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MOSAIC DOMINANCE IN THE INHERITANCE OF THE COLOUR PATTERNS OF *COELOPHORA INAEQUALIS* (F.) (COLEOPTERA: COCCINELLIDAE)

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Abstract

Crosses were made between six forms of *Coelophora inaequalis* (F.) from the Brisbane area: nine-spotted, elongated stripe, normal, black, five-spotted and broken stripe. It was established that the inheritance of colour patterns in *C. inaequalis* is governed by mosaic dominance. These six forms are governed by four alleles with a dominance order of nine-spotted > normal > black, elongated stripe > black, while the elongated stripe and nine-spotted alleles and the elongated stripe and normal alleles are co-dominant and produce the five-spotted and broken stripe forms respectively.

Examination of types confirmed the synonomy of *Coccinella novempunctata* F., *Coccinella religiosa* Lea, *Coelophora mastersi* Blackburn, *Coelophora ripponi* Crotch and *Coelophora veranioides* Blackburn with *Coelophora inaequalis*. *Lemnia desolata* Mulsant is shown to be another synonym of *Coelophora inaequalis*.

Introduction

Coelophora inaequalis is one of the most abundant coccinellids in the Brisbane region. Its colour pattern is very variable and some of the more distinctive phenotypes have in the past been described as separate species.

Inheritance of the colour patterns of *C. inaequalis* was first studied by Timberlake (1922) in Hawaii. Australian specimens of *C. inaequalis* were introduced into Hawaii by A. Koebele and the original stock of beetles with which Timberlake began his crosses was collected from Queensland. He undertook crosses with three forms: a nine-spotted (Fig. 1), normal (Fig. 2) and a black form (Fig. 3), that he later (1943) recognised as *Coccinella novempunctata*, *Coelophora inaequalis* and *Coelophora mastersi* respectively.

Hales (1976), in Sydney, studied the inheritance of another four forms of *inaequalis:* standard, zig-zag, elongated stripe and striped. She recognised that the latter form had been previously described as *Coelophora veranioides*. Britton (Hales 1977) considered that *Coelophora ripponi* and *Coccinella religiosa* were synonyms of *C. inaequalis* which had the striped and nine-spotted patterns respectively.

Tan (1946) found that the phenotypes of heterozygotes of the coccinellid *Harmonia axyridis* Pallas can be predicted by the following rule of mosaic dominance; heterozygotes form black pigment on any part of the elytra which is black pigmented in either homozygote of these alleles. By contrast heterozygotes in *C. inaequalis* form yellow pigment on any part of the elytra which is yellow pigmented in either homozygote of these alleles. The allele for black pigment in a particular area is dominant in *H. axyridis* while in *C. inaequalis* the allele for black pigment in a particular area is recessive.

Using this rule, the phenotypes of the heterozygotes of the colour forms of *C. inaequalis* can be predicted. In other words, if the colour patterns in any two different homozygotes of *C. inaequalis* are known, the colour pattern in the heterozygote can be predicted by superimposition of the patterns of the homozygotes, and leaving pigmented only those sections of the elytra which have black pigment in both homozygotes.

This study presents the results of crosses made between six forms of *inaequalis* occurring in the Brisbane area. Three were similar to those of Timberlake, one was similar to the elongated stripe form (Fig. 4) of Hales (1976) and two were new forms, a broken stripe form (Fig. 5) and a five-spotted form (Fig. 6).

Abbreviations used for Institutions mentioned are as follows: ANIC, Australian National Insect Collection, Canberra; BM, British Museum (Nat. Hist.), London; CM, Cambridge Museum, Cambridge; HM, Hope Museum, Oxford University; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide.

TABLE

INHERITANCE OF SIX ELYTRAL PATTERNS OF *COELOPHORA INAEQUALIS*

Parents		Progeny							
Phenotype	Genotype	nine-spotted	five-spotted	elongated stripe	broken stripe	normal	black	N	χ^2
five-spotted × five-spotted	$c^sc^v \times c^sc^v$	18	41	21				80	0.275
broken stripe × broken stripe	$c^vc^n \times c^vc^n$			13	21	10		44	0.500
nine-spotted × nine-spotted	$c^sc^s \times c^sc^s$	46						46	
nine-spotted × nine-spotted	$c^sc^n \times c^sc^n$	53				11		64	1.688
nine-spotted × normal	$c^sc^s \times c^nc^n$	56						56	
nine-spotted × normal	$c^sc^n \times c^nc^n$	31				21		52	1.558
five-spotted × nine-spotted	$c^sc^v \times c^sc^s$	20	28					48	1.021
five-spotted × nine-spotted	$c^sc^v \times c^sc^n$	38	13		19			70	1.543
five-spotted × elongated stripe	$c^sc^v \times c^vc^v$		25	19				44	0.568
five-spotted × broken stripe	$c^sc^v \times c^vc^n$	16	15	8	10			49	3.653
five-spotted × normal	$c^sc^v \times c^nc^n$	23			28			51	1.137
broken stripe × nine-spotted	$c^vc^n \times c^sc^s$	23	19					42	0.214
broken stripe × nine-spotted	$c^vc^n \times c^sc^n$	17	30		34	36		117	7.479
broken stripe × elongated stripe	$c^vc^n \times c^vc^v$			22	21			43	0.000
broken stripe × elongated stripe	$c^vc^n \times c^vc^b$			30	10	15		55	1.364
broken stripe × normal	$c^vc^n \times c^nc^n$				15	17		32	0.016
elongated stripe × nine-spotted	$c^vc^v \times c^sc^s$		40					40	
elongated stripe × nine-spotted	$c^vc^v \times c^sc^n$		22		20			42	0.024
elongated stripe × normal	$c^vc^v \times c^nc^n$				44			44	
elongated stripe × normal	$c^vc^b \times c^nc^b$			15	14	12	21	62	2.903
elongated stripe × black	$c^vc^v \times c^bc^b$			48				48	
elongated stripe × black	$c^vc^b \times c^bc^b$			22			26	48	0.188

Materials and methods

Adult females and larvae were field collected and unmated progeny were reared from them. These together with the occasional addition of some field males provided the material for the crosses. Soon after emergence males and females were placed in separate petri dishes and, when required, a male and an unmated female were placed together.

All stages were reared in glass petri dishes of 100 mm diameter and 20 mm deep in which a piece of folded paper was placed to induce egg-laying and as a refuge for the larvae. Cotton wool moistened with sucrose solution provided food and moisture for the adults. Eggs were removed daily. Up to 20 larvae were reared together and, providing sufficient food was available, losses due to cannibalism were small.

All feeding stages were reared on field collected aphids. These were mainly *Hyperomyzus lactucae* (L.) and *H. carduellinus* (Theobald) from milk thistles (*Sonchus* spp.), but occasionally *Toxoptera citricidus* (Kirkaldy), *T. aurantii* (Boyer de Fonscolombe) and *Hysteroneura setariae* Thomas, were used. The number of beetles reared was limited by the aphid supply.

Results

Crosses made and the results obtained in this study are shown in the Table. The symbol c^s is used for the nine-spotted allele, c^n for the normal allele, c^b for the black allele and c^v for the elongated stripe allele.

Elytral Pattern

Specimens in these breeding experiments showed slight variations in size and shape of the spots and stripes on the elytra in all forms, e.g. the size of the posterior sutural and posterior spots of the nine-spotted and five-spotted forms was variable and the latter could be reduced so as to become barely recognisable while the former was absent in some specimens. Also varying amounts of slight fusion of spots could occur in specimens of the normal form, the most common being between the posterior sutural spot and the posterior spot. It is not known whether some or all of these smaller elytral pattern variations were genetically or environmentally based.

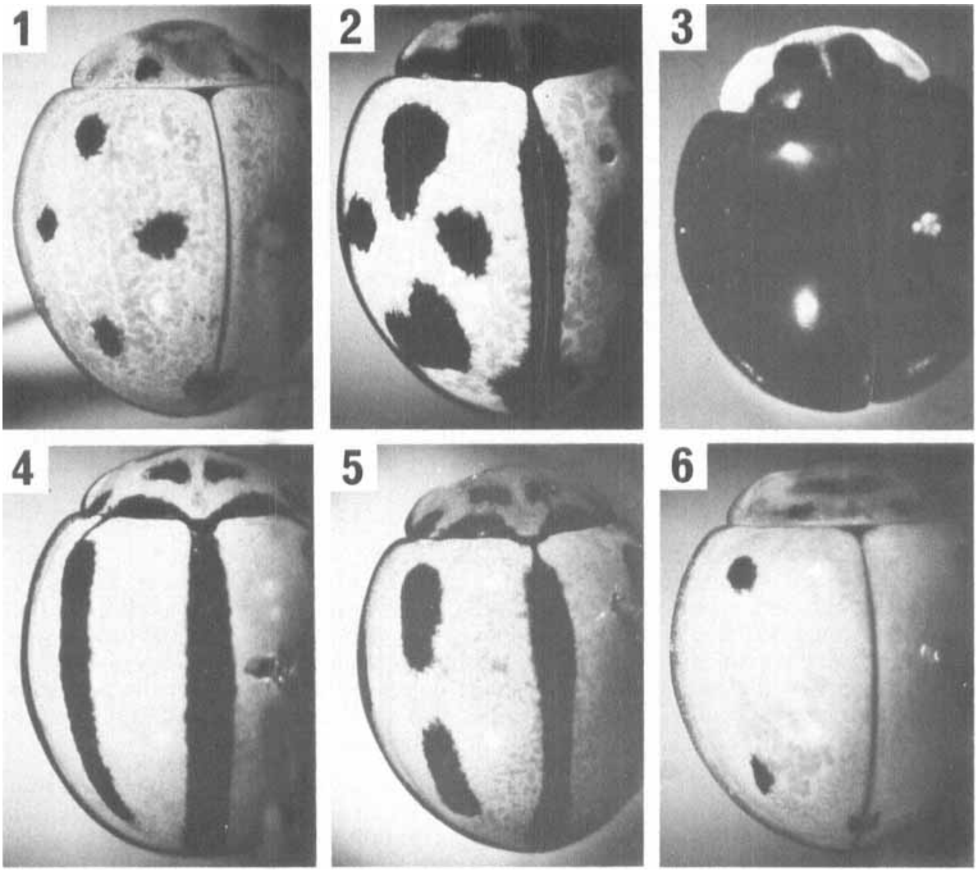
From the Table, and using Timberlake's conclusion that $c^s > c^b$, it is evident that the inheritance of these six elytral patterns is due to four alleles of a single gene, with a dominance order of $c^s > c^n > c^b$ and $c^v > c^b$ and that the five-spotted and broken stripe forms are heterozygotes, c^sc^v and c^vc^n, respectively. The alleles c^v and c^n are co-dominant, since the phenotype of their heterozygote, the broken stripe pattern (c^vc^n), is different from the phenotype of either homozygous parent (i.e. the elongated stripe c^vc^v or the normal pattern c^nc^n). Similarly c^s and c^v are co-dominant. The results were subjected to a chi square analysis, on the basis of the above conclusions, and all the probabilities were within the 5% probability limit.

It is interesting to note that the allele c^v shows varying degrees of penetrance when combined with c^s and c^n. In many specimens of c^sc^v and some specimens of c^vc^n, the stripe of the elongated stripe phenotype can be discerned as a very pale brown stripe connecting the two spots or stripes of the five-spotted or broken stripe phenotypes, respectively.

Pronotal Pattern

The pronotal patterns of c^nc^n are shown in Figs 2, 7-8 but the amount of pigmentation is variable and there is an almost continuous grade between them. Few c^nc^n specimens had the pattern of Fig. 8 which is similar to that of the zig-zag (c^zc^z) specimen figured in Hales (1976, Fig. 1d). As stated by Timberlake (1922), c^nc^b and c^bc^b have the same pronotal pattern (Figs 3, 9). Thus while $c^n > c^b$ for elytral pattern, $c^b > c^n$ for pronotal pattern. The depth of the groove of the pronotal patterns of c^nc^n, c^nc^b and c^bc^b was variable, ranging from reaching the scutellum to being almost blacked out as in Fig. 7.

The pronotal patterns of c^vc^n (Figs 4, 12-15) are the same as or variations of those of c^vc^v (Figs 4, 12-13), so $c^v > c^n$. Few specimens had the pattern of Fig. 15. Probably because there was more than twice the number of c^vc^n to c^vc^v progeny, c^vc^n appears to have a greater variation of pronotal pattern than c^vc^v. Thus the c^vc^v specimen figured in Hales (1976, Fig. 1c) has a pronotal pattern similar to that of some c^vc^n specimens (Fig. 14). The pronotal patterns of c^vc^b (Figs 10-11) are similar to those of c^vc^v except



FIGS 1-6—Colour forms of *C. inaequalis:* **(1)** nine-spotted; **(2)** normal; **(3)** black; **(4)** elongated stripe; **(5)** broken stripe; **(6)** five-spotted.

that they lack pigmented areas laterally, so c^v and c^b are co-dominant. Therefore normal and elongated stripe forms, heterozygous for the black allele (c^nc^b, c^vc^b), can be recognised by their pronotal patterns.

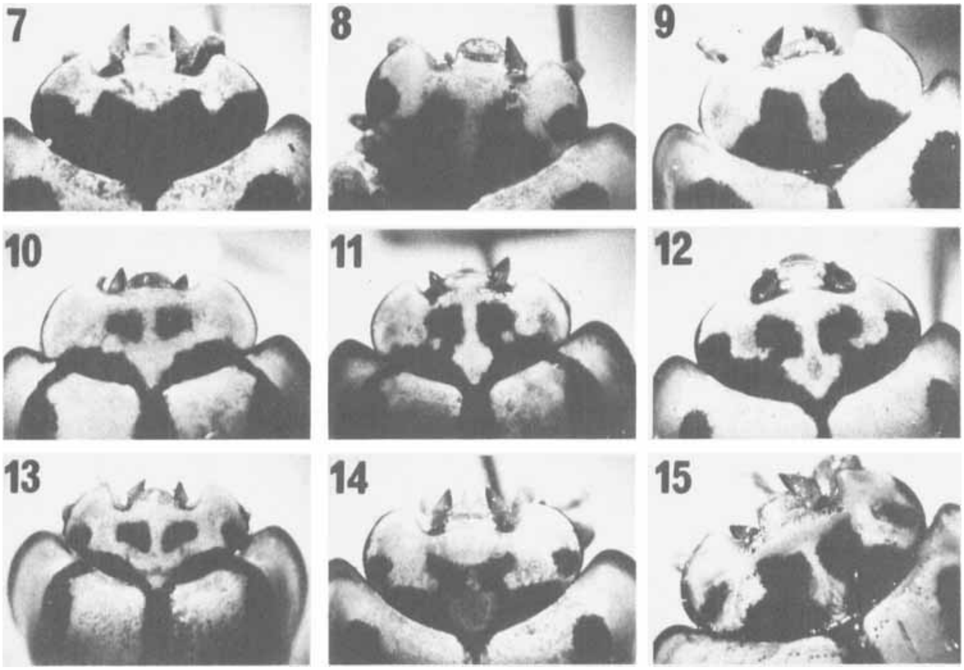
The pronotal patterns of c^sc^s, c^sc^n and c^sc^v are the same (Figs 1, 6), so $c^s > c^v$ and $c^s > c^n$. The spots varied in size and colour and were lacking in some specimens. From Timberlake (1922) it seems that $c^s > c^b$ for pronotal pattern. Whether some or all of the pronotal variations of these forms were caused by variations in penetrance due to environmental effects, or by other genes was not elucidated.

Therefore the four alleles which determine elytral pattern also partially determine the pronotal pattern, but the dominance order is different, viz.: $c^s > c^v > c^n$, $c^s > c^b > c^n$ and c^v and c^b are co-dominant.

Synonyms

All six forms of *C. inaequalis* mated freely in the laboratory in all combinations and produced fertile offspring. This crossing also occurs in natural populations since in samples collected from the field a noticeable number of specimens are heterozygous. The external morphology and the male and female genitalia of all forms were identical and agree well with *C. inaequalis* figured in Chapin (1965). Also the larvae and pupae of all forms were indistinguishable. Thus all these phenotypes must be considered to be colour forms of the one polymorphic species.

Pope (pers. comm.) has compared the types of *Coccinella novempunctata* (BM), *Coelophora inaequalis* (BM), and *Coelophora ripponi* (CM) with a series of specimens



FIGS **7-15**—Pronotal patterns of *C. inaequalis:* **(7-8)** normal; **(9)** black and heterozygous normal, c^nc^b; **(10-11)** heterozygous elongated stripe, c^ec^b; **(12-13)** elongated stripe and broken stripe; **(14-15)** broken stripe.

of all forms bred during this experiment and he confirms their synonomy. The types have the colour patterns of the nine-spotted, normal and elongated stripe forms respectively. Pope also examined the type of *Lemnia desolata* (HM), and considers it to be a synonym of *Coelophora inaequalis* with a colour pattern similar to the black form.

The types of *Coccinella religiosa* (2♀) (SAM), *Coelophora mastersi* (1♀) (BM) and *Coelophora veranioides* (1♀) (BM) were examined by the author. Their synonomy with *Coelophora inaequalis* is confirmed and their colour patterns were similar to those of the nine-spotted, black and striped forms respectively. The broken stripe pattern was previously regarded as a form of *Coelophora veranioides*.

Discussion

In his 1922 studies, Timberlake found that the black form was recessive to the nine-spotted and normal form, but he could not determine the relationship between the nine-spotted and normal forms. However from his results, Dobzhansky (1933) concluded that multiple alleles were involved, while Shull (1943) concluded that these alleles had an order of dominance of nine-spotted > normal > black. The results of the present study confirm these conclusions.

Mosaic dominance

It is evident in all heterozygotes, for both elytral and pronotal pattern, that black pigment is produced only in those areas where there is black pigment in both homozygous parents. If the black pigmented area of one homozygous parent is contained within the black pigmented area of the other homozygous parent, then the heterozygote has the pattern of the parent with the smaller area of black pigmentation. The alleles which form these inclusive heterozygotes will be either completely dominant or completely recessive. However if the patterns of the homozygous parents overlap, the heterozygote has a different phenotype from either parent e.g. the elytral pattern of the normal and elongated stripe forms overlap, so that if their patterns are superimposed and only those areas blacked in which are pigmented in both parents, the resultant pattern will be the broken stripe phenotype. The alleles which form overlapping heterozygotes are co-dominant.

The rule of mosaic dominance accurately predicts the colour patterns of heterozygotes and the order of dominance of the alleles for colour pattern in *C. inaequalis*. It also explains why some alleles have different types of dominance for elytral and pronotal patterns. For elytral pattern $c^v > c^b$, $c^n > c^b$ while c^s and c^v, c^v and c^n are co-dominant, whereas for pronotal pattern c^v and c^b are co-dominant, $c^b > c^n$, $c^s > c^v$ and $c^v > c^n$.

In *C. inaequalis* this rule is very precise and small differences in pattern can be explained by it, e.g. the black pigment along the suture of the broken stripe form (c^vc^n) is thinner at the anterior end than in the elongated stripe form (c^vc^v) because the normal form (c^nc^n) is thin anteriorly.

It is evident from the results of Hales' crosses that mosaic dominance also applies to her forms. Since the three alleles of Timberlake (c^s, c^n, c^b) and one of the alleles of Hales (c^v) are alleles of the same gene, then the other two alleles of Hales (c, c^z) must also belong to the same allelic series. The rule of mosaic dominance can be used to predict the phenotypes of heterozygotes between these alleles which have not yet been crossed in the laboratory. Thus the nine morphs of Timberlake (1922), Hales (1976) and those described in this paper are governed by six alleles, with a predicted dominance order for elytral pattern of $c^s > c^n > c > c^z > c^b$ and $c^v > c^b$ while c^s and c^v, c^v and c^n, c^v and c, c^v and c^z are co-dominant. The predicted dominance order for pronotal pattern is $c^s > c^b > c = c^n = c^z$, $c^s > c^v > c = c^n = c^z$ and c^v and c^b are co-dominant. The pronotal patterns of the standard and zig-zag specimens figured in Hales (1976, Figs 1a, d) are within the range of patterns of the normal form.

There is evidence e.g. from *Papilio* wing patterns (Clarke *et al.* 1968), that many multiple allelic genes are really supergenes, i.e. sets of very closely linked genes, so that crossing over rarely occurs, involved in a common function. That this could be the case in *C. inaequalis* is supported by the number of similar colour patterns and the mosaic inheritance of heterozygotes.

The heredity of the colour patterns of some other coccinellids also follows the rule of mosaic dominance. The results obtained by Lusis (1971) for *Calvia punctata* Mulsant and Miyazawa and Ito (Komai 1956) for *Propylea japonica* (Thunberg) can be explained by this rule. In *C. punctata* the allele for black pigment in a particular area is dominant, while in *P. japonica* it is recessive. In these two species all the patterns are inclusive but a better test for the applicability of this rule to a particular species would be to cross forms with overlapping patterns.

Comments

In Australia, and also in the Asian and Pacific areas, there are many variations of the normal form of *C. inaequalis*, involving varying amounts of fusion and/or reduction of spots. The standard and zig-zag forms are examples of this variation involving increasing amounts of fusion of the spots. No doubt other completely different patterns also occur. The approximate order of abundance of these forms in the Brisbane area is as follows: normal, broken stripe, nine-spotted, black, elongated stripe and five-spotted forms, the normal form being very common while the five-spotted form is very rare. Also the standard form is occasionally found in the Brisbane area.

Reference specimens of the forms reared in this investigation have been deposited in ANIC, BM, QM and SAM.

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