C}P^{A}$ $P^{Au}p$	6	8	14	7	2	9	5	3	8	—	—	—	31
Ratio (cross 40)				1·802			1·161			1·032				4·000
41	$P^{A}P^{Au}$ pp	—	—	—	6	8	14	—	—	—	9	5	14	28
Ratio (cross 41)							1·000						1·000	2·000

TABLE XVIII

Spectabilis × *heterozygote of* axyridis *and* aulica

		Progeny												
		spectabilis			Heterozygote of *spectabilis* and *axyridis*			*axyridis*			*aulica*			
Cross no.	Parents	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Tota
42	$P^{S}p$ $P^{A}P^{Au}$	5	3	8	4	3	7	2	6	8	5	2	7	30
Ratio (cross 42)				1·067			0·933			1·067			0·933	4·000

TABLE XIX

Forficula × aulica

		Progeny												
		forficula			Heterozygote of *forficula* and *aulica*			*aulica*			*succinea*			
Cross no.	Parents	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	Tota
43	$P^{F}p$ $P^{Au}p$	5	5	10	5	6	11	6	2	8	6	4	10	39
Ratio (cross 43)				0·865			1·189			0·865			1·081	4·000

Lastly, the cross, heterozygote of *transversifascia* and *aulica* × *aulica* produced *transversifascia* and *aulica* in an approximately 1 : 1 ratio (no. 46).

All these experiments show clearly that *aulica* belongs to the same allelomorphic series as that of all the other genes. P^{Au} will be used as the symbol for it.

TABLE XX

Nos. 44, 45, transversifascia × aulica; *no.* 45, transversifascia × aulica

Cross no.	Parents	Progeny: *transversifascia* ♀	*transversifascia* ♂	*transversifascia* Total	*aulica* ♀	*aulica* ♂	*aulica* Total	*succinea* ♀	*succinea* ♂	*succinea* Total	Total
44	$P^{T}p$ $P^{Au}p$	18	20	38	6	14	20	11	8	19	77
Ratio (cross 44)				1·974			1·039			0·987	4·000
45	$P^{T}P^{Au}$ pp	3	5	8	7	5	12	—	—	—	20
Ratio (cross 45)				0·800			1·200				2·000
46	$P^{T}P^{Au}$ $P^{Au}p$	7	16	23	8	13	21	—	—	—	44
Ratio (cross 46)				1·045			0·955				2·000

SUMMARY AND DISCUSSION

All the experiments dealt with above show beyond any doubt that *succinea*, *axyridis*, *spectabilis*, *conspicua*, *forficula*, *transversifascia* and *aulica are due to autosomal genes belonging to the same allelomorphic series*. Of these, *succinea* is largely recessive to any other gene, but the heterozygotes between it and the dominant types can often be distinguished from the respective homozygotes by the peculiarity in the shape of the anterior spot or because the spot encloses some specks, though there are cases where the heterozygote cannot be distinguished from the homozygote. Heterozygotes between *axyridis* and the other dominant types can also be told from the homozygotes, though *axyridis* is largely recessive to *spectabilis* or *conspicua*. *Conspicua* is completely dominant to *spectabilis*. Of the rarer types, *forficula*, *transversifascia* and *aulica*, *forficula* is largely recessive either to *spectabilis* or to *conspicua*, but the heterozygote can be distinguished from the homozygote by a peculiarity in the anterior spot.

Transversifascia is completely recessive to *conspicua*, and the heterozygote between it and *spectabilis* cannot be distinguished from *conspicua* phenotypically.

Aulica is completely recessive either to *spectabilis* or *conspicua*, and it is largely recessive to *transversifascia*, though the heterozygote can be distinguished from the homozygous *transversifascia*.

The fact that all the seven genes belong to the same allelomorphic series, instead of being independent of one another, is especially clear in

the experiments like nos. 9, 13, 17 or 26, where both parents are heterozygous for two dominant genes—whereas on the independent gene hypothesis the double recessive type *succinea* should have appeared among the progeny.

Tan & Li's data can also be mostly accounted for by the multiple-allelic hypothesis, except for three crosses (nos. 5, 56, 57) where a few *succinea* were obtained, besides *conspicua* and *spectabilis*, from the inbreeding of the heterozygous *conspicua*.

All these, however, are presumably due to experimental errors. Such errors could easily happen, especially in the early stages of the larva, unless great care is taken not to mix different broods. It may be added also that in the well-known experiments of *Phytodecta variabilis* by Zulueta (1925), the different pattern types were shown to be due to allelomorphic genes which are sex-linked instead of being autosomal.

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