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Allelic Frequencies and Inheritance of Colour Pattern in *Coelophora inaequalis* (F.) (Coleoptera : Coccinellidae)

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Abstract

Crosses were made between colour forms of *Coelophora inaequalis* from the Brisbane and Sydney–Newcastle areas, including two new forms ('yellow' and 'heavy'). The following alleles were involved in these crosses: 'nine-spotted', 'elongated stripe', 'normal', 'fused' (≡ 'standard'), 'zig-zag', 'black', 'yellow' and 'heavy'. All possible heterozygotes not previously described were obtained and figured. All the colour patterns produced by these alleles followed the rule of mosaic dominance. There is little difference in frequencies of the above alleles between populations in Brisbane and Mareeba (north Queensland), but the composition of the Sydney–Newcastle population is distinctly different. An examination of some major insect collections provided further information on the distribution of these alleles in Queensland and New South Wales.

Introduction

The colour pattern of *Coelophora inaequalis* (F.) is very variable. The inheritance of some of these patterns has been studied by Timberlake (1922) in Hawaii, Hales (1976) in Sydney and Houston (1979) in Brisbane. Houston showed that all the colour forms studied by these authors were controlled by multiple alleles of a single gene (or by a set of closely linked genes, i.e. a supergene) and that the pattern produced was governed by the rule of mosaic dominance, where heterozygotes form black pigment only in those areas where there is black pigment in both homozygous parents. Thus many heterozygotes are different from either parent. The above authors studied the 'nine-spotted', 'normal', 'black', 'elongated stripe', 'fused' and 'zig-zag' alleles. In this paper the name of the 'standard' allele (c) of Hales (1976) has been changed to the 'fused' allele (c^f), to avoid confusion with the 'normal' allele (c^n), which determines the pattern of *inaequalis* as it was originally described.

The 'nine-spotted', 'normal' and 'black' alleles have not been previously crossed with the 'zig-zag' and 'fused' alleles. Also, the heterozygotes of the 'zig-zag' allele with the 'fused' and 'elongated stripe' alleles were not described by Hales (1976), as the evidence for the relationship between them was incomplete. In this study crosses were made between Brisbane and Sydney–Newcastle forms to obtain these heterozygotes. Also, two new forms ('yellow' and 'heavy') were collected from the Sydney–Newcastle area and crosses were made between them and the previously studied alleles, so that all possible genotypes having either a 'yellow' or 'heavy' allele were produced.

In many coccinellids the colour pattern varies geographically (see Honek (1973) and Komai (1956) for references); there is evidence of this in *C. inaequalis* (compare the forms studied from Brisbane and Sydney). Random collections of *C. inaequalis* were made from the Sydney–Newcastle, Brisbane and Mareeba areas so that the frequency of alleles for colour pattern could be estimated and compared.

Materials and Methods

Crosses

The material for the crosses included unmated progeny of previous crosses of Houston (1979), a homozygous black male collected from Home Hill (19°40′S., 147°25′E.) in north Queensland, and unmated progeny of adults collected from the Sydney–Newcastle area. The 'yellow' allele originated from a yellow, heterozygous male collected at Hawks Nest, N.S.W. The 'heavy' allele originated from a single heterozygote collected at Eastwood, N.S.W. The 'yellow', 'nine-spotted', 'heavy' and 'black' alleles were each identical in all crosses described, having each originated from a single allele of one specimen. 'Striped', 'normal', 'fused' and 'zig-zag' alleles were introduced on several occasions, so there is the possibility that isoalleles rather than true alleles were present in the breeding stocks. Specimens were exchanged between the authors and crosses made in Brisbane and Sydney.

Sydney specimens were reared as in Hales (1976) except that additional species of aphids were used as food; these included *Acyrthosiphon kondoi* Shinji, *Aphis nerii* Boyer de Fonscolombe and *Macrosiphum euphorbiae* (Thomas). Brisbane specimens were reared as in Houston (1979) except that most aphids used as food were glasshouse-reared: *Hyperomyzus lactucae* (L.) and *H. carduellinus* (Theobald) on *Sonchus* sp., and *A. nerii* on *Asclepias* sp. Occasionally field-collected aphids were used; including the above three aphids, *Ac. kondoi, Hysteroneura setariae* Thomas and *Therioaphis trifolii* (Monell).

Iperti (1966) found that *A. nerii* from *Nerium oleander* L. is poisonous to many French coccinellids, *Adonia variegata* (Goeze) being an exception. *C. inaequalis* also develops normally on this aphid, since *A. nerii* aphids from *N. oleander, Asclepias* and *Araujia hortoruum* Fourn. were used as food in the following crosses, and many specimens of all stages of *C. inaequalis* have been collected on these in the wild.

Voucher specimens of the forms reared have been deposited in the Australian National Insect Collection, the Queensland Department of Primary Industries, and the Queensland Museum.

Allele Frequency

Samples of *C. inaequalis* were collected from three areas. Every individual encountered was collected, in order to avoid bias towards the less common phenotypes. In some cases larvae or pupae were collected and adults reared. The three areas were as follows:

Sydney–Newcastle area, November 1975–April 1978. Most specimens were from the Sydney area (33°53′S., 151°13′E.), in particular the suburbs of North Ryde, Eastwood, Castle Hill and Mosman. An additional 12 specimens were collected at Ocean Beach (33°32′S., 151°18′E.) near Woy Woy and 22 at Hawks Nest (32°41′S., 152°11′E.) on the northern side of Port Stephens. Specimens were collected from garden plants, grasses and weeds, but 30 at Castle Hill were feeding on the aphid *Schoutedenia lutea* (van der Goot) on the native plant *Breynia oblongifolia* Muell. Arg.

Brisbane area (27°28′S., 153°01′E.), February 1976–March 1978. Most specimens were from the suburbs of Long Pocket, Fig Tree Pocket and Oxley. Specimens were collected mainly from guinea grass, *Panicum maximum* Jacq.

Mareeba area (17°00′S., 145°26′E.). Specimens were collected on 12 November 1977 and 15 April 1978, from sorghum.

Each specimen was assigned a genotype by reference to reared specimens of known genotype. In some cases the genotype was known from breeding data. Because of the overlap and variability of phenotypes, it was frequently not possible to be certain of both alleles contributing to the pattern of an individual specimen, but in nearly all cases at least one allele could be identified with reasonable confidence. The frequency of some alleles could be counted directly, while that of others could be calculated by the Hardy-Weinberg method from the frequency of homozygotes or homozygotes plus heterozygotes. Further notes on the methods of calculation are given in Table 3.

Terminology and Abbreviations

Symbols used for the alleles are: c^y, yellow; c^h, heavy; c^s, nine-spotted; c^v, elongated stripe; c^n, normal; c^f, fused; c^z, zig-zag; c^b, black. For ease of description, the elytral markings of the nine-spotted form have been named as anterior, posterior, dorsal, ventral and sutural. The first four of these are situated at the four corners of an imaginary diamond on each elytron, and the sutural spot is formed by the apposition of black marks on the suture of both elytra, posteriorly. The same terminology is applied to other 'spotted' phenotypes (e.g. normal, zig-zag, etc.), but their patterns are complicated by the greater pigmentation.

The following abbreviations are used for institutions:

ANIC	Australian National Insect Collection, Canberra
BPBM	Bernice P. Bishop Museum, Honolulu
NSWDA	New South Wales Department of Agriculture, Sydney
QDPI	Queensland Department of Primary Industries, Brisbane
QM	Queensland Museum, Brisbane
UQ	University of Queensland Insect Collection, Brisbane

Table 1. Results of crosses involving eight alleles for colour pattern of *C. inaequalis*

The phenotypes of the parents and progeny are shown in Fig. 1. *P < 0·05

Parental genotype	Genotype and number of progeny				N	χ^2
$c^yc^y \times c^vc^n$	c^yc^v (36);	c^yc^n (34)			70	0·014
$c^yc^s \times c^yc^s$	c^yc^y (22);	c^yc^s (51);	c^hc^b (11)		84	6·738*
$c^yc^v \times c^fc^b$	c^yc^f (20);	c^yc^b (20);	c^vc^f (14);	c^vc^b (21)	75	1·640
$c^yc^v \times c^hc^b$	c^yc^h (14);	c^yc^b (14);	c^vc^h (19);	c^vc^b (11)	58	2·276
$c^yc^n \times c^sc^n$	c^yc^s (17);	c^yc^n (8);	c^sc^n (13);	c^nc^n (14)	52	3·231
$c^yc^n \times c^zc^{bA}$	c^yc^z (11);	c^yc^b (12);	c^nc^z (9);	c^nc^b (4)	36	4·222
$c^yc^n \times c^bc^b$	c^yc^b (8);	c^nc^b (14)			22	1·136
$c^yc^f \times c^sc^b$	c^yc^s (14);	c^yc^b (15);	c^sc^f (14);	c^fc^b (12)	55	0·345
$c^yc^f \times c^vc^h$	c^yc^v (12);	c^yc^h (11);	c^vc^f (6);	c^fc^h (9)	38	2·211
$c^yc^f \times c^nc^z$	c^yc^n (13);	c^yc^z (7);	c^nc^f (9);	c^fc^z (13)	42	2·381
$c^yc^h \times c^sc^n$	c^yc^s (7);	c^yc^n (10);	c^sc^h (10);	c^nc^h (10)	37	0·730
$c^yc^z \times c^sc^v$	c^yc^s (8);	c^yc^v (11);	c^sc^z (16);	c^vc^z (15)	50	2·480
$c^yc^b \times c^sc^v$	c^yc^s (10);	c^yc^v (13);	c^sc^b (9);	c^vc^b (16)	48	2·500
$c^yc^b \times c^bc^b$	c^yc^b (7);	c^bc^b (13)			20	1·250
$c^hc^z \times c^vc^z$	c^vc^h (14);	c^vc^z (12);	c^hc^z (14);	c^zc^z (13)	53	0·208
$c^hc^z \times c^bc^b$	c^hc^b (29);	c^zc^b (25)			54	0·167
$c^hc^b \times c^nc^h$	c^nc^h (14);	c^nc^b (9);	c^hc^h (7);	c^hc^b (13)	43	3·047
$c^vc^h \times c^zc^b$	c^vc^z (5);	c^vc^b (13);	c^hc^z (5);	c^hc^b (11)	34	6·000
$c^nc^h \times c^bc^b$	c^nc^b (16);	c^hc^b (11)			27	0·593
$c^nc^n \times c^fc^b$	c^nc^f (11);	c^nc^b (9)			20	0·050
$c^fc^z \times c^bc^b$	c^fc^b (26);	c^zc^b (27)			53	0·000
$c^zc^z \times c^bc^b$	c^zc^b (65)				65	
$c^zc^b \times c^zc^b$	c^zc^z (2);	c^zc^b (8);	c^bc^b (4)		14	0·857

[A]Two female parents (c^zc^b) were used in this cross.

Results

Crosses

The crosses made and the results obtained are shown in Table 1. The phenotypes of the 36 possible combinations of the eight alleles are shown in Fig. 1, most heterozygotes precisely following the rule of mosaic dominance. Some groups of genotypes have similar phenotypes, but can be distinguished by minor differences. Also, all genotypes, even those with identical alleles, showed slight variations in

the size and shape of their spots or stripes. Some observations are listed below (all the examples of variation within a genotype are taken from progeny with identical alleles, unless indicated otherwise).

(i) *Yellow forms*

All heterozygotes with a c^y allele have a 'yellow' phenotype but most are recognizable by slight differences in either the width of the black elytral margin, the pronotal pattern, the underlying pattern or a combination of these.

Black elytral margin. Both $c^y c^y$ and $c^y c^b$ have a thick black line along the outer elytral margin, while $c^y c^v$ and $c^y c^h$ are similar but have narrower margins anteriorly. The $c^y c^s$ phenotype lacks black pigment on the outer elytral margin, but $c^y c^n$, $c^y c^f$ and $c^y c^z$ all have a thin black line slightly expanded medially.

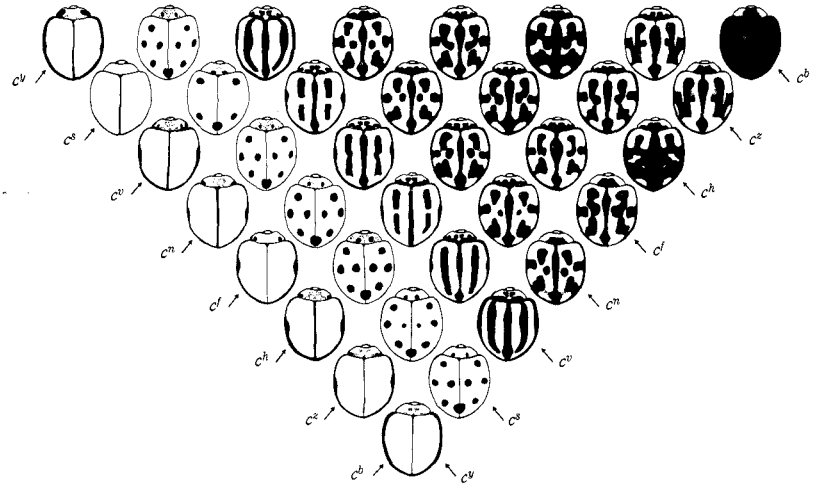

Fig. 1. Phenotypes of *C. inaequalis* for all the genotypes possible between eight alleles for colour pattern. Abbreviations: c^y, yellow; c^s, nine-spotted; c^v, elongated stripe; c^n, normal; c^f, fused; c^h, heavy; c^z, zig-zag; c^b, black.

Pronotal pattern. The $c^y c^y$, $c^y c^n$, $c^y c^f$, $c^y c^z$, $c^y c^h$ and $c^y c^v$ all have two dark lateral spots on the pronotum, but the size varies and they are barely visible or lacking in some specimens; $c^y c^v$ specimens tend to have smaller spots than do other phenotypes. Lateral spots are lacking in $c^y c^s$ and $c^y c^b$. Some specimens of $c^y c^y$, $c^y c^s$, $c^y c^v$, $c^y c^n$, $c^y c^z$, $c^y c^h$ and $c^y c^b$ have two small diffuse median spots in a similar position to those on the nine-spotted phenotype.

Elytral pattern. In $c^y c^v$, $c^y c^n$, $c^y c^f$, $c^y c^z$ and $c^y c^h$ heterozygotes, the pattern due to the recessive allele is present in light brown on the elytra of live specimens; $c^y c^y$ and $c^y c^b$ have some light yellow patches on the elytra. In addition to these underlying patterns, which fade after death, some specimens of all eight possible genotypes involving the c^y allele have small diffuse black marks on the callus (anterior spot). Of these, some specimens of $c^y c^s$, $c^y c^v$, $c^y c^n$, $c^y c^z$ and $c^y c^h$ also have diffuse black marks at some other spots (e.g. the dorsal, ventral and posterior spots). An extreme case is one $c^y c^b$ specimen from the $c^y c^f \times c^s c^b$ cross, which has two large median pronotal spots and small black marks at the anterior, ventral and

posterior spots. This suggests that this specimen may have three alleles, $c^v c^b c^s$, or that crossing-over within a supergene may have transferred part of the c^s allele into the c^b allele.

(ii) *Nine-spotted forms*

The dorsal spot of most $c^s c^z$ specimens is about half the size of the anterior spot (larger in some and barely discernible in others).

(iii) *Striped forms*

Specimens of $c^v c^f$ may have either a stripe constricted medially or a broken stripe with only a small break between pigmented areas. The break in the stripe of $c^v c^h$ specimens is often large but may be small. The pronotal patterns of $c^v c^f$, $c^v c^h$ and $c^v c^z$ are within the range of patterns of the 'broken stripe' form ($c^v c^n$) of Houston (1979, figs 4, 12–15).

(iv) *Homozygotes of* c^f, c^h, c^z *and their heterozygotes with* c^b

The 'heavy' form ($c^h c^h$, $c^h c^b$) is variable, some specimens having a small break between two or more of the following spots: anterior and ventral, anterior and dorsal, dorsal and sutural margin, dorsal and posterior spots. Also, the amount of fusion between the sutural margin, dorsal and posterior spots is variable and in some $c^h c^b$ specimens this entire area is pigmented black. There is varying amounts of fusion between the combined anterior and dorsal spots and the posterior spot in $c^f c^b$ progeny; some have a complete break, as in the $c^f c^f$ in Fig. 1. The dorsal spot of $c^z c^z$ and $c^z c^b$ is barely indicated in some specimens; of these, some $c^z c^z$ have the dorsal spot separated from the combined anterior and posterior spots. Heterozygotes of c^f, c^z, and c^h with c^b each have a pronotal pattern similar to that of the 'black' form.

(v) *Heterozygotes between* c^n, c^f, c^h *and* c^z

Both $c^n c^f$ and $c^n c^h$ are similar to the 'normal' form ($c^n c^n$). Five $c^f c^h$ progeny of the Brisbane cross shown in Table 1 are similar to the 'normal' form but with the anterior and posterior spots elongated towards each other. However, in four specimens the dorsal spot is slightly fused to the anterior spot; of these, two also have the dorsal spot slightly fused to the posterior spot. The $c^f c^h$ progeny (Fig. 1) from a Sydney cross differ from the Brisbane $c^f c^h$ in that the posterior spot is joined to the suture; the $c^h c^z$ pattern in Fig. 1 was also produced by a cross in Sydney. Neither of these Sydney crosses is in Table 1, as only a small number of progeny were reared. The $c^h c^z$ progeny of the Brisbane crosses in Table 1 are similar to the $c^n c^z$ phenotype (Fig. 1), but in the former the anterior and posterior spots are closer together. The dorsal spot is slightly fused to the anterior spot in some $c^n c^z$ and $c^h c^z$ progeny, and the dorsal spot is barely visible in some $c^n c^z$. The $c^f c^z$ phenotype is similar to the 'fused' pattern but with a small dorsal spot; in some specimens the combined anterior and dorsal spots are not fused to the posterior spot (e.g. the $c^f c^z$ in Fig. 1). Progeny which have any combination of the alleles c^n, c^f, c^z and c^h, including homozygotes, have a pronotal pattern that is within the range of the 'normal' form described by Houston (1979, figs 2, 7–8).

Allele Frequency

The number of specimens collected in the three areas and their presumed genotypes are shown in Table 2, and the allelic frequencies are estimated in Table 3.

Although only two small samples were collected in the Mareeba area, they have been included because they give an indication of the composition of a north Queensland population. The allele frequencies from year to year cannot be compared, because regular samples were not taken; however, our observations indicated that in the Brisbane and Sydney populations the frequencies appeared to be fairly constant, most of the rarer alleles being present in any one year.

Table 2. Genotype frequencies for colour pattern of *C. inaequalis* collected in the Sydney-Newcastle, Brisbane and Mareeba areas

Genotype	Number of specimens		
	Sydney-Newcastle	Brisbane	Mareeba
$c^y c^n$	1		
$c^s c^{?A}$		5	5
$c^v c^v$	1		
$c^v c^n$	11	14	
$c^v c^f$	11		
$c^v c^h$	3		
$c^v c^b$		1	1
$c^n c^z$	8		
$c^n c^b$		14	9
$c^n c^{?B}$	150	229	27
$c^f c^f$		3	
$c^f c^z$	9		
$c^f c^b$		2	1
$c^f c^{?C}$	48		
$c^h c^h$	1	1	
$c^h c^z$	4		
$c^b c^b$			2
Total	247	269	45

[A]? indicates *s, n, f, h* or *b*. [B]? indicates *n, f* or *h*. [C]? indicates *f* or *h*.

Since the distribution of certain alleles appears to be limited, further information was sought by studying specimens from Queensland and New South Wales in the following collections: ANIC, BPBM, NSWDA, QDPI, QM and UQ. The following pattern has emerged:

c^y There are no specimens of the 'yellow' form in any collection examined.

c^s The 'nine-spotted' form is widespread throughout Queensland but rare in New South Wales. [In NSWDA there is one specimen from Narrabri, N.S.W. (30°20′S., 149°47′E.) and one from Dharug National Park near Wiseman's Ferry, N.S.W. (33°23′S., 150°59′E.).]

c^v 'Striped' forms are widespread in both States.

c^n The 'normal' form is the most common phenotype.

c^f The 'fused' form occurs widely in both states but is common only in New South Wales. (There were 'fused' forms among Timberlake's reared specimens in BPBM.)

c^h There is one c^hc^b specimen from Brisbane in QDPI, a 'c^hc^b' specimen from Harlin, Qld (26°58′S., 152°22′E.) in QDPI, a 'c^hc^b' specimen from Abernethy, N.S.W. (32°53′S., 151°24′E.) in QM (both of these 'c^hc^b' specimens had anterior and posterior spots fused) and a 'c^hc^b', with reduced pigmentation, from Bundaberg, Qld (24°52′S., 152°21′E.) in BPBM. Also there are several possible c^hc^z heterozygotes from the Sydney region in NSWDA.

c^z There is no definite evidence of this allele in Queensland, although there is a possible c^nc^z and a possible c^fc^z specimen from the Bunya Mountains (26°51′S., 151°34′E.) in QDPI. There is a c^zc^z specimen from New South Wales in ANIC and a 'c^zc^z' specimen (with dorsal spot not joined to rest of pattern) from the Sydney suburb of Ashfield, in NSWDA.

c^b The c^b allele is widespread in Queensland but is more common in the north, while the c^hc^b record from Abernethy is the most southerly example of c^b seen in any collection.

Table 3. Allelic frequencies for colour pattern of *C. inaequalis* in the Sydney-Newcastle, Brisbane and Mareeba areas

Allele	Sydney–Newcastle	Brisbane	Mareeba	Method of calculation
c^y	0·002	0·000	0·000	Direct counting
c^s	0·000	0·009	0·056	Direct counting (assume no c^sc^s)
c^v	0·055	0·028	0·011	Direct counting
c^n	0·442[A]	0·764[B]	0·689[C]	–
c^f	0·394[A]	0·106[B]	0·077[C]	–
c^h	0·064	0·061	?	Homozygote frequency
c^z	0·043	?	?	Direct counting
c^b	0·000	0·032	0·167	Direct counting (assume no c^sc^b)

[A]Frequency of c^n calculated from homozygote plus heterozygote frequency and frequency of c^f obtained by subtraction.
[B]Frequency of c^f calculated from homozygote frequency and frequency of c^n obtained by subtraction.
[C]Frequency of $c^n + c^f$ obtained by subtraction and portioned in the ratio of (number of c^nc^b)/(number of c^fc^b).

The study of the above collections and the allele frequencies found in the three areas sampled are largely in agreement. However, while the c^s and c^b alleles were not represented in the Sydney–Newcastle sample, they have been previously recorded from this area (one specimen with c^s from Wiseman's Ferry and one with c^b from Abernethy).

Discussion

Dominance Order of the Alleles

From the results of the crosses shown in Table 1 and the results of previous authors, it can be seen that the inheritance of the elytral patterns in Fig. 1 is governed by eight alleles of a single gene or supergene, with the following order of dominance: $c^y > c^s > c^n > c^f > c^z > c^b$; $c^y > c^v > c^z > c^b$; $c^y > c^s > c^n > c^h > c^b$; c^s and c^v, c^v and c^n, c^v and c^f, c^v and c^h, c^z and c^h, c^f and c^h are codominant. However, c^y is not completely dominant over c^s, c^v, c^n, c^f, c^h and c^z, and c^s, c^v,

c^n and c^f are not completely dominant over c^z, since their heterozygotes have slightly different elytral patterns to those of the dominant alleles. All these alleles follow the rule of mosaic dominance for elytral and pronotal pattern. The dorsal spot of the 'zig-zag' form is slightly more anterior and ventral than that of the 'normal', 'fused' and 'heavy' forms, and is often reduced, so that heterozygotes between the latter alleles and the c^z allele can usually be recognized by their smaller dorsal spots. The results were subjected to a χ^2 analysis on the basis of the above conclusions, and all the probabilities were within the 5% probability limit, except for the $c^y c^s \times c^y c^s$ cross. This deviation from the expected ratio may have been brought about by differential survival of the larvae in crowded conditions.

Similarly it is obvious that these alleles also partly control pronotal pattern: $c^y > c^v > c^n = c^f = c^z = c^h$; $c^s > c^v > c^n = c^f = c^z = c^h$; $c^s > c^b > c^n = c^f = c^z = c^h$; c^v and c^b, c^y and c^b, c^y and c^s are codominant. All forms can have a range of pronotal patterns but the reason for these variations was not elucidated.

Geographic Variation in Allelic Frequencies

From Table 3, it is evident that there are distinct differences in the frequencies of the alleles in the three localities sampled. The absence of c^s and c^b from the Sydney–Newcastle population (both alleles can be recognized in a single dose) contrasts with the situation in Brisbane and more particularly in north Queensland. In Brisbane and Mareeba, c^n is by far the most common allele but in Sydney–Newcastle c^f is almost as common; c^y is rare, being represented in a single specimen. The c^z allele is probably absent from Brisbane, although the frequencies of both c^z and c^h are difficult to determine because of the rarity of homozygotes and uncertain recognition in heterozygotes (the 'heavy' specimen from Brisbane had a light pattern with reduced pigmentation along the suture and between the posterior and sutural spots). In the Mareeba population the frequency of c^v is perhaps underestimated and that of c^s and c^b overestimated as a result of the small sample size; in the Sydney sample the former may be slightly overestimated as a result of the founder effect in certain subsamples. On comparing the three areas it can be seen that the frequencies of c^s and c^b increase, and those of c^v and c^f decrease, from south to north. This indicates the possibility of a clinal distribution of frequencies for some alleles, although many more sites in the intervening regions need to be sampled before any definite conclusions can be made. At this stage we are unable to speculate on the adaptive value of the various alleles or the reason for the different allelic frequencies in the three sampling areas.

Phenotypic Variation

It was noted in the results that the $c^h c^z$ progeny reared in Sydney were much darker than those from Brisbane, where the same c^h allele was involved although the c^z alleles may have been isoalleles. However, anterior and posterior spots were almost joined in some of the $c^h c^b$ progeny reared in Sydney. Thus, these Sydney specimens of $c^h c^b$ and $c^h c^z$ may have been produced by an extreme fused expression of the c^h allele, but the rearing conditions in Brisbane caused the pigmented areas produced by this allele to be much smaller. Also, there were many cases in which progeny with identical alleles from different crosses or from a single cross had

different amounts of pigmentation and so had slightly different patterns (for example, the variation of the $c^h c^b$ genotype was particularly large). The cause of these changes in the expression of the alleles is not known but they may be due to environmental conditions, the presence of isoalleles, the effects of a variety of modifer genes, or a combination of these. Timofeeff-Ressovsky (1941) showed that in *Epilachna chrysomelina* F. the area of black pigmentation decreases as the temperature rises, although other environmental agents (e.g. humidity) had no effect.

In the course of examining our collections and those in the institutions mentioned above, we have noted numerous specimens which differ to some degree from any of the phenotypes illustrated in Fig. 1 (e.g. the 'zig-zag' specimen from Ashfield, Sydney and the 'heavy' specimens from Harlin and Abernethy). Most differences involve the pattern of fusion or degree of fusion of the spots, the reduction or absence of one or more elytral spots, or variations in the pronotal pattern. While some of these differences may be brought about by environmental effects on the expression of the eight alleles described, we believe that many are produced by genetically distinct alleles, some of which differ only slightly from those described, or by unknown rare alleles in the heterozygous condition. The presence of these uncharacterized alleles may have caused minor distortions in the calculation of allelic frequencies.

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