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ON POLYMORPHISM IN ELYTRAL COLORATION PATTERN IN *COELOPHORA QUADRIVITTATA* (COLEOPTERA, COCCINELLIDAE)

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The genetics of polymorphism in elytral coloration pattern was studied in the endemic New Caledonian coccinellid *Coelophora quadrivittata* Fauvel. Cross-breeding results can be explained by recognizing that the three basic types of pattern (*pale, spotted,* and *striped*) are due to the occurrence of three different alleles (or pseudo-allelic genes) designated a^p, a^m, and a^q respectively, the order of dominance being $a^q > a^m > a^p$. Other genes participate in local extensions of melanic areas.

In New Caledonia and in the New Hebrides many different polymorphic ladybirds are reputed to display very similar colour patterns. This may be ascribed to similar genetic mechanisms operating in different species. Furthermore, it is possible that environmental factors are involved, as, in some species (for example, *Henosepilachna chrysomelina* (F.)) high temperature and low humidity tend to reduce the melanic area, while low temperature and high humidity increase it (Komai, 1956). But ecological and biogeographic data are scarce, and a study of inheritance and genetic control of the patterns may constitute a useful approach to the problem. This has been attempted for the New Caledonian species, *Coelophora quadrivittata*.

Phenotypes studied (Fig. 1)

Five elytral patterns (black spots on dark yellow background) were recorded:
1) *pale 1*: 2 basal spots, 1 medio-lateral outer spot;
2) *pale 2*: 2 basal spots, 2 lateral outer spots (middle and rear);
3) *spotted*: 2 basal spots, 2 lateral outer spots (middle and rear), 1 median inner spot;
4) *spotted+*: distinct from spotted by partially joined lateral outer spots;
5) *striped*: 2 longitudinal stripes (pattern of the species type specimen).
As a rule, spots in phenotypes *pale 1* and *pale 2* are smaller than in *spotted* and *spoteed +*.

MATERIAL AND METHODS

All stages were reared under controlled conditions (temperature 25,5° ± 0,5°;

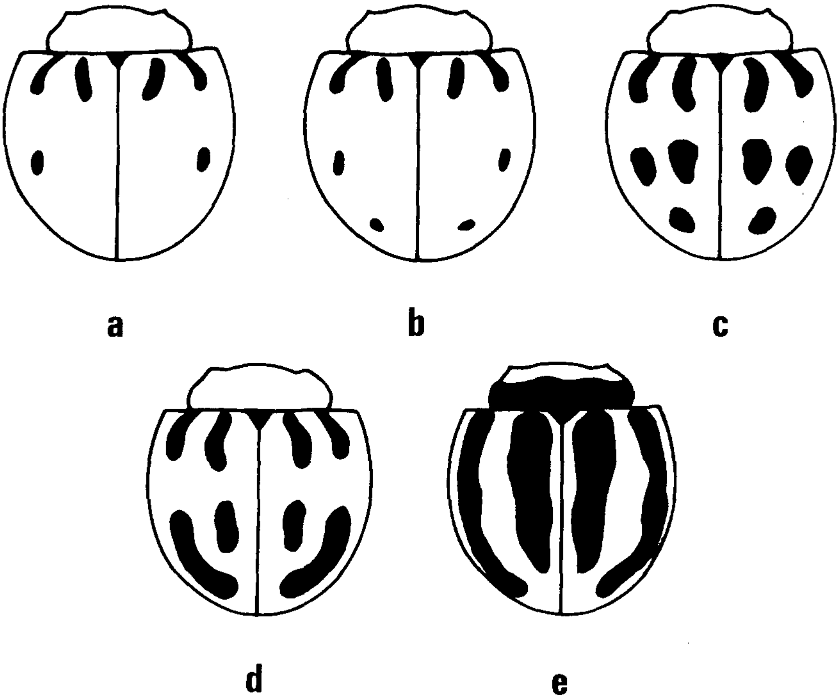

Fig. 1. Elytral patterns in *Coelophora quadrivittata*. a: *pale 1* — b: *pale 2* — c: *spotted* — d: *spotted +* — e: *striped*.

r.h. 55%—80%), in plastic boxes (inner dimensions: 62 x 48 x 14 mm) covered with a wire netting and lined with wet filter paper. Food was provided daily in the form of a piece of leaf of *Plumeria* sp. (*Apocynaceae*) infested by *Coccus viridis* Green (Homoptera, *Lecanidae*).

All specimens studied originated from one single field-collected female of the striped pattern (Nouméa, 10.VII.1978, predator of *Coccus viridis* on *Plumeria* sp.). This female laid 201 fertile and 8 sterile eggs in 25 days; 182 specimens were raised to the adult stage: 53 *pale 1* and *pale 2*, 5 *spotted* and 124 *striped*.

All female parents in the 15 crosses formed were virgin, except female 3. Each cross consisted of a single pair. Both parents in crosses 1, 2, 4, 5, 6, 7, 8 and 9 were taken from the 182 specimens originating from the wild female. Cross 3 resulted from the cross of this female with a male from her progeny, after she had produced only sterile eggs during 5 days. Both parents in crosses 10 and 12, and the males in crosses 11 and 13, were taken from the progeny of cross 3. Female 11 was taken from the progeny of cross 1.

Females 13, 14 and 15 were respectively taken from the progeny of crosses 9, 6 and 13. The male in crosses 14 and 15 was a field-collected specimen (Nouméa, XI.1978, predator of *Coccus viridis* on *Plumeria* sp.).

The entire progeny of each cross (hundreds of larvae for each female) could not be reared for food supply and handling reasons; therefore, specimens examined originated from the first days of oviposition.

RESULTS

The results (Table I) of crosses where phenotypes *pale 1* and *pale 2* appear in the F_1 cannot be simply explained by the assumption of independent inheritance. Intermediate patterns between both phenotypes can be observed (rear spot sometimes hardly noticeable), and a stereomicroscope had to be used at a

TABLE I

Inheritance of elytral patterns in Coelophora quadrivittata; a^p: *allele for phenotypes* pale 1 *and* pale 2, a^m: *allele for phenotypes* spotted *and* spotted +; a^q: *allele for* striped *phenotype; (Numbers in parentheses represent expected values)*

	Parents		F_1					
Cross	Phenotypes	Genotypes	Phenotypes of specimens reared					
	♀ ♂	♀ ♂	pale 1 + pale 2	spotted	striped	spotted +	χ^2	P
1	pale 2 × pale 1	$a^pa^p \times a^pa^p$	30 + 18 = 48 (*48*)	—	—	—		
2	pale 2 × pale 2	$a^pa^p \times a^pa^p$	4 + 29 = 33 (*33*)	—	—	—		
3	striped × striped	$a^pa^q \times a^ma^q$	—	15 (*15.75*)	48 (*47.25*)	—	0.05	0.80—0.90
4	striped × striped	$a^ma^q \times a^pa^q$	—	9 (*11*)	35 (*33*)	—	0.48	0.30—0.50
5	striped × striped	$a^pa^q \times a^pa^q$	10 + 9 = 19 (*16*)	—	45 (*48*)	—	0.75	0.30—0.50
6	striped × striped	$a^pa^q \times a^pa^q$	0 + 13 = 13 (*9.5*)	—	25 (*28.5*)	—	1.72	0.10—0.20
7	pale 2 × striped	$a^pa^p \times a^pa^q$	14 + 4 = 18 (*18*)	—	18 (*18*)	—		
8	pale 2 × striped	$a^pa^p \times a^ma^q$	—	21 (*22.5*,	24 (*22.5*)	—	0.20	0.50—0.70
9	pale 2 × striped	$a^pa^p \times a^qa^q$	—	—	53 (*53*)	—		
10	spotted × spotted	$a^pa^m \times a^pa^m$	5 + 9 = 14 (*12.5*)	36 (*37.5*)	—	—	0.24	0.50—0.70
11	pale 2 × spotted	$a^pa^p \times a^pa^m$	15 + 11 = 26 (*28.5*)	31 (*28.5*)	—	—	0.22	0.50—0.70
12	spotted × striped	$a^pa^m \times a^qa^q$	—	—	37 (*37*)	—		
13	striped × spotted	$a^pa^q \times a^pa^m$	0 + 15 = 15 (*14*)	12 (*14*)	29 (*28*)	—	0.40	0.80—0.90
14	pale 2 × spotted +	$a^pa^p \times a^pa^m$	5 + 16 = 21 (*23*)	24 (*23*)	—	1	0.34	0.50—0.70
15	spotted × spotted +	$a^pa^m \times a^pa^m$	0 + 7 = 7 (*6.5*)	17 (*19.5*)	—	2	0.05	0.80—0.90

moderate magnification to separate both types. These observations and the numerical values for *pale 1* and *pale 2* suggested that these phenoptypes had to be treated together initially.

Results in Table I may then be explained by the existence of three basic pattern types (*pale, spotted* and *striped*) dependent on three alleles (or pseudo-allelic genes) respectively designated a^p, a^m and a^q, in order of dominance $a^q>a^m>a^p$. The relationship between a^p and a^q is proved by the results of crosses 5, 6, 8 and 9. The dominance of a^m over a^p is proved by the results of cross 10. The dominance of a^q over a^m is proved by the results of crosses 3, 4 and 12.

Genotypes given for parents in crosses 1 to 3 and 5 to 12 are inferred by their origin, by the order of dominance, and by ratios of different patterns in the F_1. Doubt in the case of cross 4 ($a^ma^q \times a^pa^q$, or $a^pa^q \times a^ma^q$, or $a^ma^q \times a^ma^q$) was removed by crossing the male with two females of the *pale 1* pattern (*pale 1* and *pale 2* patterns thus obtained in the F_1).

Cross 13 was conducted to check the genotypes inferred by the above analysis.

Crosses 14 and 15 were conducted to establish the genotype of a field-collected male of *spotted* + phenotype. It should be mentioned that the specimen classified as *spotted* + in the F_1 of cross 14, and one of the two specimens classified as *spotted* + in the F_1 of cross 15, show an intermediate pattern between *spotted* and *spotted* + (the spot-joining stripe is very narrow). It may thus be concluded that this pattern is not inherited through the control of a fourth allele. Consequently, the χ^2 values for these crosses were calculated by adding the numbers observed for patterns *spotted* and *spotted* +.

DISCUSSION

The explanation of genetic control and inheritance of the elytral patterns recorded in *C. quadrivittata* appears to present no initial difficulty. The values of χ^2 are always low despite limited size of the F_1 samples studied. This can be partly attributed to the homogeneity of the strain originating from one single female. The occurrence of *pale 1*, *pale 2*, *spotted* and *striped* patterns in the F_1 of this female can be explained by multiple fertilization by several males.

However, the existence of distinguishable phenotypes *pale 1* and *pale 2* and the results of crosses 14 and 15, giving rise to *spotted* + beside *spotted*, prove that other genes participate in the control of elytral pattern, the intricate mechanism of which cannot be completely explained by the present work.

Action of these genes may affect more than one body segment. Thus, the presence of a pronotal black spot of variable extension was always observed in *striped* specimens; in specimens *pale 1*, *pale 2* and *spotted*, the pronotum was usually spotless; but this spot was apparent in two specimens *pale 2* and *spotted* in the F_1 of cross 14, the male parent of which was *spotted* +.

It was furthermore observed that inheritance of the scutellum pattern (usually black, but occasionally a light colour) and of the pattern of the abdominal sternites (dark yellow or brown) cannot be simply related to inheritance of the elytral pattern.

The above observations correspond to those of Hales (1976) on *Coelophora inaequalis* (F.) and concur with her explanation of Timberlake's results on the same species. As described in Komai's review (1956), multi-allelic series (or series of pseudo-allelic genes) are commonplace in Coccinellidae. Operation of such similar mechanisms might partially explain the occurrence of common pattern types in *C. quadrivittata* and *Coelophora mulsanti* (Mont.) in New Caledonia, in *Harmonia novaehebridensis* (Kors.) and *Coelophora auberti* Chazeau, or in *Coelophora inaequalis* (F.) and *Menochilus sexmaculatus* (F.) in the New Hebrides (Chazeau, 1978). Only *C. inaequalis* had been previously studied (Timberlake, 1922; Hales, 1976; Houston, 1979). Houston's results indicate that inheritance of colour patterns in *C. inaequalis* is governed by mosaic dominance, but this could not be established for *C. quadrivittata.*

Nevertheless, no comprehensive analysis has yet been conducted of genetic control and inheritance owing to the complexity of patterns. Since this complexity is related to the great number of phenotypes recorded in most of the species examined, a relatively simple species like *C. quadrivittata* may be suitable for a more thorough study of pigmentation. More particularly, it can be adapted for an analysis of relationships between different body segments.

RÉSUMÉ

SUR LE POLYMORPHISME OBSERVÉ DANS LA COLORATION ÉLYTRALE DE COELOPHORA QUADRIVITTATA *(COLEOPTERA, COCCINELLIDAE)*

Le problème posé par la grande similitude des types de coloration élytrale, observée chez certaines coccinelles polymorphes de Nouvelle-Calédonie et des Nouvelles-Hébrides, a été abordé par l'étude de la transmission de ces caractères chez une espèce néo-calédonienne endémique: *Coelophora quadrivittata* Fauvel. Les résultats des croisements effectués peuvent s'interpréter par l'existence de trois types de coloration de base: clair (*pale*), taché (*spotted*) et rayé (*striped*), sous la dépendance de trois gènes allèles (ou pseudo-allèles) respectivement notés a^p, a^m et a^q, dans l'ordre de dominance $a^q>a^m>a^p$. D'autres gènes interviennent en outre dans l'extension locale de la mélanisation.

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