



	PAGE		PAGE
VII. FURTHER DATA ON THE GENETICS OF <i>THUNBERGI</i> , <i>BUTLERIANUS</i> AND <i>AGENOR</i>	54	4. The possible origin of the polymorphic forms unique to Java and Sumatra	60
VIII. DISCUSSION	56	(a) f. <i>isarcha</i>	61
1. The effect of modifiers on the resemblance between the mimetic forms and their models	57	(b) f. <i>achates</i> with orange epaulettes	61
2. Dominance relationships in pure races and hybrids	57	(c) f. <i>anceus</i>	61
3. The super-gene	59	REFERENCES	63
		APPENDIX	64

*Papilio memnon* is a Swallowtail butterfly widely distributed in South-East Asia. The females are highly polymorphic and many of them are Batesian mimics. A previous paper gives an account of the mode of inheritance of seventeen of these female forms and here we describe the inheritance of nine from Java and Sumatra, an area we had not investigated before. We have also obtained further information on some of the forms whose modes of inheritance are not clear in the earlier paper.

The nine new forms and one of those previously investigated (f. *thunbergi*) have been shown to be determined by the same complex locus or super-gene which controls the polymorphism already studied. The results from the present genetic investigation confirm the previous findings in *P. memnon* and *P. dardanus* that the resemblance of a form to its model is greater in the gene complex of the race in which the form is found than it is in intra-specific hybrid gene complexes. This suggests that the detailed resemblance of the mimic to its model has been built up gradually by the accumulation of modifiers. Of particular interest in this connexion is the mimic f. *achates* in Java and South Sumatra in which the heterozygote is a better mimic than the homozygote in the gene complex of its own race.

Evidence has also been accumulated on the nature of dominance. Previously, complete dominance was present between most sympatric forms and absent between allopatric ones, both in *P. dardanus* and *P. memnon*. In contrast, the forms found in Java and Sumatra show only partial dominance between sympatric forms in most instances. However, in a hybrid gene complex the heterozygotes are even more intermediate. Thus, on these two islands the evolution of dominance has proceeded less far than elsewhere. There is ample evidence for the presence of dominance modifiers, but we are uncertain whether the absence of full dominance results from the modifiers having other, more powerful, selective forces acting upon them, or whether insufficient time has elapsed for full dominance to have evolved.

In a complex Batesian mimetic polymorphism the forms must either be controlled by multiple allelomorphs at a single locus, by a group of closely linked loci (a super-gene), or by independent genes having complex epistatic interactions. In both *P. dardanus* and *P. memnon* it has been established that super-genes have been evolved. The present study throws further light on the super-gene in *P. memnon*.

We have reason to believe that a number of very rare forms (some of which we have bred) result from crossing over rather than from point mutations, since if mutations were responsible we should have expected some of the patterns to be controlled by loci unassociated with the super-gene. This is not the case. Furthermore, in one instance, a double mutation would be required to explain the pattern.

On the assumption that crossing over is the explanation of these rare forms we have postulated five loci. These control the presence or absence of tails (*T*), hindwing pattern (*W*), forewing pattern (*F*), colour of the basal triangle or epaulette on the forewing (*E*), and abdomen colour (*B*). Previously we had deduced that *W* must lie between *T* and *B*. The present study has given independent support to this order and also suggested that neither *W* nor *B* lies between *E* and *F*, and that *T* does not lie between *W* and *E*, the probable order being *TWFE**B*. If the hypothesis is correct the initial mimic of *P. sycorax* could have been produced by a single crossover, and f. *anceus*, the modern mimic, evolved by subsequent minor modifications.

In our investigations into the genetics of Batesian mimicry we have found that the polymorphism is controlled by a multiple allelic series at one locus or by a super-gene in *P. dardanus*, *P. memnon* and *P. polytes* (unpublished). This contrasts with the situation in Müllerian mimicry. In order to see whether the evolution of such super-genes is a general phenomenon or whether in other genera of Lepidoptera, and perhaps in other orders, complex epistatic interactions have been developed rather than super-genes, it will be necessary to extend this investigation outside the genus *Papilio*. We have already started to study *Pseudacraea eurytus* from Africa, which seems a particularly suitable species to use since the Batesian relationships of its forms are well documented.

## I. INTRODUCTION

In a previous paper (Clarke, Sheppard & Thornton 1968) we investigated the genetics of some of the mimetic and non-mimetic forms of *Papilio memnon* in order to compare the genetic control of the various forms with that in *P. dardanus*. Striking parallels were found and it was possible to draw some conclusions on the evolution of Batesian mimicry in general.

Material at that time was not available from a number of critical areas, notably Java and Sumatra. It has now been possible to obtain living butterflies from both, and the present paper reports on the genetics of races from these two islands. In addition, it has been possible to produce some more hybrids between races whose genetics have already been reported.

## II. MATERIALS AND METHODS

Eggs, larvae, pupae or butterflies of *P. memnon* have been sent to us from various localities, particularly from Bogor (Djakarta) in Java, Dolok Merangir, Medan in North West Sumatra and Palembang in South East Sumatra. We also received *P. polymnestor parinda* from Ceylon.

On arrival in this country the insects were reared in heated greenhouses and the larvae fed on *Citrus* which was grown in the Liverpool University Botanical Gardens at Ness, as well as on plants kindly provided by a large number of private individuals throughout the United Kingdom. All the matings in the laboratory were carried out by the hand-mating technique (Clarke & Sheppard 1956) and the breeding procedure was that used in the previous study (Clarke, Sheppard & Thornton 1968).

## III. DESCRIPTION OF THE FEMALE FORMS FROM JAVA AND SUMATRA

1. *Polymorphic forms*(a) *f. achates* (tailed) (plate 1 a to c)

In Java, southern Sumatra and some outlying islands, for example, Bali, Bawean, Batu and Billiton, the *achates* (plate 1 a, b) are all of the same general form, resembling *distantianus* from Malaya and Thailand but differing in some important aspects. Thus the veins on the hindwing are very black, agreeing in this with the model. The scarlet-orange on the hindwing is replaced by orange of the same colour as the abdomen and also agreeing with the model, the colour atlas score of both model and mimic being about O† or OOY/12/17 for hue, degree of chromaticity and lightness value respectively (Villalobos-Dominguez & Villalobos 1947).

The forewing basal triangles (epaulettes) of *achates* from these localities are variable. In some they are almost white (there are a few black scales present and some faintly pigmented ones of colour scores OOS/6/19), in others the epaulettes are far more scarlet. The most extreme of these has a score of SSO/11/11, but the average is slightly more orange than this (being about OOS) and at least some are orange (about O).

In central and northern Sumatra, as well as Nias, the *achates* (plate 1 c) are more like *distantianus*. They differ, however, in that although the epaulettes are usually more scarlet than those from South Sumatra and Java, varying between RS and OOS, they are sometimes flecked with white scales distally and then tend to be more orange varying between S and SO. The pigmented

† The colours ranging from ruby (R) through scarlet (S) and orange (O) to yellow (Y) are indicated by R, RS, S, SSO, SO, OOS, O, OOY, OY, YYO, Y.

scales at the distal edge of the central white area of the hindwing (the window) and those encircling the eye spot at the anal angle of the hindwing are more orange (SSO to OOS) than in typical *distantianus* (S to SSO) and although the body is yellow with a black dorsal stripe this may be absent on the terminal segments.

(b) *f. agenor* (tailless) (plate 1*d, e*)

The *agenor*-like specimens in Java are variable with regard to the area of the window on the hindwing and two distinct phenotypes are apparent. In one this window is large (*f. isarcha*, plate 1*d*), the white extending well into the cell on the hindwing. It is extremely like that of *f. venusia* (plate 2*g*) and *f. zephyria* (see Clarke, Sheppard & Thornton 1968, plate 8*b*), though in the former it is suffused with yellow. In addition, *isarcha* has a broad black area on the hindwing between the costal margin and vein 7. This is much reduced or absent in *venusia* and *zephyria*. In *isarcha* the epaulettes vary between RS and SSO, the great majority being S.

In the other phenotype (*f. hiera*, plate 1*e*) all the white spots making up the window are reduced in length and the white does not extend into the cell of the hindwing. This form is therefore much more like typical *agenor*. The colour of the epaulettes shows the same range as does *isarcha*, and the body is either black or has a yellow tip as do some *laomedon*.

(c) *f. laomedon* (tailless) (plate 1*f*)

*F. laomedon* from Java are very similar to those from Borneo, and like them some (3 out of 10 examined) have a yellow tip to the abdomen. The colour of the epaulettes shows the same range as does *agenor* from Java.

#### DESCRIPTION OF PLATE I

Some female forms of *P. memnon* found in Java and Sumatra.

- (a) *P. m. f. achates*. The homozygote found in Java and South Sumatra. Note the white patches (epaulettes) at the bases of the forewings found in many homozygotes. In others they are very pale orange.
- (b) *P. m. f. achates*. Heterozygote. The epaulettes here are orange and characteristic of the Java heterozygote.
- (c) *P. m. f. achates* from North Sumatra. The epaulettes from this region are red in both heterozygotes and homozygotes.
- (d) *P. m. f. agenor (isarcha)* from Java. This homozygote has a large white area (window) on the hindwings.
- (e) *P. m. f. agenor (hiera)* from Java. Note the small window and characteristic absence of a white subapical forewing patch in these heterozygotes with *laomedon*.
- (f) *P. m. f. laomedon* from Java. In this specimen the subapical white patch, though present, is much reduced.
- (g) *P. m. f. trochila* from Sumatra. There is a well-developed white subapical forewing patch in this specimen and a close resemblance between this form and *laomedon*.
- (h) *P. m. f. anceus* from Sumatra. Note the white epaulettes, the absence of a white subapical forewing patch and the yellow area on the distal part of the abdomen.
- (i) *P. m. f. titania* from Java. The only example of the form that we know of from this area. It closely resembles *hiera* except for the presence of tails on the hindwing. It is also found in Formosa where it is excessively rare.
- (j) *P. m. f. gerania* from Sumatra. Note the white subapical forewing patch, the large white window on the hindwing and the distal yellow patch on the abdomen.
- (k) *P. m. f. ityla* from Sumatra. This rare form differs from *gerania* only in that it has a black abdomen.
- (l) *P. memnon* ♀, a unique unnamed form from Sumatra resembling *f. gerania*. It differs, however, in having no white subapical forewing patch and white instead of red epaulettes.



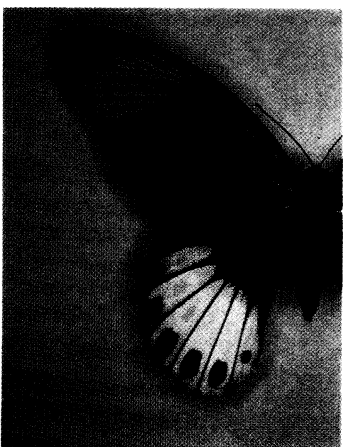
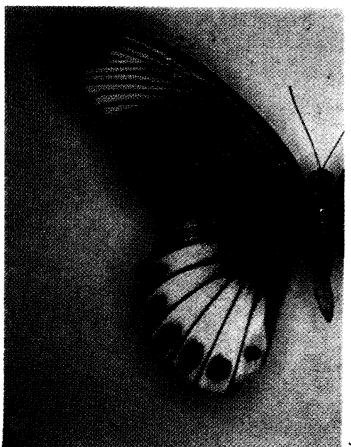
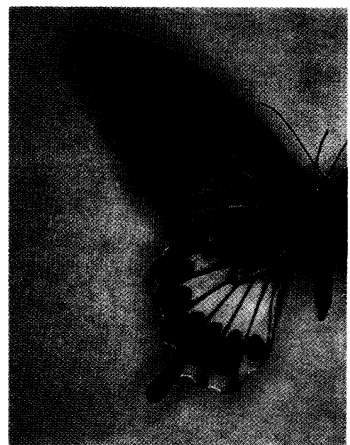
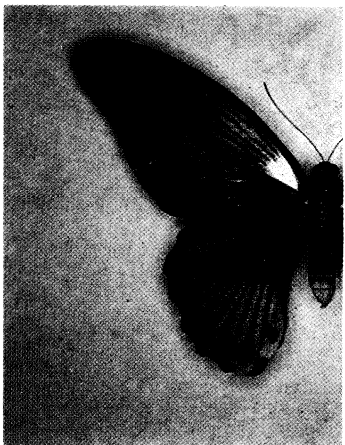
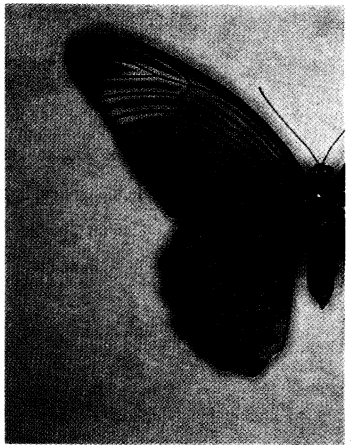
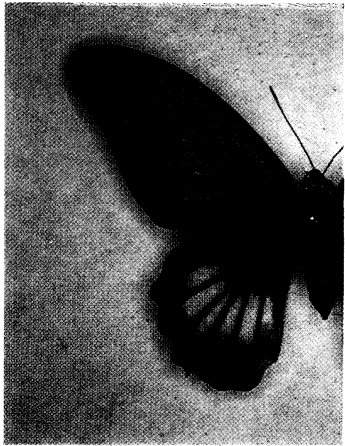
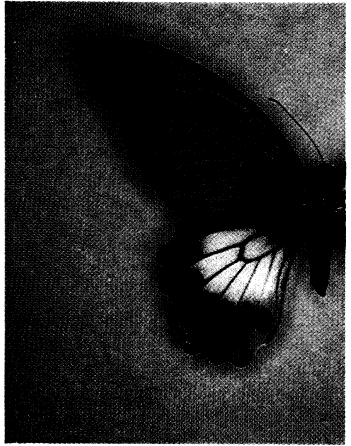


PLATE 1. For legend see facing page

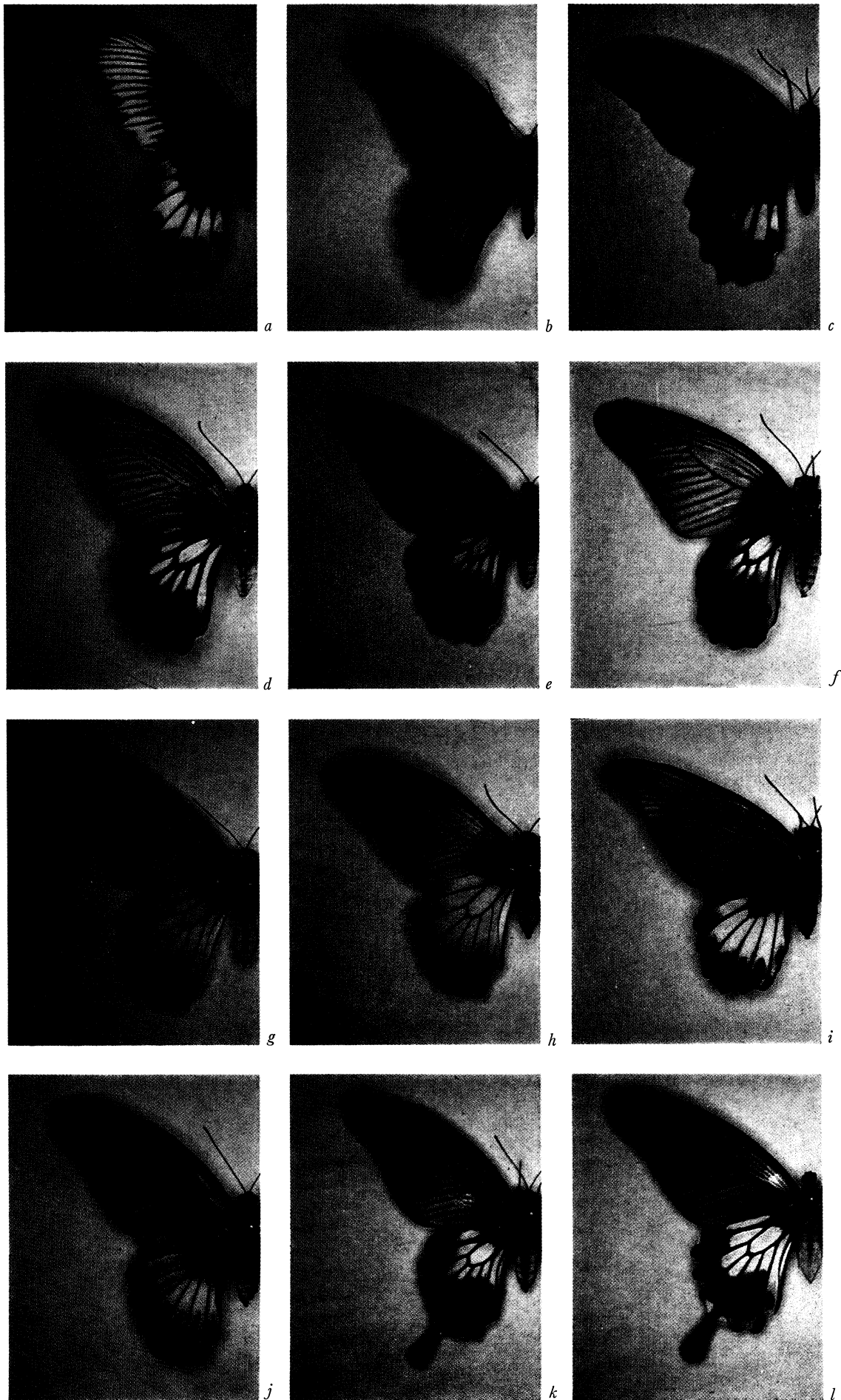


PLATE 2. For legend see facing page

(d) f. *trochila* and f. *erebinus* (tailless) (plate 1g)

In Sumatra and some outlying islands, for example Nias and Sabang, f. *laomedon* is absent and is replaced by two named forms, f. *trochila* and f. *erebinus*, which appear to differ from one another chiefly in the degree of expression of the subapical white patch on the forewing and the amount of blue scaling on the hindwing. Since both these characters are highly variable we have combined the forms under the single name *trochila*. *Trochila*, so defined, differs from *laomedon* chiefly in its hindwing pattern. Thus it has more blue scaling, a more prominent inner submarginal row of black spots on its upper side, and more pronounced yellow markings at the anal angle. The forewing subapical white patch on average tends to be more pronounced than in *laomedon* but can vary from complete absence to as an extreme a white patch as is found in *esperis* (plate 3g). The abdomen may be either black or have yellow on it. This can vary from a few scales to a patch of yellow on the dorsal surface extending over more than a quarter of the abdomen. The epaulettes are scarlet, varying from RS to SO with the majority being S and SSO, and as in *achates* from Sumatra, white scaling may be present.

(e) f. *anceus* (tailless) (plate 1h)

*F. anceus*, which is confined to Sumatra and some outlying islands, differs in two important respects from *trochila*. The subapical white patch on the forewing of *trochila* is absent in *anceus* except in the island of Nias. The epaulettes on the forewings are a brilliant white though there are occasionally a few red scales scattered amongst the majority of white ones. The hindwing is

#### DESCRIPTION OF PLATE 2

Some forms of *P. memnon* from Java, Sumatra, North Borneo and Japan, together with some race hybrids.

- (a) *P. m. f. caeruleus* ♀ from an island off the west coast of Sumatra. The hindwing is tailed.
- (b) *P. memnon* ♂ from the area where f. *caeruleus* is found. It has far more blue scaling than *P. memnon* males from the rest of Sumatra.
- (c) *P. m. f. thunbergi*. This is the only ♀ form found in Japan, but varies somewhat in the amount of white scaling on both the fore and hindwing.
- (d) *P. m. f. anura* from Java and Enggano. The form only differs from the f. *achates* from the same area in that it has no tails. Note its very close resemblance to f. *anura* from Borneo, from which it differs chiefly in having orange rather than red epaulettes.
- (e) *P. m. f. anura* from North Borneo (cf. plate 2d).
- (f) *anura*-like ♀ 9045. Note that the epaulettes are redder than those in plate 2d (see p. 42).
- (g) *P. m. f. venusia* from North Borneo.
- (h) *venusia*-like ♀ (*venusia/isarcha* heterozygote) 9023. The sister of insect in plate 2i.
- (i) *agenor (isarcha)-laomedon* ♀ 9023. Note the presence of a white subapical forewing patch showing the insect to be heterozygous for *laomedon* from Borneo, and the small hindwing window characteristic of *hiera*, see plate 1e and pp. 44 and 45.
- (j) *anceus-parinda* heterozygote 10275, similar in appearance to the equivalent genotypes in broods 10113 and 10416. The butterfly has no subapical forewing patch, some white scaling in the epaulettes and yellow terminal segments on the abdomen, demonstrating that it is *anceus-parinda* and not *anceus-trochila*.
- (k) *P. m. f. achates* 10417 of pure North Sumatra genotype. The epaulettes have no white scaling in them and the abdomen has a full black dorsal line to its end. Thus in this insect *achates* is fully dominant to f. *anceus*.
- (l) *P. m. f. achates* 10529 of pure North Sumatra genotype. The epaulettes have many white scales and the black dorsal line on the abdomen stops well before the terminal segments. Thus in this butterfly *achates* is not fully dominant to f. *anceus* in contrast to the insect in plate 2k.

very similar to that of *trochila* except that there is a tendency for more pale blue and white scaling to be present. Thus on average the hindwing is paler, although in some specimens it is almost indistinguishable from that of *trochila*. On the abdomen there is normally a yellow dorsal area covering between a half and a quarter of the distal end; however, specimens are known in which the abdomen is black.

## 2. Rare forms

There are a number of forms both named and unnamed in Java and Sumatra which are either uncommon or excessively rare but which are important in any discussion of the evolution of the colour patterns.

### (a) f. *gerania* (tailless) (plate 1j)

This form is confined to Sumatra, but occasional specimens similar to it have been found in Singapore (Clarke, Clarke & Sheppard 1968). The forewings are very similar to those of

## DESCRIPTION OF PLATE 3

Female forms of *P. memnon* from Sumatra and the Malay Peninsula together with various race hybrids.

- (a) *agenor-trochila* 9811. The presence of a white subapical forewing patch, the absence of white scaling in the epaulettes, the black or almost black body and the reduced hindwing window show that the insect is heterozygous for f. *trochila* (cf. plate 3b).
- (b) *agenor-anceus* 9811. Note the absence of a white subapical forewing patch, the presence of white scaling in the epaulettes, the yellow terminal segments on the abdomen and the reduced white hindwing window, showing that the insect is heterozygous for f. *anceus* (cf. plate 3a).
- (c) *trochila-parinda* 10374. The butterfly has a subapical forewing white patch and yellow scales on the terminal segment of the abdomen, showing that it is heterozygous for f. *trochila*. The reduced epaulettes are scarlet (cf. plate 2j for the *anceus-parinda* phenotype).
- (d) *achates* 9101, first backcross of the Java f. *achates* to the Hong Kong race. The epaulette colour is much redder than in pure Java *achates* heterozygotes (cf. plate 1b), showing the tendency of Java epaulette colour to become recessive on outcrossing.
- (e) *trochila-anceus* 10383, in a race hybrid gene complex. The heterozygote shows the characteristic yellow terminal segments on the abdomen typical of *anceus* and the subapical forewing patch of *trochila*. This insect is unusual in that most similar genotypes have some white scaling in the epaulettes, a reduced yellow area at the distal end of the abdomen and a dark hindwing (see p. 50).
- (f) *P. m. f. trochila* from Sumatra, heterozygous for f. *anceus*. Note the differences between this pure Sumatra insect and the same heterozygote in a hybrid gene complex (plate 3e).
- (g) *P. m. f. esperi* from the Malay Peninsula. Note the white subapical forewing patch similar in position to the much less marked ones in f. *laomedon* and f. *trochila* (see plate 1f and g).
- (h) *P. m. f. butlerianus* from the Malay Peninsula. Note its similarity to f. *esperi* except for the absence of the white forewing subapical patch and the presence of a white patch near the inner margin of the forewing.
- (i) *thunbergi-anceus* 10842. There are many white scales in the epaulettes and the yellow area at the tip of the abdomen typical of f. *anceus* is much reduced in this heterozygote.
- (j) *achates/trochila* heterozygote 10494. The presence of *trochila* is indicated in this race hybrid by a white subapical forewing patch which is reduced to a few white scales.
- (k) *butlerianus-trochila* heterozygote 10494. The *butlerianus* patch appears to be recessive in this insect. The subapical white forewing patch typical of *trochila* appears to be more marked (i.e. more like *esperi*) than is usual in the pure race (see plate 3f and g).
- (l) *butlerianus/anceus* heterozygote 10494. The insect is intermediate in appearance, having a *butlerianus* patch on the forewing and *anceus*-like epaulettes and abdomen, suggesting that all three characters are semi-dominant in this hybrid.

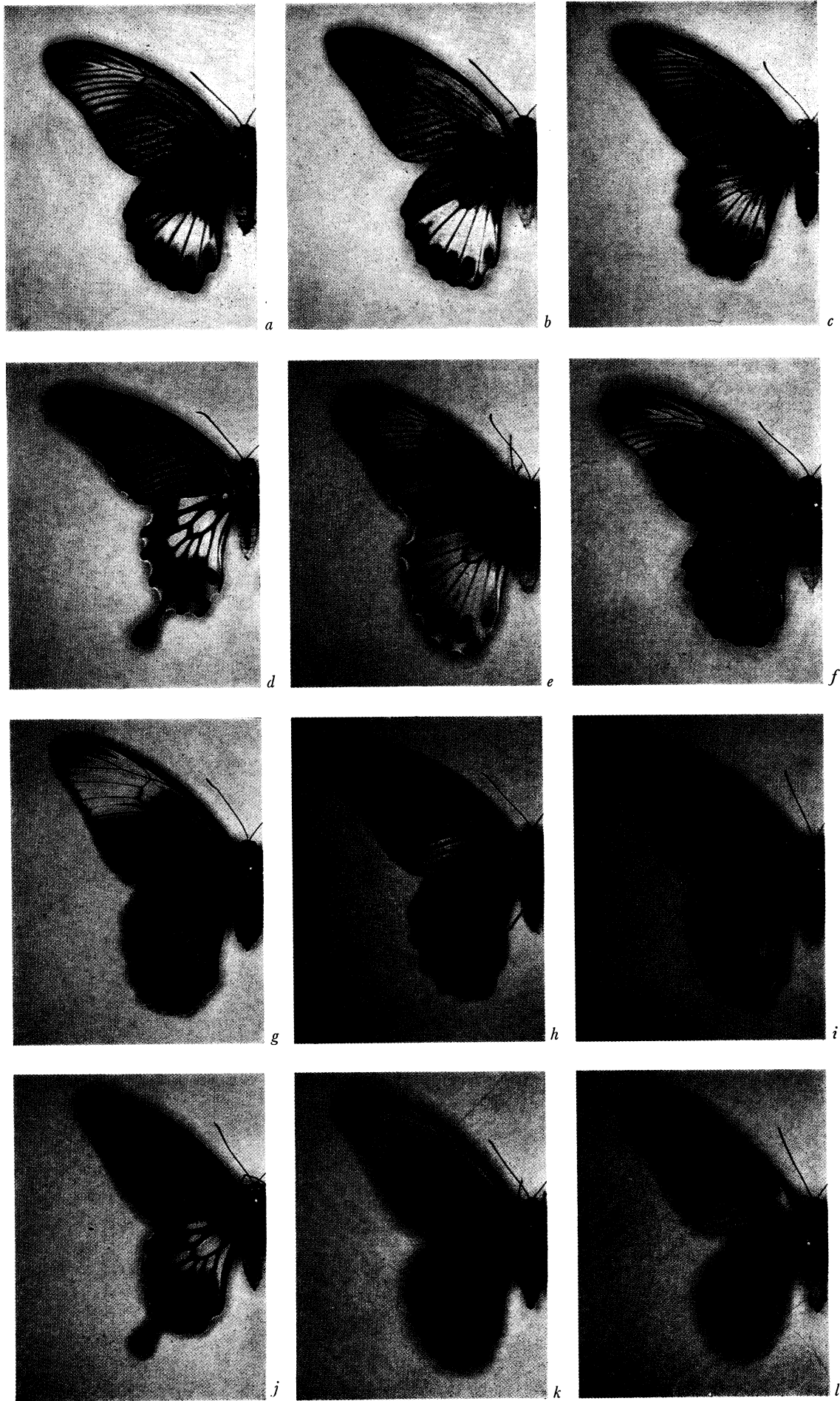


PLATE 3. For legend see facing page



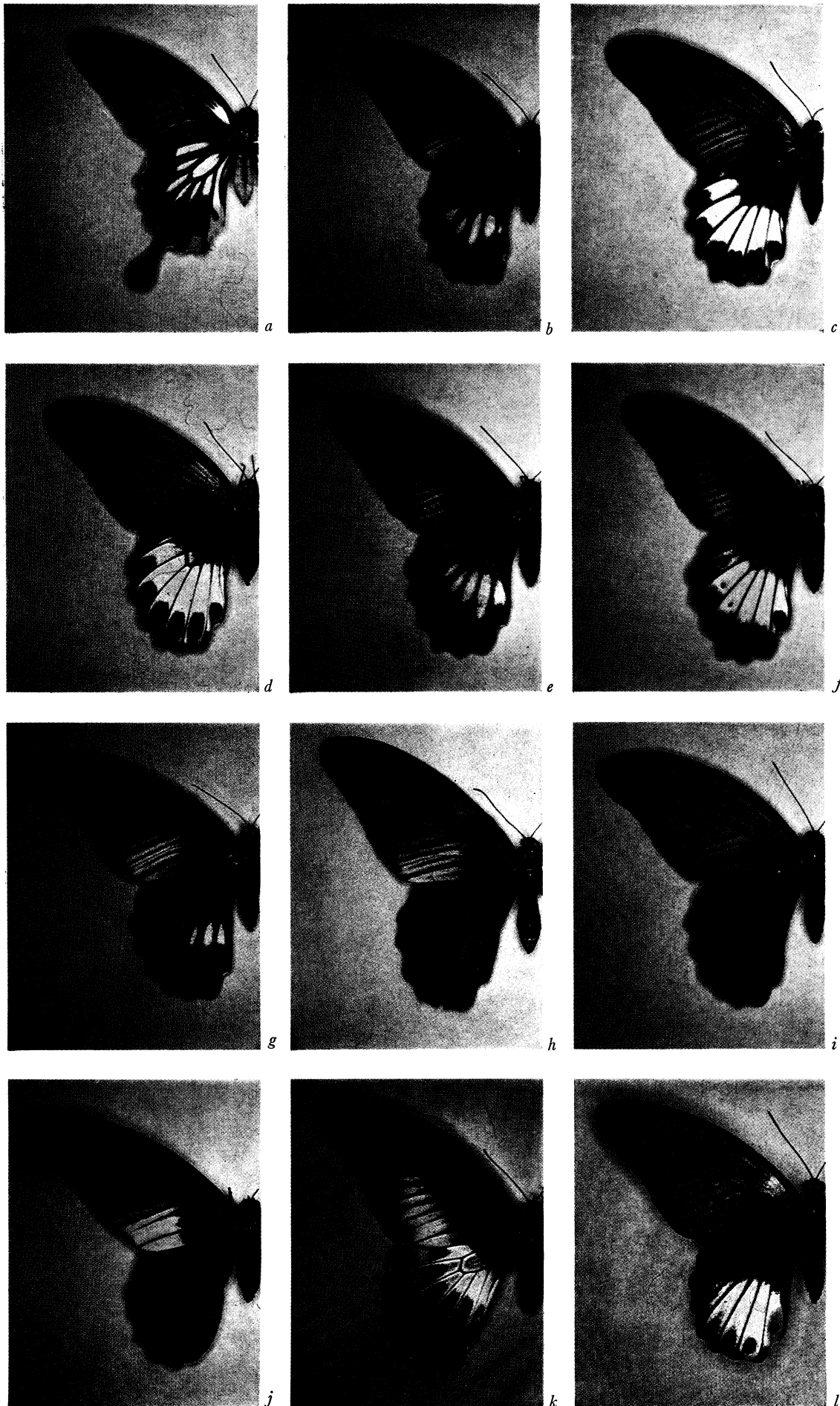


PLATE 4. For legend see facing page

*trochila* but the subapical white patch on the forewings is always marked. The epaulettes are the same colour as in *trochila*, averaging between SSO and S. White scales may or may not be present. The hindwing has a white window extremely similar to that found in *agenor*, except that in some specimens it is enlarged and extends to all three margins distally, leaving a submarginal row of black spots as in *venusia* (plate 2g). It differs from *venusia*, however, in not extending so far into the cell. The body is the same as that of *anceus*, having a large yellow dorsal area on the distal end of the abdomen.

We have obtained living material of a previously unknown variety of *gerania* (plate 1l). It appeared among the progeny of a female *anceus* mated to a male from South Sumatra. The new form appears to be identical to *gerania* except that it lacks the typical subapical light forewing patch and the epaulettes are white and not the usual scarlet of *gerania*.

(b) f. *ityla* (tailless) (plate 1k)

This form is found in Sumatra and is like *gerania* except that the body is black. In the British Museum there are insects without a varietal name which are like *ityla* except that the hindwing window is reduced in size and has a suffusion of black scales round its border. The hindwing pattern of these insects is extremely similar to that produced by hybridizing *agenor* from Hong Kong with *laomedon* from Borneo (see Clarke, Sheppard & Thornton 1968, plate 9i).

#### DESCRIPTION OF PLATE 4

♀ *P. polymnestor parinda* and various *P. memnon* hybrids between races from Java, Sumatra, Hong Kong, the Malay Peninsula and Japan, together with hybrids between *P. memnon* and *P. p. parinda*.

- (a) Java × Sumatra *achates* hybrid 10805, heterozygous for *anceus*. The epaulettes are white, despite the fact that the insect is neither homozygous Java nor South Sumatra *achates*. This shows that the allelomorph controlling white epaulettes in *anceus* is non-complementary with that controlling them in Java and South Sumatra *achates*.
- (b) *thunbergi*-like hybrid 9713, homozygous for *thunbergi*, cf. the pure form, plate 2c.
- (c) *agenor*-like hybrid 9713, heterozygous *agenor/thunbergi*. Note the large white hindwing window compared with its sib (plate 4b).
- (d) *agenor*-like hybrid 9713, a homozygous *agenor*. The hindwing white window is even larger than in the heterozygote (cf. plate 4c; see also p. 54).
- (e) Hybrid *P. memnon* × *P. p. parinda*, heterozygous for *thunbergi* (brood 9752). Compare the small white hindwing window with that in plate 4b.
- (f) Hybrid *P. memnon* × *P. p. parinda*, heterozygous for *agenor*. Compare the white hindwing window with the smaller one of its sib in plate 4e and the similar one in 4c. Note the clear-cut segregation in brood 9752.
- (g) *thunbergi-butlerianus* heterozygote 9592. The white patch near the inner margin of the forewing characteristic of *butlerianus* is present, as is the reduced white window of *thunbergi* on the hindwing.
- (h) *thunbergi-butlerianus* heterozygote 9592. It differs from its sib (plate 4g) in that there is no white area on the hindwing, indicating that the difference in dominance is due to modifiers.
- (i) *thunbergi-laomedon* heterozygote 9179. Compare the hindwing with that of the insect in plate 4h, showing that here again the absence of white on the hindwing is behaving as a dominant in this insect though it does not in all such heterozygotes.
- (j) *butlerianus*-like hybrid 9548. The very white forewing patches suggest that this insect is a homozygote for *butlerianus* and not a heterozygote (cf. plate 4h).
- (k) *P. p. parinda* ♀ from Ceylon.
- (l) *agenor-anceus* hybrid 9807. Compare with plate 3b, in which the terminal segments of the abdomen are yellow. The super-gene producing black-bodied *anceus* is very rare but segregated in brood 9807 (see p. 49).

*(c) f. caeruleus* (tailed) (plate 2*a, b*)

This form is recorded from islands off the west coast of Sumatra. The forewings and hindwings are heavily suffused with blue scaling and the forewing white subapical patch typical of *trochila* extends down the outer margin of the wing to the anal angle, giving the forewing a very pale appearance. The hindwings are also heavily suffused with blue, which extends over the *agenor*-like white window. The tails are variable in length, the shorter ones being pointed in shape and the longer more spatulate. The two females we have been able to measure had tails of 8.5 and 16.5 mm respectively. The body is black. The males from the same locality are also heavily suffused with blue but the hindwings are tailless.

*(d) f. titania* (tailed)

This form is found in Taiwan (Clarke, Sheppard & Thornton 1968) and resembles a typical *agenor* except that it has long tails on the hindwing. There is a very similar specimen which is unnamed amongst the Java insects in the British Museum (plate 1*i*). Its forewings are the same as *agenor* from Java and the epaulettes are scarlet (RS/11/10). The hindwing is identical to the small-windowed *agenor* (*f. hiera*), except that it has long tails (tail length 11.5 mm, total length of hindwing 55.5 mm). The body is black with a yellow tip.

*(e) f. anura* (tailless)

This form is found in Borneo (plate 2*e*) and resembles a tailless *achates*, though the window is much more orange. A specimen extremely similar to it has been found in Java (plate 2*d*). It differs from *anura* in that the window is white and the epaulettes far more orange (OOS/12/16) instead of being scarlet (RS/11/10) as in *anura*. Thus the epaulettes are the same colour as those of many Java *achates*, and known Java *achates*/Borneo *laomedon* heterozygotes in a hybrid gene complex (brood 9045). They are, however, much more orange (OOS to O) than the *anura/agenor* and *anura*-like sibs (SSO to S) of these hybrids (plate 2*f*). The Java specimen also differs from the Borneo *anura* and *anura/agenor* hybrids in that the hindwing is not suffused with orange. In fact, the insect is typical of Java *achates* except that it is tailless (tail length 2.5 mm, total length of hindwing 42.0 mm). Two other specimens, one from Java, the other from the island of Enggano, also look like tailless Java *achates*, but have a vestige of a tail. The one from Java has a tail length of 5.0 mm and total wing length of 48.0 mm and has orange epaulettes. The other, from Enggano, has a tail length of 5.0 mm and a total wing length of 58.0 mm. The epaulettes are absent on the dorsal side of the forewing but on the ventral side are orange. We also know of a single *f. anura* like the previous ones but with red epaulettes from North Sumatra.

## IV. GENETICS OF THE FEMALE FORMS FROM JAVA

1. *f. achates* (plate 1*a, b*)

Most of the elements of the *achates* pattern in Java are dominant to those of *agenor* and *laomedon* (de Meijere 1910; Baur 1911; Clarke, Sheppard & Thornton 1968), but the situation as far as the colour of the basal forewing triangles (epaulettes or shoulders) is concerned is more complex. They are variable in Java (plate 1*a, b*), but when not white they always tend to be more orange than in *achates* from other places (except South Sumatra). A number of pure Java *achates* with orange epaulettes have been tested and found to be heterozygous for *achates*. Thus



brood 8979, derived from a wild orange-shouldered *achates*, segregated for three orange-shouldered *achates* and two white. Broods derived from two of the former (broods 9040 and 9055) segregated for *agenor* showing that the *achates* females were heterozygous. In brood 9039 one of the 8979 white-shouldered *achates*, mated to a sib, produced two white-shouldered *achates* and a male which when test-mated (see brood 9176) proved to be heterozygous for *achates*. In brood 9135, one of these white-shouldered 9039 females, mated to a sib, produced five *achates* offspring, segregating for white and orange epaulettes, and a male which was probably homozygous for *achates* (see brood 9272). Thus in these broods the *achates* with white epaulettes have produced only *achates* females or males carrying this form, suggesting that they are the homozygotes. This view is strengthened on consideration of broods 9014 and 9015 and their descendants. Broods 9014 and 9015 resulted from two Java orange-shouldered *achates* mated to Hong Kong males, so that the offspring could not be homozygous for *achates* derived from Java. In 9089 an *achates* 9014 with orange epaulettes and therefore carrying the *achates* allele from Java, was mated to a male 9015 (shown to be homozygous *achates*, see brood 9082) and which must therefore have derived one of its *achates* genes from Java and the other from Hong Kong, the two being allelic.† Brood 9089 segregated for red shoulders and non-red shoulders in a 1:1 ratio and among the non-red-shouldered *achates* there were two forms, three insects having orange and one white shoulders, the segregation of white shoulders suggesting that this is a homozygote for the allele from Java.

Brood 9040 was a mating between a Java orange-shouldered *achates* and a Thai male (see above). Both the ratio of *achates* to *agenor* and the fact that the eight *achates* did not segregate for epaulette colour (all being SO)—in contrast to 9015 which did—suggest that the male was homozygous *agenor* and therefore that all the *achates* offspring were heterozygous Java *achates*/Thai *agenor*.

One of these heterozygous *achates* (brood 9096) mated to the same male as 9089 (and 9082) produced a brood in which the female offspring were all *achates* and segregated for red, orange and white epaulettes. If white-shouldered *achates* are homozygotes then the expected ratio of epaulette colour would be the same in 9089 and 9096 (whether the female parent of 9089 be homozygous or heterozygous for *achates*). Combining these two broods we find that the ratio 1 red to 2 orange to 1 white-shouldered *achates*, on the assumption that white is a homozygote and orange a heterozygote, is very close to the expected ( $\chi^2_2 = 2.45$ ,  $p > 0.1$ ).

Subsequent broods (9199 and 9206) demonstrate not only that at least two of these putative white-shouldered homozygotes are, in fact, homozygous for *achates* but also that there is no segregation for epaulette colour among their offspring. The same male that produced the homozygous white-shouldered *achates* in 9089 and 9096 also produced a homozygous red-shouldered *achates*, presumably because the allelomorphs of the latter both came from the Hong Kong rather than the Java ancestor. Thus in brood 9085 a red-shouldered *achates* of brood 9015 when mated to its sib (the father of 9082, 9089 and 9096) produced a brood segregating for red- and orange-shouldered *achates*. One of the females with red epaulettes was subsequently proved to be homozygous (brood 9186).

Thus the Java *achates* appears to be controlled by an allelomorph of the supergene controlling *achates* from Hong Kong but differing in the expression of the colour of the epaulettes, which are orange in heterozygotes, but white or nearly white in *achates* homozygotes which are hybrids.

† Brood 9082 shows that the two types of *achates* are allelic since all the offspring were *achates*, whereas if the two genes were independent a further form would be expected ( $P < 0.05$ ).

Although in the Java race itself some *achates* homozygotes have white shoulders there is evidence that not all do so, that is to say dominance is sometimes complete and sometimes incomplete. Thus in brood 10764 an *achates* with orange epaulettes mated wild produced 14 females, 12 of which were *achates* and two of which were *agenor*. This result strongly indicates that the mating was between two *achates* heterozygotes, but two fathers were involved (see below, p. 45). None of the *achates* had white shoulders and one of the two *achates* with particularly pale orange shoulders was shown to be a heterozygote (brood 10824). The absence of white-shouldered *achates* suggests that some homozygotes may have orange shoulders since homozygotes would have been expected. However, the matter is not as certain as would appear, because the likelihood of homozygous *achates* being present in brood 10764 might be reduced since two males were responsible and the brood may be a mixture between a 3:1 and a 1:1 ratio.

Since the heterozygote *achates* is recognizable and resembles the model in colour more closely than the homozygote it is important to discuss the appearance of the heterozygote when genes from other races are introduced by hybridization.

#### *Dominance of epaulette colour*

*Achates* heterozygotes in the  $F_1$  with other races have redder epaulette colour (between SSO and SO) than do those of pure Java stock, in which the average is about OOS. The first backcross to non-Java material tends to produce even redder epaulettes (compare plates 1*b* and 3*d*) so that frequently they cannot be distinguished from those of their non-*achates* sibs, the average of the *achates* being between SSO and SO but much closer to SSO, whereas the average of the *agenor* is between SSO and S but much closer to SSO. In fact, the majority of both phenotypes are SSO, the chief difference being in the intensity of the colour, the *achates* tending to have less pigment. In the first backcross sibbed, again many of the *achates* and *agenor* epaulettes are indistinguishable from one another in colour, but a few of the *achates* still tend to have less pigment. In contrast to this, the cross between the first backcross and pure Java (brood 9176) restores the intermediate epaulette colour of the heterozygotes, the *achates* mean being between SO and OOS, but slightly closer to SO, so that the colour is intermediate between pure Java and the  $F_1$  as would be expected if the degree of dominance of epaulette colour in the heterozygotes were under multifactorial control.

There is strong evidence therefore that the epaulette colour of the Java *achates* tends to become recessive on out-crossing to races not possessing this allelomorph of the supergene but to be intermediate and similar to the body colour of the model in the pure Java gene complex.

#### 2. *f. agenor* (*f. isarcha* and *f. hiera*) (plate 1*d, e*)

Brood 9044 resulted from a mating between a large-windowed Java *agenor* 9012 and a Java male 8979. The offspring segregated one large-windowed and one small-windowed *agenor*. The small-windowed *agenor* was mated to a pure *thunbergi* (plate 2*c*) (brood 9102) and segregated into *thunbergi*-like and *thunbergi-agenor*-like, showing that the female parent must have been a heterozygote. Since *achates* is not involved, it is only likely to be heterozygous for *laomedon*, or big-windowed *agenor* if the two are controlled by different allelomorphs. However, in a race cross the Java *agenor/laomedon* heterozygotes (the *laomedon* coming from Borneo) have small windows (see below). The data suggest therefore that the small-windowed *agenor* in brood 9044 is heterozygous for *laomedon* (the large-windowed being homozygous *agenor*) and that within pure Java as well as in race crosses the Java *agenor/laomedon* heterozygotes have small windows

(*f. hiera*). In this connexion it is interesting that de Meijere illustrated a small-windowed *agenor* and it is known from his broods that many of his *agenor* were heterozygous *laomedon*. Unfortunately, however, it is impossible to determine which particular insect he figured. It is important to note that neither this small-windowed *agenor* nor that illustrated by de Meijere has a trace of *laomedon* forewing patch, whereas it was present in our Java *agenor*/Borneo *laomedon* heterozygotes. This would suggest that the character is recessive in the pure Java gene complex but not in the hybrids. Subsequent broods have shown that the *laomedon* patch is sometimes apparent in the *agenor*/*laomedon* heterozygotes of pure Java stock and also that the heterozygote between *laomedon* and Java *agenor* has a small window. Thus a small-windowed *agenor* with a *laomedon* patch (brood 10764) mated to a sib produced *laomedon* and small-windowed *agenor* with variable white subapical patches, only just detectable in one insect and absent in another (brood 10828). In a similar sib mating (brood 10815) a small-windowed *agenor* has appeared in which there is no trace of a *laomedon* patch.

If all Java *agenor*/*laomedon* heterozygotes have a small window, as seems likely, then the mother of brood 10764 must have mated with at least two males, since she produced both large and small-windowed *agenor*, and it is known (Clarke, Sheppard & Thornton 1968) that *achates*, *agenor* and *laomedon* are controlled by an allelomorphous series. Subsequently, she was shown to have mated twice, since her abdomen contained two spermatophores.

(a) *The relationship between f. agenor and the Borneo forms f. laomedon, f. venusia and f. anura*

Brood 9023 was a mating between a big-windowed *agenor* 9012 from Java and a Borneo male 8948. His sisters segregated for *laomedon* and *vensusia*. The female offspring consisted of three *vensusia*-like and four *agenor*-like with a small window (plate 2*h, i*). The latter must have been heterozygous for *laomedon* (and at least one had a marked *laomedon* patch on the forewing) and the results suggest that the big-windowed *agenor* heterozygous for *laomedon* from Borneo has a small window. Brood 9109 supports this view since a sib mating from 9023 using a *vensusia*-like female segregated 12 *vensusia*-like to one *agenor*-like with a big window (and no *laomedon* patch). This mating is clearly producing a 3:1 ratio suggesting that the big-windowed *agenor* is a homozygote. The same male mated to an *agenor*-like sib (brood 9111) segregated 10 *vensusia*-like, three *agenor* large window and one *agenor* small window (with a *laomedon* patch) again demonstrating that the small-windowed *agenor* are the *laomedon* heterozygotes. These matings also demonstrate the dominance of *vensusia* over large-windowed *agenor*.

Brood 9110 was a sib mating of brood 9023 using an *agenor*-like female. It produced six *laomedon*-like insects and 19 *agenor*-like. These 19 insects were variable in the size of the hindwing window and could not be divided into two distinct classes. However, those with a *laomedon* forewing patch tended to have smaller windows, again suggesting that the heterozygotes are associated with a reduction in the hindwing window, but that there is also segregation of modifiers affecting the dominance relationships in these  $F_2$  hybrids.

Brood 9045 resulted from the mating between an *anura*-like female (itself resulting from race hybridization) mated to a Java male 9012. It segregated 11 *achates*, six *agenor*/*laomedon* heterozygotes and four *anura*-like insects (plate 2*f*), suggesting that *anura* is recessive to *achates* and dominant to big-windowed *agenor*. This view is strengthened by the fact that two of the *agenor*/*laomedon* heterozygotes mated to a sib produced no *anura* (broods 9140 and 9161). A third such female mated to a sib (brood 9162) segregated three *anura*-like and five *agenor*, four of which had a bigish window suggesting that the male must have been heterozygous *anura*/*agenor*.

(b) *Allelomorphism with agenor from Hong Kong (see Clarke, Sheppard & Thornton, 1968, plate 9d)*

Brood 9024 was an  $F_1$  hybrid between *agenor* from Hong Kong and a Java male (brood 9012) and produced three *agenor*-like offspring. One of these was mated to a male of *P. polymnestor parinda* (plate 4k)\* (brood 9147C). If the two types of *agenor* were controlled by unlinked loci, one in four of the offspring should not be *agenor*-like. In fact, all 21 females were *agenor*-like, showing that the genes responsible for the two forms are either allelomorphic or linked ( $P = 0.0024$ ). Since Java *achates* is allelomorphic with *achates* from elsewhere (p. 43) large-windowed *agenor* and *achates* from Java must be allelomorphic or linked.

## V. GENETICS OF THE FEMALE FORMS FROM NORTH SUMATRA

### 1. f. *achates* (plate 1c)

(a) *With f. trochila* (plate 1g)

Brood 10018 shows that *achates* is not recessive to *trochila*, for it will be seen that a pure Sumatra *achates*, when outcrossed to another race which does not possess the form *trochila*, segregated for *achates*-like phenotypes and others which were clearly heterozygous for *trochila* (see plate 3a for a similar phenotype). They showed not only the characteristic subapical forewing patch but also on many occasions the yellow scaling at the tip of the abdomen. Furthermore, the size of the white window was also reduced as in typical *agenor*/male-like heterozygotes (Clarke, Sheppard & Thornton 1968, plate 9h, i).

Since the known heterozygous *achates*/*trochila* females (assuming for the moment that *achates* and *trochila* are allelomorphic) are indistinguishable from the known homozygous Sumatra *achates* (for example the mothers of 10418 and 10437), this form must be dominant to *trochila* in the pure Sumatra gene complex.

(b) *With f. anceus* (plate 1h)

Broods 10113 and 10416 show that *achates* is not recessive to *anceus*, since on outcrossing to insects not possessing this form the offspring segregated for insects which were clearly heterozygous for *anceus*, having no subapical forewing patch, some white scaling in the epaulettes and yellow on the terminal segments of the abdomen (see plate 2j for similar phenotype). However, it may be that not all *achates* are fully dominant. Thus the mother of brood 10113 appeared to be a normal *achates* except for a few white scales distally in the epaulettes and a narrowing of the black dorsal line towards the tip of the abdomen. Furthermore, the *achates* female parent of 10416 not only had some white scaling in the epaulettes but also the dorsal black line on the abdomen was completely missing on the last few segments. Since *anceus* usually has a yellow tip to the abdomen without a black dorsal line and has white epaulettes, the appearance of the known heterozygotes suggests that the two characters under discussion may sometimes at least manifest themselves to a small degree in the heterozygote. The matter can be investigated further by examining known *achates*/*anceus* heterozygotes and scoring them for white scaling in the epaulettes and the extent of the black line in the abdomen. If the mothers of 9930, 10113, 10301, and 10416, all the offspring of brood 10417 and those of brood 10529 are combined, in only two out of the total 16 insects does *achates* appear to be fully dominant.

A comparison of these insects (table 1 and see plate 2k, l) suggests that the number of white scales is correlated with the expression of the dorsal black stripe, those insects with a reduced

\* The male is similar to the female but has more blue scaling.

stripe tending to have more white scales. However, the results cannot be fully explained by merely postulating variability in the degree of dominance of *achates* over *anceus*. Thus the clear segregation of abdomen type in brood 10417, where all the *achates* are heterozygous for *anceus*, suggests that the difference between a shortened dorsal stripe and a full one may be due to a single gene modifier of *achates* independent of the *anceus* locus. That the effect of the modifier is independent of the presence of *anceus* is demonstrated by the results of brood 10514, where an *achates/anceus* male 10417 mated to a female homozygous for the male-like gene (derived from *parinda*) segregated for short and long black dorsal line among the *achates*. These cannot be heterozygous for *anceus* because the two forms are allelomorphous (see below). The brood also shows that the modifier is genetically independent of the *achates* allelomorph, because all the *achates* are derived from a single heterozygous parent. However, the deficiency of the full dorsal line phenotype indicates that linkage may be involved.

Again, in brood 10520 half the *achates* should be heterozygous for *anceus* and yet only two of the 18 *achates* scorable for these characters had a full dorsal black stripe on the abdomen. This further suggests that the absence of the stripe on the terminal segments can be independent of the presence of the allelomorph controlling *anceus*. However, in brood 10520 the proportion of insects having white scaling in the epaulettes is greater than in brood 10514, suggesting that this character may be more closely associated with heterozygosity for *anceus*.

The situation with respect to the abdomen pattern is even more complex than this, because it cannot be explained solely by the presence of a modifier of *achates*, since *achates* homozygotes and *achates/trochila* heterozygotes have a full dorsal line in those cases where we are certain of the genotype. Thus in the pure Sumatra race the modifier responsible for a short dorsal line may only be effective in *achates/anceus* heterozygotes, but can produce a short dorsal line in its own right in *achates* hybrids with *parinda* (brood 10514 and other broods). It is not known whether this only applies to such *achates*/male-like heterozygotes, in which case the gene can still be considered a modifier of dominance, or whether it can also exert its effect in *achates* homozygotes in *parinda* hybrids.

In summary, the evidence suggests that there is a modifier of abdomen pattern which reduces the length of the black dorsal line on the abdomen of *achates* in *anceus* heterozygotes but not in *trochila* heterozygotes or *achates* homozygotes. It also exerts its effect in the absence of *anceus* in Sumatra  $\times$  *parinda* hybrids. It is not certain, however, whether or not the gene can be considered a dominance modifier since its effect on *achates* homozygotes in a hybrid gene complex has not been investigated. The white epaulette colour of *anceus* appears to be semi-recessive or recessive, the number of white scales in heterozygotes being variable.

### (c) Allelomorphism

We have no certain information as to whether North Sumatra *achates* is allelomorphous with *trochila* or *anceus*, nor in fact whether it is allelomorphous with *achates* from other areas, but in view of the great similarity in pattern it almost certainly is. The dominance relationships between Sumatra *achates* and *anceus* (see above) and Thai *achates* and *anceus* (see below) also suggest that they are controlled by the same allelomorph.

The results from brood 10514 and 10574 are in agreement with the view that *anceus* and *achates* from Sumatra are allelomorphous. A pure Sumatra *achates* mated to a *parinda* segregated for *achates-parinda* and *anceus-parinda* only. An *achates* from these offspring backcrossed to *parinda* produced two non-*achates* offspring, neither of which was phenotypically heterozygous for *anceus*, the situation expected if *anceus* and *achates* were allelomorphs.

*(d) Dominance of North Sumatra achates in a hybrid gene complex*

Sumatra *achates* shows the same dominance relationships as does *achates* from Thailand and Hong Kong, the *achates* characters being dominant and the differences between the pure stock and the hybrids being due to the segregation of non-specific modifiers of the pattern, particularly in hybrids with *parinda*.

Since there is evidence that *achates/anceus* heterozygotes are sometimes recognizable even in pure Sumatra material, it is important to investigate whether the dominance relationships change in a gene complex which is not pure Sumatra (see below).

**2. f. *trochila*** (plate 1g)*(a) With f. anceus*

Brood 9811 shows that *trochila* is dominant to *anceus* with respect to epaulette colour and forewing subapical white patch (assuming for the moment that the forms are allelomorphic). Here a *trochila* female from North Sumatra (with red epaulettes) and a yellow tip to the body and the typical dark *trochila* hindwing) whose female parent was *anceus*, when crossed to a Thai male produced *agenor-trochila* (plate 3a) heterozygotes and *agenor-anceus* heterozygotes (plate 3b), showing that the *trochila* mother was heterozygous for *anceus*. The *agenor-trochila* had the forewing subapical white patch typical of *trochila*, no white scaling in the scarlet epaulettes and a slightly reduced white window on the hindwing. The body was black in four females and had a variable sized yellow tip in five (see plate 3a). The *agenor-anceus*, on the other hand (plate 3b), had no subapical forewing patch, a considerable amount of white scaling in the epaulettes, a reduced white *agenor* window on the hindwing and a marked but variable yellow area on the last few segments of the abdomen, this area being less than a typical *anceus* but more than in their *trochila* heterozygous sibs. Thus the *trochila* heterozygote mother of 9811 was fully dominant to *anceus* with respect to the epaulettes and the colour of the hindwing. Similarly, in brood 10374 a *trochila* with red shoulders and a yellow area to the end of the body from brood 10268 was mated to *parinda* and the brood segregated 11 *anceus-parinda* and nine *trochila-parinda*.

The *trochila-parinda* (plate 3c) had a subapical white patch similar to that in many *trochila*, epaulettes which were reduced in size or absent, and where present were scarlet (RS to S). The hindwing was dark, with a scattering of blue scales, and some pale fawn scaling between the cell and the inner row of black submarginal spots. The abdomen was black, with a small yellow tip which was absent, or almost absent, in some insects. The *anceus-parinda* had no subapical white patch on the forewings, the epaulettes were of normal size or only very slightly reduced, and were scarlet (S to SSO) with no white scaling present. The hindwings were similar to the *trochila-parinda* sib except that the pale area of scaling was more extensive and grey rather than fawn. The abdomen had a yellow area, heavily suffused with black scales, extending over the distal third to a quarter of the abdomen. It appears therefore that *trochila* is dominant to *anceus* with respect to subapical forewing white patch and with respect to the red on the epaulettes but that the yellow patch on the abdomen characteristic of *anceus* is either dominant or intermediate in the heterozygote. In brood 10313 at least one of the known *trochila/anceus* heterozygotes (mother of 10439) had the yellow body so reduced as to be almost identical with normal *trochila*. That is to say the yellow body is virtually recessive in this specimen. It is possible that

the same allelomorph which is modifying the dominance in the *achates/anceus* heterozygotes (see above) is also modifying dominance here.

(b) *Allelomorphism with achates from Thailand*

Broods 10127, 10128 and 10132 result from the backcross to *parinda* of insects heterozygous for *trochila* from Sumatra and *achates* from Thailand. If the genes controlling the two forms were not allelomorphic one would expect half the non-*achates* offspring to be heterozygous for *trochila* and half not heterozygous. All 18 of the insects were clearly carrying the gene for *trochila*, indicating that the genes are allelomorphic or at least the loci are extremely closely linked. An *achates* from one of these broods backcrossed to a *parinda* brood (brood 10251) segregated for *achates* and non-*achates*; the latter were not heterozygous for *trochila*, thus agreeing with the hypothesis that *achates* and *trochila* are allelomorphic.

3. f. *anceus* (plate 1h)

Although most *anceus* have an extensive yellow area on the distal part of the abdomen we have obtained one female (wild) in which the body was black. Black body appears to be recessive to the normal *anceus* body, since in brood 9807 a pure Sumatra *anceus* with the distal half of the body yellow, when mated to a Thai male, produced two distinct types of *agenor/anceus* heterozygotes. In nine the body was black (plate 4l) and in four had a yellow area. Since the Thai race is monomorphic for black body (excluding *achates*) the yellow-bodied *anceus* mother must have been heterozygous for the black-bodied condition, showing that black body is recessive in the Sumatra gene complex.

The yellow area on the abdomen of *anceus* is controlled by the same gene as that controlling the other associated characters or by a closely linked gene, since the yellow body does not segregate independently of the other characters. This is shown by the fact that in brood 9965, which is a second backcross of the Sumatra race to the Thai race, and in broods 10358 and 10372, all of the ten *anceus* heterozygotes (recognized by white scaling in the epaulettes) had yellow on the abdomen, whereas the nine individuals without white scaling had black bodies (one insect in 10372 was not scorable for epaulettes or body).

(a) *Allelomorphism with trochila* (plate 1g)

*Anceus* and *trochila* are controlled by allelomorphs at the same locus or closely linked genes. Thus the female parent of brood 10275 carried both *trochila* and *anceus* and was mated to a *parinda*. The offspring segregated six *trochila-parinda* and ten *anceus-parinda*. If the two forms were not allelomorphic, at least some *trochila-anceus*-like insects should have appeared. That such insects are recognizable in this line is shown by brood 10383 in which an *anceus-parinda* female mated to its sib produced amongst its offspring three *trochila-anceus* females (plate 3e). To confirm that the *trochila* in brood 10275 were not carrying *anceus* one of the *trochila-parinda* females was backcrossed to *parinda*. The brood (10390) segregated 15 *trochila-parinda* and 16 *parinda*-like. Thus the female could not have been carrying the gene for *anceus* as would have been the case if the two loci were unlinked. Since *trochila* and *achates* from Thailand are allelomorphic, *anceus* and *achates* must also be allelomorphic (or very closely linked).

*(b) Dominance relationships with trochila in race hybrids*

In a number of broods obtained by hybridizing Sumatra insects with those from other races, and then producing further generations, either by  $F_2$ s or by further outcrossing and then intercrossing, *trochila/anceus* heterozygotes have been obtained in a gene complex which is not pure Sumatra. In these insects the forewing apical patch is very variable and in at least one insect was absent or almost absent. The epaulettes on the forewings almost always had some yellow or white scaling but the amount varied from insect to insect, and the colour in some tended to be more orange. The yellow patch on the tip of the abdomen tended to be much smaller than in the pure Sumatra *trochila/anceus* heterozygotes. The hindwings in the majority of specimens were dark and showed no trace of the pale scaling typical of *anceus*. Thus the heterozygotes were more intermediate in appearance than pure *trochila/anceus* heterozygotes (plate 3f) with respect to the colour of the epaulettes and the yellow on the abdomen. On the other hand, the dark hindwing of *trochila* appeared to remain dominant in many but not all specimens (for example see plate 3e). The butterfly figured not only differs from those described above with respect to the hindwing but also where epaulettes, forewing patch and body colour are concerned, thus highlighting the extreme variability in such complex hybrids. However, little can be said about the subapical forewing patch since it is so variable in *trochila* itself.

4. *Hybrids with races from Malaya, Borneo and South Japan*

10367 was an  $F_1$  between a *trochila/anceus* 10268 and a Malayan male with three *esperi* sisters and subsequently shown to be carrying *esperi*. Any offspring carrying this form will therefore be *esperi/trochila* or *esperi/anceus*. No scorable females were produced, but we mated a male to a *parinda*-like butterfly (brood 10513) and the offspring were seven *esperi-parinda* and seven *anceus-parinda*. Since all the offspring were either carrying *anceus* or *esperi*, but not both together, the data suggest that *anceus* and *esperi* are allelomorphic. This is what would be expected from a consideration of all the other colour patterns tested which appear to be controlled by a supergene.

Brood 10522 was a mating between a pure Sumatra *trochila/anceus* and a Singapore male with six *esperi* (plate 3g) sisters. It produced eight males and three phenotypically different females. One was *esperi*-like, and since it did not have a yellow tip to the abdomen and no white scales in the epaulettes was probably *esperi-trochila*. One was indistinguishable from *trochila*, having the forewings of that form and a black body. Presumably therefore, it was heterozygous for *trochila* (plate 1g) and *butlerianus* (plate 3h), this being the only other common form from Malaya excluding *achates*. The third form had no subapical forewing white patch, a faint patch of white scaling at the inner margin of the forewing (fainter than in *butlerianus*), some white scaling in the epaulettes and a yellow patch on the last third of the abdomen. It was presumably therefore a *butlerianus-anceus* heterozygote.

We have reason to believe (p. 61 and table 2) that *trochila* and *laomedon* are identical as far as the supergene is concerned. In 10522 *esperi* appeared to be fully dominant to *trochila*. That in hybrids *esperi* is also dominant to *laomedon* is shown by brood 10579 where an *esperi-parinda* 10513 was mated to a male from north Borneo and produced a female which had an *esperi*-like subapical patch but must have been heterozygous for *laomedon*. Had this female carried *venusia* or *anura* from Borneo it would have had yellow on the abdomen (Clarke, Sheppard & Thornton 1968). Thus *trochila* and *laomedon* behave similarly with regard to dominance in heterozygotes with *esperi*.



In brood 10470 a *thunbergi* female was mated to a pure Sumatra male homozygous for *anceus* (see brood 10512) and produced a female heterozygote which is intermediate between the two forms (see plate 3i for a similar phenotype), having much white scaling in the epaulettes and a yellow patch reduced and indistinct on the abdomen—not much greater than that found in many *trochila*. The window on the hindwing is not distinguishable with certainty from pure *thunbergi*.

TABLE 1.

brood	dorsal line	white scaling in epaulettes		
		none	few	many
mothers of 9930, 10113, 10301, and 10416, all offspring of brood 10417, and <i>achates</i> offspring of brood 10529†	short	0	1	8
	full	2	5	0
10514†	short	5	0	0
	full	1	0	0
10520†	short	6	4	6
	full	1	0	1

† One female deformed and unscorable.

TABLE 2. CLOSELY LINKED LOCI WITHIN THE SUPER-GENE

form	super-gene	super-genes, sympatric and recessive in effect	super-genes, sympatric and showing no dominance
<i>achates</i> ( <i>distantianus</i> )	$TW^aFE^sBY$	$twF^lE^sb^y$ , $twF^lE^sb$ , $twFE^wB^y$ , $twFE^wb$	$twFE^wB^y$ , $twFE^wb$
<i>achates</i> ( <i>distantianus</i> ) Java and South Sumatra)	$TW^aFE^wBY$	—	$twF^lE^sb^y$ , $twF^lE^sb$ , $tW^iFE^sb$ , $twFE^wB^y$
<i>laomedon</i> (yellow tip)	$twF^lE^sb^y$		$tW^iFE^sb^*$
<i>laomedon</i>	$twF^lE^sb$		$tW^iFE^sb^*$
<i>trochila</i> (yellow tip)	$twF^lE^sb^y$	$twFE^wB^y$	$twFE^wB^y$
<i>trochila</i>	$twF^lE^sb$		$twFE^wB^y$
<i>isarcha</i>	$tW^iFE^sb$		$twF^lE^sb^y^*$ , $twF^lE^sb^*$
<i>anceus</i>	$twFE^wB^y$	$twFE^wb$	$twF^lE^sb^y$ , $twF^lE^sb$
<i>anceus</i> (black body)	$twFE^wb$		
<i>titania</i> (Java)	$TW^iFE^sb$		
<i>anura</i> (Java)	$tW^aFE^wBY$		
<i>gerania</i>	$tW^gF^lE^sB^y$		
<i>ityla</i>	$tW^gF^lE^sb$		
new <i>gerania</i> -like form	$tW^gFE^wB^y$		$twF^lE^sb^y$

Table 2 shows the super-genes and the dominance relationships, where known, between the various loci within them in sympatric forms. Where dominance is sometimes present and sometimes absent the super-gene has been entered twice. The loci producing an intermediate heterozygote are indicated by bold type. Where more than one locus within a super-gene is so indicated it does not necessarily mean that both produce an intermediate effect in any given individual if the super-gene is also sometimes completely recessive in effect.

\* An asterisk indicates that the  $F^l$  locus is usually recessive but occasionally manifests itself.

Brood 10494 was a *trochila/anceus* 10393 female mated to a male from Selangor. The male must have been an *achates* but heterozygous, since only half its offspring were of this form. Three of the *achates* were typical, suggesting that it is dominant to *trochila* (one was shown to be heterozygous for *trochila*, see brood 10558 below). However, a fourth (plate 3j) had a much reduced but very noticeable subapical forewing streak which is possibly a manifestation of the *trochila* forewing patch. The fifth *achates* had much white scaling in the epaulettes and a very much shortened dorsal black line on the abdomen, clearly demonstrating that it is an *achates/anceus*

heterozygote. The next insect must be a *butlerianus/trochila* (plate 3k) heterozygote, having a very marked forewing white subapical patch, no white scaling in the epaulettes and a black abdomen. The very conspicuous subapical white patch suggests that modifiers have been introduced accentuating this feature so that it is as extreme as in some *esperi*. The remaining five insects are *butlerianus/anceus* (plate 3l); all have the white scaling at the inner margin of the forewing characteristic of *butlerianus*. The epaulettes are white with a sprinkling of red scales, often reduced to a very few. The distal third to a half of the abdomen is yellow and the hindwing pattern is typical of *anceus*. Thus the heterozygotes are intermediate between *anceus* and *butlerianus* but, unlike the genetically similar insect in brood 10522, the white epaulettes of *anceus* are almost fully dominant. That is to say, the dominance is reversed compared with all the other crosses involving *anceus*.

The *laomedon/anceus* heterozygote in a hybrid gene complex (brood 10458) is recognizable. The forewing apical patch of *laomedon* appears to be much reduced and the epaulettes have no white scaling. The blue scaling on the hindwings typical of *anceus* is reduced and replaced by a blackish brown suffusion. The last third of the abdomen is yellow. In brood 10564, which included part of the *thunbergi* gene complex, the *laomedon/anceus* heterozygote was much the same except that the hindwing had rather more pale fawn scaling. In contrast to these hybrids, the *laomedon/anceus* heterozygotes which include some *parinda* gene complex (10573) have a marked *laomedon* subapical patch, no white scales in the epaulettes, a very black hindwing with a few blue scales, and a black body with a very reduced yellow patch on the last two segments.

In brood 10558 a typical *achates* 10494 was mated to a male from North Borneo almost certainly homozygous for *laomedon* and segregated for five *achates* and one *laomedon*-like insect. The latter had a quite marked white subapical forewing patch, no white scaling in the epaulettes, a black body and very dark hindwings with the double row of black spots typical of *laomedon*. It was therefore not heterozygous for *anceus* and was presumably *trochila/laomedon*.

## VI. THE GENETIC RELATIONSHIP BETWEEN SOME OF THE FEMALE FORMS IN JAVA, SOUTH SUMATRA, AND NORTH SUMATRA

### 1. f. *achates*

#### (a) *Dominance of epaulette colour*

Many of the *achates* in South Sumatra are similar in appearance to those in Java. It was therefore decided to investigate the relationship between these two forms and the other forms sympatric with them. In brood 10765 a Java *achates* with orange shoulders was mated to a male from Palembang in South Sumatra. Of the 12 female offspring eight were *achates*, suggesting a 3:1 ratio. The four non-*achates* offspring were obviously heterozygous for *anceus*, since the end of the abdomen had the yellow patch characteristic of this form, but the epaulettes were red without the white scaling found in many *anceus* hybrids. The *achates* could also be subdivided into those carrying *anceus* by the absence of the black line on the last few segments of the abdomen. These *achates* could be divided into three phenotypes, those with the characteristic short dorsal line on the abdomen, which all had very pale orange epaulettes, those with a full dorsal line and orange epaulettes, and the final category which had a full dorsal line and very pale orange epaulettes. It seems likely that these are *achates-anceus*, *achates/agenor*, and *achates* homozygotes respectively. Test matings showed that the putative genotypes were correct in the four individuals where broods were successfully raised (10821, 10822, 10836 and 10838).

Brood 10765 must have been a cross between two individuals heterozygous for *achates*, since one of the male offspring was shown to be homozygous *achates* (brood 10805). Nevertheless, none of the *achates* females had white shoulders, suggesting that homozygous *achates* may not always have white shoulders. This conclusion is in accord with the evidence that not all homozygous Java *achates* have white shoulders (p. 44).

(b) *South Sumatra f. achates and f. trochila*

Brood 10836 resulted from an *achates* 10765 mated to a South Sumatra male. It produced two normal orange-shouldered *achates* with a full dorsal line and two small-windowed *agenor*, one with a just detectable white subapical patch on the forewing. Since the *agenor* allelomorph can only have come from Java, the *achates* allelomorph must have originated from South Sumatra. The male parent of 10836 must have been carrying *trochila*, since none of the offspring, judged by their appearance, were heterozygous for *anceus*; therefore *trochila* is behaving with respect to Palembang *achates* as *laomedon* does with Java *achates*, producing intermediate epaulette colour but recessiveness as far as forewing patch is concerned. Thus the brood provides further evidence that *trochila* and *laomedon* are genetically the same as far as the major gene is concerned, both with respect to *achates* and large-windowed *agenor*.

(c) *Java f. achates with f. anceus from South Sumatra*

Brood 10765 (see (a) above) produced recognizable *achates/anceus* heterozygotes. A subsequent brood (10822) conclusively demonstrated the presence of *anceus* in one of these *achates* heterozygotes. An examination of the phenotypes in 10765 showed that the *achates/anceus* heterozygotes not only had a short dorsal line on the abdomen, but also epaulettes which were neither white nor the orange typical of other heterozygotes, but were an intermediate orange-white.

(d) *Java and South Sumatra f. achates with f. anceus from North Sumatra*

Brood 10805 was the product of a mating between a female *anceus* from North Sumatra and a male from brood 10765. It contained 25 *achates* and no other female form, demonstrating that the male was a homozygote and had therefore obtained one of its *achates* allelomorphs from South Sumatra and the other from Java. All the offspring must have been heterozygous for *anceus* and all had large white epaulettes and a short dorsal line (plate 4a). Thus the brood shows that the *achates* allelomorph from Java and that from Palembang behave alike with respect to North Sumatra *anceus*. However, in contrast to similar heterozygotes using *anceus* from South Sumatra, the epaulettes are white rather than orange-white. The differences may well be due to the gene complexes, rather than the major gene, not being the same. A similar mating (10806), in which the male proved to be an *achates/anceus* heterozygote, not only showed the presence of *anceus* in 10765 but also confirmed that Java *achates* in heterozygotes with *anceus* from North Sumatra have white shoulders. The *achates* allelomorph must have come from Java since the *anceus* allelomorph in the male could only have come from South Sumatra.

(e) *Epaulette colour in South Sumatra achates/thunbergi heterozygotes*

Java *achates*  $F_1$ s with other races have an epaulette colour between SSO and SO, in contrast to pure Java heterozygotes in which it is more orange (p. 42). Broods 10824 (an  $F_1$  between Java *achates* and *thunbergi* from Japan), 10842 and 10847, in which similar heterozygotes were produced but in a more hybrid gene complex, confirm this finding. In all these broods there

was a strong tendency for the epaulette size to be reduced. Brood 10821 produced similar *achates/thunbergi* heterozygotes in which the *achates* allelomorph came from South Sumatra. The epaulette colour again was between SSO and SO, and the epaulette size reduced. Thus yet again the *achates* allelomorphs from Java and South Sumatra behave similarly.

#### VII. FURTHER DATA ON THE GENETICS OF *THUNBERGI*, *BUTLERIANUS* AND *AGENOR*

In a previous paper (Clarke, Sheppard & Thornton 1968) we reported conflicting evidence on the genetic determination of the difference between *thunbergi* on the one hand and *agenor* from Hong Kong and Thailand on the other. We could not decide whether the difference was multifactorial or due to a major gene determining the distribution of white on the hindwing (the window). A number of new broods have now been produced in some of which the distinction between the phenotypes was clearer than in the earlier ones. In the light of this, on rescoring the broods reported previously we find that with this increased experience we can distinguish two and possibly three genotypes, *thunbergi*, *agenor*-like (probably the heterozygote, see below), and *agenor* (probably the homozygote). The *thunbergi* (plate 4*b*) in these broods had a white window smaller than *agenor* but tending to be larger than in pure *thunbergi*. In the *agenor*-like insects (plate 4*c*) the window was slightly smaller than in typical *agenor*, with an indistinct outline and prominent black veins, though not as broad as in *thunbergi*. The presumed *agenor* homozygotes (plate 4*d*) had the white window characteristic of this form, with a clear outline and black veins narrower than in the other two phenotypes.

Summing the results from the matings between putative *agenor/thunbergi* heterozygotes (broods 8969, 8984, 8990, 9709, 9712, 9713 and 9717) the resulting progeny have been scored as 29 *thunbergi*, 48 *agenor*-like and 22 *agenor*, which gives a satisfactory approximation to the expected 1:2:1 ratio. That the Mendelian ratios given above are not due to the arbitrary division of a continuous range of variation, and that *agenor* and *thunbergi* differ by a pair of allelomorphs, is proved by the crosses to *parinda* (broods 9690, 9691, 9752 and 9771), where the offspring could unambiguously be divided into two phenotypes, nine *thunbergi-parinda* (plate 4*e*) and 12 *agenor-parinda* (plate 4*f*), giving satisfactory approximation to the expected 1:1 ratio.

Other attempts to confirm our scoring by genotyping individuals of different phenotypes were made. A *thunbergi* from the  $F_2$  brood, brood 9713, mated to a pure *parinda* (brood 9766) produced four *thunbergi-parinda*, thus strongly supporting the view that the female parent was homozygous *thunbergi*. The difference in phenotype between the putative *agenor*-like heterozygotes and *agenor* homozygotes is far less distinct than that between *thunbergi* and *agenor*-like. We therefore genotyped some of the individuals to test whether dominance was complete or incomplete. Thus the presumed heterozygous females in broods 9752 and 9771 were shown to be heterozygous for *thunbergi* by backcrossing to pure *parinda*. The presumed homozygous *agenor* mother of 9827 was backcrossed to a male from Sumatra known not to be heterozygous for *agenor*. This produced seven *agenor-anceus* females (and no *thunbergi-anceus*, see p. 51), confirming that the mother was homozygous *agenor*. In every case, therefore, the genotype as judged by the phenotype has been confirmed, strongly supporting the view that the dominance of *agenor* in race crosses with *thunbergi* is incomplete.

Previously (Clarke, Sheppard & Thornton 1968) we had no evidence that the gene producing *butlerianus* (plate 3*h*) existed as far east as Thailand, although we knew that its model occurred

there. Since then we have seen a dead specimen from Vientiane (Laos), which was typical of our *agenor*-*butlerianus* hybrids (see Clarke, Sheppard & Thornton 1968, plate 9*l*). The genetic results from a male from central Thailand (brood 9477) support the view that the Laos insect really was an *agenor*/*butlerianus* heterozygote and proves that the *butlerianus* gene is found, albeit probably as a great rarity, as far east as central Thailand. The male in question was mated to a pure *thunbergi* from Japan and produced offspring in subsequent generations which, as will be seen below, were obviously carrying the gene for *butlerianus*.

Previous work showed that *thunbergi* was either allelomorphous or closely linked to the supergene determining other polymorphic forms including *agenor*, *butlerianus* and *achates*. The doubt as to whether *thunbergi* is allelic or closely linked arises because one insect was male-like in appearance (i.e. had no white in the hindwing) and this could have been due to either a change in dominance (because of the segregation of modifiers) or a crossover between *achates* and *thunbergi*. Present investigations support the view that the former hypothesis is the correct one. In brood 9477 three distinct types of female appeared, *agenor*-*thunbergi*, *thunbergi*-*butlerianus* and *butlerianus*-like. These last insects, although far darker than typical *butlerianus* and with a slightly reduced amount of white on the forewing patch, had no white window on the hindwing, a character found in their sibs designated *thunbergi*-*butlerianus*. Since the female parent was pure *thunbergi* all the offspring must be heterozygous for *thunbergi*. Subsequently, a *butlerianus*-like individual was shown to be heterozygous for *thunbergi* by backcrossing it to *parinda* (brood 9671). The distinction between the two kinds of *butlerianus* females in 9477 must therefore be due to segregation of one or more modifiers of dominance with respect to the *thunbergi* hindwing window. The *thunbergi*-*butlerianus* individuals are intermediate or recessive for the character absence of white on the hindwing and the *butlerianus*-like females are dominant for this character. Subsequent broods (9546, 9548, 9549, 9551, 9560, 9583, 9592) tend to fall into clear-cut classes (plate 4*g*, *h*) with respect to the presence or absence of white on the hindwing in the *thunbergi*/*butlerianus* heterozygotes, suggesting that one or at most very few modifiers are involved.

Previously (Clarke, Sheppard & Thornton 1968) we had data which suggested that the absence of white on the hindwing (this time derived from a Borneo *laomedon*) could sometimes be dominant to *thunbergi* but not always. Three subsequent broods (9054, 9147(N) and 9179, plate 4*i*) confirm this.

The  $F_1$ , 9054, between a pure Borneo and a pure *thunbergi*, produced 14 females, seven with no white on the hindwing (male-like) and seven with a variable amount of white, in most insects this being less than in typical *thunbergi* (*thunbergi*-*laomedon*). A male from 9054 mated to *thunbergi* (9147N) segregated for one *thunbergi*-like and one male-like. Brood 9179, from a female *thunbergi*-*laomedon* 9054 mated to a pure *thunbergi* male, segregated for three forms, eight *thunbergi*-like, eight male-like and three *thunbergi*-*laomedon*. Thus here again there appear to be modifiers of dominance so that the absence of white on the hindwings is dominant in some individuals but intermediate in the heterozygote in others. Thus the male-like individual in brood 8650 (table 7*d* of Clarke, Sheppard & Thornton 1968), which suggests that *laomedon* might be linked with rather than allelic to *achates*, was probably not a cross-over but a male-like *thunbergi* heterozygote in which the absence of the white on the hindwing was dominant..

The insects derived from the wild Thai male carrying the gene for *butlerianus* (brood 9477) also give useful information on the dominance relationship of the presence or absence of the white area in the region of the inner margin of the forewing (the '*butlerianus* patch'). In the  $F_1$  a *butlerianus* patch was present in all insects not heterozygous for *agenor* and absent in all those

that were, as would be expected, the two forms being allelomorphous and the male a heterozygote. However, in a number of the  $F_2$ s in which the female parent possessed the patch, insects appeared which were male-like, having no white on the hindwings and no patch on the forewings. These could have either been due to the *butlerianus* patch being recessive in these insects or to crossing over within the supergene. Broods 9672 and 9682 show that the absence of the forewing patch is not due to crossing over but to a change in dominance. On crossing male-like females to *parinda*, segregating broods were produced in which five of the six non-*thunbergi-parinda* individuals possessed the *butlerianus* patch despite its absence in the mothers.

The breeding work also suggests that the *butlerianus* patch when manifested in the heterozygote is not fully dominant. Thus among the  $F_2$  broods only one (brood 9548) could have been between a *butlerianus*-like female and a male heterozygous for the gene, since in the others *agenor* segregated. Thus only this brood could have produced homozygous *butlerianus*, and in fact it produced two insects in which the *butlerianus* patch was markedly whiter (plate 4j) than in all other insects in this series of broods. This strongly suggests that *butlerianus* is not dominant and that these two insects are homozygotes.

### VIII. DISCUSSION

Polymorphic Batesian mimicry to be effective requires that the various forms are controlled by single switch genes. Moreover, when several forms are present in the same population the genes concerned must either be tightly linked within a super-gene and have particular dominance relationships, or if unlinked show complex epistatic interactions. In the absence of one or other of these two situations imperfect mimics will be produced in some heterozygotes. Consequently one would expect dominance to be evolved if it were absent initially and super-genes to evolve either by the accumulation of advantageous mutants which happened to be tightly linked to the locus initially responsible for the original mimicry, or by increasing linkage between interacting loci. For a discussion of the relative likelihood of these two alternative methods of evolution see Clarke, Sheppard & Thornton (1968), Sheppard (1969).

As pointed out by Fisher and Ford (see Ford 1953) mimicry is often so good that it is unlikely that a new mutant when it first appeared could produce so perfect a likeness of the mimic to its protected model. Thus in the evolution of mimicry one would expect that the effect of a mutant would be gradually altered towards the production of a more perfect resemblance by the accumulation of modifiers under the influence of natural selection.

This general thesis concerning the events which occur during the evolution of a complex Batesian mimetic situation was developed as a result of the analysis of the genetics of the butterfly *Papilio dardanus*.

In order to obtain independent evidence on the validity of these deductions it was decided to investigate genetically other examples of mimicry both Batesian and Müllerian. In the former type of mimicry super-genes together with complex dominance relationships between sympatric but not allopatric forms should be the rule, and in the absence of linkage appropriate epistatic interactions should determine the patterns among sympatric but not necessarily allopatric forms. Here there will be no opportunity for modifiers of dominance or epistasis to be accumulated as a result of selection for mimicry. In Müllerian mimicry there is selection for monomorphism, not polymorphism. Hence there should be no selection for the evolution of super-genes nor of suitable epistatic interactions (except in the region of hybridization between

monomorphic races), but there should be selection for modifiers improving the mimicry where this is dependent on the presence of a major gene (Sheppard 1969).

Investigations of the Batesian mimics *P. memnon* (Clarke, Sheppard & Thornton 1968) and *Papilio polytes* (C. A. Clarke & P. M. Sheppard, unpublished; Sheppard 1969) are in agreement with the thesis that the genetic control of the mimicry closely parallels that of *P. dardanus* (Clarke & Sheppard 1960*a, b, c*, 1963). The genetic studies of the Müllerian mimics *Heliconius melpomene*, *H. erato* and *Zygaena ephialtes* are also in agreement with our ideas on the evolution of mimicry, although in the two Heliconid species linkage has been found between some of the loci involved in the mimicry (Bovey 1941, 1966; Dryja 1959; Emsley 1964, unpublished; Sbordonì, Bullini & Ragazzini 1969; Sheppard 1963; Turner & Crane 1962; J. R. G. Turner, unpublished).

The previous study of the genetics of *P. memnon* was somewhat incomplete since at that time material from Java and Sumatra, where the polymorphism appeared particularly complex, was not available. Now that the races inhabiting these two islands have been investigated it is important to see what further light this new information throws on the evolution of the polymorphism.

(1) *The effect of modifiers on the resemblance between the mimetic forms and their models*

In the previous investigation it was found that the resemblance between mimetic forms and their models was usually greater when the super-gene responsible was in the gene complex of a race possessing that form rather than in a hybrid. This is the situation one would expect if the effects of the major genes are modified to produce an optimum phenotype under the influence of natural selection. In the present investigation a further nine mimetic forms in their natural gene complex and in race hybrids have been examined. A comparison of the resemblances between mimic and model within races and with those in race crosses shows that the resemblance in the hybrids is better in no cases, as good in three, and poorer in 16. The results are in good agreement with those in the previous investigation where the ratio was 0:10:35.

(2) *Dominance relationships in pure races and hybrids*

As has been pointed out previously, if there are two optimum phenotypes controlled by a pair of allelomorphs then if dominance is absent there will be a genotype which produces a non-optimum phenotype and consequently there will be selection for the evolution of dominance. Thus with complex mimicry one would expect dominance to be present between most sympatric forms. If dominance were not present initially and had been evolved one would expect it to break down in race crosses in which allopatric forms were involved. In the previous investigation full dominance was present in nine heterozygotes between sympatric forms and absent in none. In hybrids between allopatric forms it was present in six and absent in 19. In the present investigation dominance is present in one case (*achates*/*trochila*) out of six when sympatric forms are involved, and nine out of 26 for allopatric ones. Thus, in the present study, particularly in forms from Java and Sumatra, complete dominance is absent more frequently than in the other races examined. However, if one considers how intermediate the heterozygotes are in appearance in the three where they can be specifically compared in a pure and a hybrid gene complex, it is found that there is a greater degree of dominance in the former. Thus, although Sumatra *trochila* is recessive to *achates*, the presence of *anceus* in the heterozygote with *achates* can sometimes be recognized by the presence of a few white scales in the red epaulette on the base of the forewings. Furthermore, the distal black stripe on the abdomen of the heterozygote may be

somewhat reduced in length. The *anceus/trochila* heterozygote may also have some white scales in the epaulettes and the abdomen has a yellow patch similar to but smaller than that found in *anceus*. However, these manifestations of the presence of *anceus* are not always to be seen and, when they are, produce an effect less evident than in the corresponding heterozygote in a race hybrid.

In Java the *isarcha/laomedon* heterozygote has a reduced white window on the hindwing (*hiera*) but the white subapical forewing patch typical of *laomedon* is very much reduced or absent. This is confirmed in British Museum (Natural History) material, where only five out of 27 *hiera* examined have any trace of this character. However, we have found that in the same heterozygote produced by a race-cross using *laomedon* from Borneo the white patch is clearly visible. These observations suggest that there has been some modification of dominance but that the process has not been completed. This may mean either that not enough time has passed since the polymorphisms were established for dominance to have evolved, or that a sufficient supply of nearly selectively neutral modifiers is not available (see O'Donald 1968, 1969). O'Donald showed that a small heterozygote advantage among the modifiers of dominance could prevent, even in a mimetic polymorphism, complete dominance evolving. The results in *P. memnon* demonstrate that there is no lack of modifiers of dominance in any of the races studied.

It is perhaps important to note that in the case of the tailed *achates* in Java it is the heterozygote with *laomedon* or *agenor* which is the better mimic, rather than the homozygous *achates*. This is because the colour of the epaulettes is orange, as are the thoracic marks of the model rather than pale orange or white as in the homozygote. Thus it is *achates* which is an exception to the rule that the heterozygote, if intermediate in appearance, is more so in race crosses, for on backcrossing to the Hong Kong race the pale orange or white epaulettes of the Java race tend to become recessive to the scarlet ones of Hong Kong. Such a result can be expected if the heterozygote can be more easily modified than the homozygote. Nevertheless, since there is some evidence from the Java material that not all Java homozygous *achates* have white epaulettes as they appear to have in race crosses, there has been a tendency for the evolution of this homozygote towards the mimetic heterozygote.

There is one exception to the rule that these homozygous *achates* in race crosses have white epaulettes, and this concerns crosses with South Sumatra material, where the Java type of *achates* is also found (see p. 52). In the Java  $\times$  Sumatra  $F_1$  we failed to get white epaulettes in a cross where homozygous *achates* was expected. However, some epaulettes were pale orange, as they are sometimes in pure Java homozygotes. In the cross there were also *achates* (Java)/*anceus* heterozygotes which in other race crosses have white epaulettes but which here had pale orange ones. Since there is reason to believe that the allelomorph controlling epaulette colour in *anceus* is the same as that controlling it in these *achates* (p. 53), the presence of pale orange epaulettes instead of white ones in these heterozygotes is further evidence for some dominance of orange epaulette colour in *achates* having evolved in Java and Sumatra. However, white epaulettes are still present in South Sumatra (British Museum (Natural History) material) despite the fact that selection against them would be stronger than in Java. This is because they are potentially produced by both *achates/anceus* heterozygotes and *achates* homozygotes, whereas in Java they could only appear in the latter, since *anceus* is absent.

Thus the genetic studies on *achates* from Java and South Sumatra show that the homozygous individuals and those homozygous for the allelomorph producing 'white' epaulettes (*achates/anceus* heterozygotes) are more like the mimetic *achates* heterozygote in their own gene complex



than they are in hybrid gene complexes. That is to say that there is partial dominance of the mimetic form.

The genetic comparison of sympatric and allopatric forms gives ample evidence for an abundance of modifiers of dominance in wild populations and also of the evolution of dominance. However, in both *P. dardanus* and *P. memnon* full dominance between sympatric forms has not always occurred, although where the heterozygote is particularly intermediate in appearance it is usually mimetic.

### 3. *The super-gene*

In previous investigations into the genetics of *P. memnon*, *P. dardanus* and *P. polytes* (Clarke, Sheppard & Thornton 1968; Clarke & Sheppard 1960*b*, 1963; C. A. Clarke & P. M. Sheppard, unpublished; Sheppard 1969) it has been shown that the complex mimicry is controlled by what appears to be a multiple allelomorphous series. In contrast, the Müllerian mimics *H. melpomene*, *H. erato* and *Zygaena ephialtes* (Bovey 1941, 1966; Dryja 1959; Emsley 1964, unpublished; Sbordoni, Bullini & Ragazzini 1969; Sheppard 1963; Turner & Crane 1962; J. R. G. Turner, unpublished) show a considerable amount of independent assortment between the genes controlling the allopatric mimetic forms. It appears likely that the multiple allelomorphous series in the Batesian mimics is really a super-gene composed of several closely linked loci and that it has evolved as the result of the action of disruptive selection (Fisher 1930; Sheppard 1953; Mather 1955). Furthermore, it was pointed out by Clarke, Sheppard & Thornton (1968) that if the very rare forms of *P. memnon* which have been found in Hong Kong and Taiwan are products of crossing over within the super-gene and not of mutation, then the order of the genes within the super-gene can be deduced. The argument used was that employed by Fisher (1953) when developing his hypothesis about the order of the units in the Rhesus blood group system in Man. However, in mimicry we are more fortunate than Fisher was, since we have a better idea of the direction of selection on the various combinations of allelomorphs. Although both mimetic and non-mimetic forms may be maintained by frequency dependent selection, imperfect mimics will be at a disadvantage because of the disruptive selection. The rare imperfect mimics are therefore likely to result from single crossovers within the super-gene rather than by a double crossover. On this basis Clarke, Sheppard & Thornton (1968) suggested that the locus controlling the pattern on the hindwing lies between that determining the presence or absence of tails and that determining the colour pattern on the abdomen.

In the present investigation we have obtained another of these rare forms, *anceus* with a black abdomen rather than the normal one in which the distal third to a half is yellow (plate 1*h*). In fact, this form was obtained twice from the same locality, suggesting that the insects were related, for we have never obtained the form since, nor seen it in a museum collection. The only black-bodied form with which *anceus* is likely to produce a heterozygote in this area of Sumatra is *trochila*. Thus, if the event which gave rise to this rare form were a crossover within the super-gene we can deduce that the locus determining body colour is at one end of it, since all the other features of the insect were typical of *anceus*. This is in agreement with the previous conclusion.

A number of other rare forms which we have been unable to obtain alive have been seen in museums and also give evidence about the super-gene, if again we assume crossing over is more common than mutation. The form *ityla* (p. 41, plate 1*k*) resembles *gerania* except that it has a black abdomen, again suggesting that the locus responsible for abdomen colour is at one end of the super-gene. The very rare tailed *agenor* from Java (f. *titania*, p. 42, plate 1*i*) again

supports our previous conclusion that the locus controlling the presence or absence of tails is at the opposite end of the super-gene to that controlling body colour. The tailless *anura*-like form from Java (p. 42, plate 2*d*) appears to be the reciprocal crossover class to that of *titania*. The insect in question cannot be the descendant of an immigrant from Borneo where *anura* is a common mimic, since it had the orange epaulettes of the typical Java *achates* and not the scarlet ones of *anura* (p. 42, plate 2*e*). The single *anura* with red epaulettes from North Sumatra has probably arisen from yet another such crossover but involving the North Sumatra *achates*, hence the red epaulettes.

The examination of these rare forms and the genetic analysis of two of them could suggest that the loci controlling body colour and the presence or absence of tails mutate more frequently in both directions than do the other loci in the super-gene. Alternatively, and more likely, these two loci are at opposite ends of the super-gene and are more loosely linked than are others in the block of loci controlling hindwing pattern (*W*), epaulette colour (*E*), and forewing pattern (*F*).

Crossing over probably does not occur in female Lepidoptera. We have therefore examined our 55 backcross broods in which the male has been proved to be an *achates* heterozygote by the production of both *achates* and non-*achates* progeny. Overall, these came to 299 *achates* and 244 non-*achates*, without a single crossover between *T* and *B*; thus the 95 % confidence limits are 0 to 0.6 % crossing over between the two loci. The data also suggest an excess of *achates* ( $P < 0.01$ ), suggesting that the non-*achates* have a selective disadvantage of about 18 % with 95 % confidence limits of 3 to 31 %.

A new *gerania*-like form (plate 1*l*), throws further light on the order of the loci in the super-gene. The phenotype of this insect is like that of *gerania* except that there is no subapical forewing patch and the epaulettes are white, not scarlet. The form must be excessively rare since we can find no description of it in the literature nor specimens in the British Museum (Natural History), the University Museum, Oxford, the Manchester Museum, nor the Rijksmuseum van Natuurlijke Historie, Leiden. It is therefore likely to have arisen either through a crossover or a new mutation. If it arose by a single mutation, then it must either have occurred in the super-gene producing *anceus* to modify the appearance of the hindwing, or must be altering the super-gene's effect on at least three characters. However, that controlling this new form could have been produced by a single crossover in a *gerania/anceus* heterozygote if the order of the loci is *TWFE<sup>v</sup>B<sup>v</sup>*. The heterozygote would have been genetically  $tW^gF^vE^sB^{v\dagger}/twFE^wB^v$  and the new chromosome derived by crossing over  $tW^gFE^wB^v$ , the crossover having occurred between the locus controlling hindwing pattern and those controlling forewing pattern.

Figure 1 shows one possible order of the loci and the minimum number of independent crossover events of which we have evidence, together with the limits within which the crossover must have occurred. Similar diagrams can be constructed for the other possible orders of the loci.

Thus although the order of all the elements has not yet been determined, they can almost certainly be separated by crossing over (see table 2) and *W* lies between *T* and *B*. Furthermore, apparently neither *W* nor *B* lies between *E* and *F* nor *T* between *E* and *W* or *E* and *B*.

#### 4. The possible origin of the polymorphic forms unique to Java and Sumatra

The genetic evidence suggests that *trochila* from Sumatra is very similar to both *esperi* from the Malay Peninsula and *laomedon* from Java and Borneo. It probably differs from *esperi* in

†  $W^g$  may be the same as  $W^v$  from Borneo.

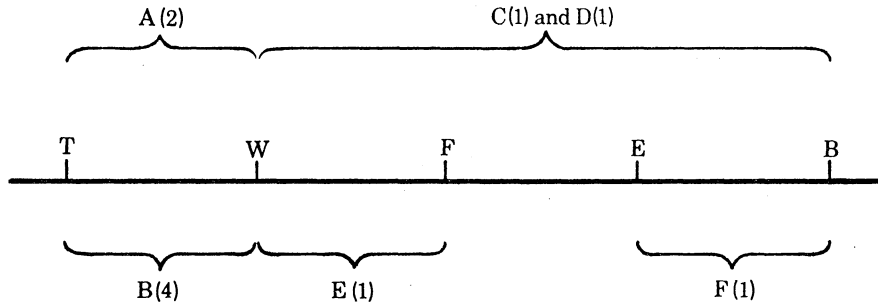


FIGURE 1. Diagram indicating by means of brackets the loci between which crossing over must have occurred if the very rare forms result from this phenomenon rather than from mutation. The particular form produced in each case is indicated by a letter and a number showing the minimum independent occasions on which it must have been produced by crossing over to account for the insects we know of. Note that A and B are reciprocal classes. A, *titania*; B, *anura*; C, *titania* Hong Kong; D, *ityla*; E, new *gerania*-like form; F, black-bodied *anceus*. Similar diagrams can be constructed for the other six possible orders of the genes, FTEWB, TEFWB, TFEWB, TWEFB, TWBEF and TWBFE which are still possible on our present data from rare forms. However, if the polymorphic forms *anceus* and *anceus* from Nias are taken into account then the only likely order is that given in the figure (see (c) below).

having a different allelomorph controlling the expression of the forewing subapical white patch. However, it may be identical with *laomedon* except for the presence of unlinked modifiers, particularly those controlling the amount of blue on the hindwings. Thus it could have arisen as a single mutation from the male-like form without subapical forewing patches ( $F \rightarrow F^i$ ). Since both the model, *Parides nox*, and the mimic are widespread, the place of origin of *laomedon* is likely to remain unknown.

(a) *f. isarcha*

This form is very similar to the allopatric *venusia* from Borneo, and the widespread non-mimetic *agenor*. However, genetic analysis has revealed that it probably differs from both at the locus controlling the pattern on the hindwing, *venusia* having the allelomorph  $W^v$ , *agenor*  $W$ , and *isarcha*  $W^i$ . It could not have arisen as a single mutation or crossover event from either *achates* or *laomedon*, which are the only common forms currently sympatric with it.

(b) *achates with orange epaulettes*

This mimic of *Parides coon* is only found in Java, South Sumatra, and some small off-shore islands. The super-gene differs from that controlling *achates* (*distantianus*) at the locus determining epaulette colour, where the allelomorph  $E^s$  has been replaced by  $E^w$ . This form could have arisen as the result of a single mutation at the locus  $E$ .

(c) *f. anceus*

This mimic of *Parides sycorax* could not have arisen as the result of a single mutation or crossover. It differs from the sympatric form *trochila* (*laomedon*) in three respects, the white epaulettes, the absence of a forewing subapical white patch, and the amount of yellow on the abdomen. All these characters are important in determining the mimetic resemblance. Consequently it is worth inquiring whether any single crossover could have produced a form which was a tolerable mimic of *P. sycorax* and which could subsequently be modified.

The genetic and morphological evidence shows that the form of *achates* found in Java is also present in South Sumatra. The genetic evidence also points to the conclusion that the part of

the super-gene controlling epaulette colour is the same in Java *achates* as in *anceus*. Thus the epaulette colour in the *achates/anceus* heterozygotes is indistinguishable from that in *achates* homozygotes. The actual colour was pale orange in our Java and Sumatra material but white, like the *anceus* homozygotes, in hybrids, showing that the allelomorphs are non-complementary. If the allelomorph  $E^w$  is common to South Sumatra *achates* and to *anceus*, then a single crossover in a *trochila (laomedon)/achates* heterozygote in this locality would produce a good mimic of *P. sycorax* if the order of the loci in the super-gene is *TWFEB* as suggested above. If this were the order the heterozygote would be  $TW^dFE^wB^Y/twF^lE^sb$  and a single crossover could produce the chromosome  $twFE^wB^Y$ . This chromosome in the homozygote would produce an insect which was like *anceus* except that it would have the yellow body typical of *achates*. A mutation or a crossover within the *B* locus converting  $B^Y$  to  $B^y$  would complete the transformation, as would the accumulation of linked modifiers. The same argument would apply if the order of the loci were *TWEFB*, *TWBEB* or *TWBEF* (see figure 1). Thus, if *anceus* and Java *achates* have the common allelomorph  $E^w$  it is likely that the *anceus* evolved from *achates* rather than the reverse since to produce *anceus* from other forms would require a number of steps, whereas to produce Java *achates* from *distantianus* would require just one mutation.

On the island of Nias in North-West Sumatra there is a form of *anceus* which has the white subapical forewing patch of *trochila*. If this form also arose as a single crossover then the possible orders of the loci in the super-gene are reduced to two, *TWFEB* or *TWBEB*. If the latter were the order, then one might expect more crossovers between *W* and *E* or *F* than between *W* and *B*. This appears not to be the case. The most likely order therefore is *TWFEB*. If our deductions are correct, then it is interesting to note that the three loci affecting wing pattern are situated next to each other. This raises the question of whether they may initially have arisen by duplication rather than by introduction from elsewhere within the genome.

We are extremely grateful to the following for sending or supplying us with living material of *Papilio memnon* and allied species from various areas:

- Dr Shigeru A. Ae, Nanzan University, Japan;
- Mr Yong Teik Chin and Mr Tho Yow Pong, Penang, W. Malaysia;
- Dr E. W. Diehl, Dolok Merangir, North Sumatra;
- Mrs W. Thelma T. P. Gunawardane and Mr P. B. Karunaratne, National Museum, Colombo, Ceylon;
- Mr O. H. U. Heathcote and Mr Stephen Kueh, Sarawak;
- Colonel and Mrs B. R. Johnston, formerly of Djakarta;
- Mr Lim Eng Leon, Singapore;
- Mr S. Limprasutr, Bangkok;
- Mr Nalliah Pandian, Selangor;
- Dr Somadikarta, Bogor, Indonesia;
- Mr V. G. Bennett, The British Council, Djakarta, Indonesia;
- Monsignor J. H. Soudant, s.c.j., Bishop of Palembang, Sumatra;
- Professor Ian Thornton, La Trobe University, Melbourne;
- Mr V. F. Wong, Sabah, East Malaysia;
- Mr K. K. Yeung and Mr Ah So, Hong Kong University.

We also wish to thank Mr J. K. Hulme, Director of Ness Gardens, University of Liverpool, and Mr J. S. Wright and Miss R. Lyon of Ness Gardens, for growing and caring for *Citrus*

plants; Mr J. A. Attaway, of the Florida Citrus Commission for sending *Citrus* leaves and many people for sending supplies of *Citrus* and of *Choisya ternata* in response to our appeals; also Mr M. D. L. Easton for dissecting out spermatophores.

We are greatly indebted to Dr Paul Freeman, Keeper of Entomology, British Museum, for allowing us access to the collections of *P. memnon*, and to Mr T. G. Howarth and Mr N. H. Bennett of the British Museum (Natural History) and Dr A. Diakonoff, Rijksmuseum van Natuurlijke Historie, Leiden, for much helpful advice about the specimens. In addition we would like to thank Mr A. Brindle for showing us the material in the Manchester Museum. We are also grateful to Mr D. J. Kidd, Liverpool University, for drawing the diagram; and to Mrs C. A. Clarke, Mrs A. C. L. Gill, Mrs W. Cross, Mrs J. Mills, Mrs V. Dodd, Mrs A. Williams, Mrs P. Thorpe and Mrs J. A. Qureshi for secretarial and general help.

Finally we are extremely grateful to Professor E. B. Ford, F.R.S., for many helpful discussions.

This work could not have been carried out without the most generous grants from the Nuffield Foundation and the Briggs-Bury bequest to the Department of Medicine, University of Liverpool.

## REFERENCES

- Baur, E. 1911 *Einführung in die experimentelle Vererbungslehre*, pp. 155–159. Berlin: Verlag von Gebrüder Borntraeger.
- Bovey, P. 1941 Contribution à l'étude génétique et biogéographique de *Zygaena ephialtes* (L.). *Rev. Suisse de Zool.* **48**, 1–90.
- Bovey, P. 1966 Le problème des formes oranges chez *Zygaena ephialtes* (L.). *Revue suisse Zool.* **73**, 193–218.
- Clarke, C. A. & Sheppard, P. M. 1956 Hand-pairing of butterflies. *Lepid. News* **10**, 47–53.
- Clarke, C. A. & Sheppard, P. M. 1960a The evolution of dominance under disruptive selection. *Heredity, Lond.* **14**, 73–87.
- Clarke, C. A. & Sheppard, P. M. 1960b Super-genes and mimicry. *Heredity, Lond.* **14**, 175–185.
- Clarke, C. A. & Sheppard, P. M. 1960c The evolution of mimicry in the butterfly *Papilio dardanus*. *Heredity, Lond.* **14**, 163–173.
- Clarke, C. A. & Sheppard, P. M. 1963 Interactions between major genes and polygenes in the determination of the mimetic patterns of *Papilio dardanus*. *Evolution* **17**, 404–413.
- Clarke, C. A., Clarke, F. M. M. & Sheppard, P. M. 1968 Mimicry in *Papilio memnon*, some breeding results from England *Malay. Nat. J.* **21**, 201–219.
- Clarke, C. A., Sheppard, P. M. & Thornton, I. W. B. 1968 The genetics of the mimetic butterfly *Papilio memnon* L. *Phil. Trans. Roy. Soc. Lond.* **254**, 37–89.
- Dryja, A. 1959 Badania nad polimorfizmem krasnika zmiennego (*Zygaena ephialtes* L.). *Panstwowe wydawnictwo naukowe. Warszawa*, pp. 1–402.
- Emsley, M. G. 1964 The geographical distribution of the colour-pattern components of *Heliconius erato* and *Heliconius melpomene* with genetical evidence for the systematic relationships between the two species. *Zoologica* **49**, 245–286.
- Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford University Press.
- Fisher, R. A. 1953 Population genetics. *Proc. R. Soc. Lond. B* **141**, 510–523.
- Ford, E. B. 1953 The genetics of polymorphism in the Lepidoptera. *Adv. Genet.* **5**, 43–87.
- Mather, K. 1955 Polymorphism as an outcome of disruptive selection. *Evolution* **9**, 52–61.
- de Meijere, J. C. H. 1910 Über Jacobsons Zuchtungsversuche bezüglich des Polymorphismus von *Papilio memnon* L. ♀ und über die Vererbung sekundärer Geschlechtsmerkmale. *Z. induct. Abstamm. u. VererbLehre* **3**, 161–181.
- O'Donald, P. 1968 Models of the evolution of dominance. *Proc. R. Soc. Lond.* **171**, 127–143.
- O'Donald, P. 1969 The selective coefficients that keep modifying genes in a population. *Genetics* **62**, 435–444.
- Sbordoni, V., Bullini, L. & Ragazzini, P. 1969 Mimetismo mülleriano in popolazioni Italiane di *Zygaena ephialtes* (L.) (Lepidoptera Zygaenidae). *Archo. zool. ital.* **54**, 181–214.
- Sheppard, P. M. 1953 Polymorphism, linkage and the blood groups. *Am. Nat.* **87**, 283–294.
- Sheppard, P. M. 1963 Some genetic studies of Müllerian mimics in butterflies of the genus *Heliconius*. *Zoologica* **48**, 145–154.
- Sheppard, P. M. 1969 Evolutionary genetics of animal populations: the study of natural populations. *Proc. XII Int. Congr. Genet.* **3**, 271–279.

- Turner, J. R. G. & Crane, J. 1962 The genetics of some polymorphic forms of the butterflies *Heliconius melpomene* Linnaeus and *H. erato* Linnaeus. I. Major genes. *Zoologica* **47**, 141-152.  
 Villalobos-Dominguez, C. & Villalobos, J. 1947 *Colour atlas*. Buenos Aires: E. L. Ateneo.

## APPENDIX

(1) *F. achates* described as having 'full dorsal line' has on the yellow abdomen a black dorsal line extending to the terminal segments. Those described as having a 'short dorsal line' have the black line missing on the last few segments.

(2) Where the colour of the shoulders in *f. achates* is mentioned this refers to the colour of the triangular patch at the base of the forewings, which are also referred to in the text as the 'epaulettes'. The colour is only mentioned when *achates* from Java or South Sumatra may be involved, otherwise the shoulders are red.

brood no.	mother	father	phenotype of offspring	
			males	females
8838	<i>anura</i> N. Borneo	Hong Kong	6	4 1 <i>anura-agenor</i> 3 <i>agenor-laomedon</i>
8920	<i>venusia</i> N. Borneo	Hong Kong	3	19 8 <i>venusia-agenor</i> 11 <i>anura-agenor</i>
8924	<i>laomedon</i> N. Borneo	8838	24	10 4 <i>agenor-like</i> 6 male-like
8940	<i>thunbergi</i> Japan	Hong Kong	9	4 <i>agenor-like</i>
8948	<i>venusia</i> Borneo	Borneo	24	17 5 <i>venusia</i> 12 <i>laomedon</i>
8957	male-like 8924	8920	38	18 9 <i>anura-like</i> 9 <i>agenor-like</i>
8969	<i>agenor-like</i> 8940	8940	10	7 1 <i>agenor</i> 1 <i>agenor-like</i> 4 <i>thunbergi</i> 1 unscorable
8979	<i>achates</i> orange shoulders, Java	Java	3	5 3 <i>achates</i> orange shoulders 2 <i>achates</i> white shoulders
8984	<i>agenor-like</i> 8940	8940	31	44 10 <i>agenor</i> 23 <i>agenor-like</i> 11 <i>thunbergi</i>
8990	<i>agenor-like</i> 8940	8940	10	6 2 <i>agenor</i> 1 <i>agenor-like</i> 3 unscorable
9012	<i>agenor</i> , big window, Java	Java	4	6 3 <i>achates</i> orange shoulders 3 <i>agenor</i> big window
9013	<i>achates</i> orange shoulders, Java	Hong Kong	15	5 <i>achates</i> orange shoulders
9014	<i>achates</i> orange shoulders, Java	Hong Kong	8	1 <i>achates</i> orange shoulders
9015	<i>achates</i> orange shoulders, Java	Hong Kong	4	3 2 <i>achates</i> red shoulders 1 <i>achates</i> orange shoulders
9023	<i>agenor</i> , big window, Java, 9012	N. Borneo 8948	12	7 3 <i>venusia-like</i> 4 <i>agenor-like</i> small window
9204	<i>agenor</i> Hong Kong	Java 9012	1	3 <i>agenor-like</i>
9039	<i>achates</i> white shoulders, Java 8979	8979	13	2 <i>achates</i> white shoulders
9040	<i>achates</i> orange shoulders, Java 8979	Thailand	24	12 8 <i>achates</i> orange shoulders 4 <i>agenor</i>
9044	<i>agenor</i> , big window, Java 9012	Java 8979	2	2 1 <i>agenor</i> big window 1 <i>agenor</i> small window
9045	<i>anura-like</i> 8957	Java 9012	34	21 11 <i>achates</i> orange shoulders 4 <i>anura-like</i> 6 <i>agenor-like</i>
9054	<i>thunbergi</i> Japan	N. Borneo 8948	31	14 7 <i>thunbergi-laomedon</i> 7 male-like

brood no.	mother	father	phenotype of offspring		
			males	females	
9055	<i>achates</i> orange shoulders, Java 8979	<i>parinda</i> Ceylon	4	4	3 <i>achates</i> orange shoulders 1 <i>agenor</i> -like big window
9082	<i>laomedon</i> 8963	9015	16	13	3 <i>achates</i> red shoulders 9 <i>achates</i> orange shoulders 1 <i>achates</i> unscorable for shoulders
9085	<i>achates</i> red shoulders, Java/Hong Kong 9015	9015 (same as 9082, 9089 and 9096)	7	5	3 <i>achates</i> red shoulders 2 <i>achates</i> orange shoulders
9089	<i>achates</i> orange shoulders, Java/Hong Kong 9014	9015	9	13	6 <i>achates</i> red shoulders 4 <i>achates</i> orange shoulders 1 <i>achates</i> white shoulders 2 <i>achates</i> unscorable for shoulders
9096	<i>achates</i> Java/Thai 9040	9015	26	22	6 <i>achates</i> red shoulders 11 <i>achates</i> orange shoulders 5 <i>achates</i> white shoulders
9101	<i>agenor</i> Hong Kong	9013	53	25	7 <i>achates</i> red shoulders 6 <i>achates</i> orange shoulders 2 <i>achates</i> unscorable for shoulders 10 <i>agenor</i> -like
9102	<i>agenor</i> Java, small window 9044	Japan	13	18	8 <i>agenor-thunbergi</i> -like 10 <i>thunbergi</i> -like
9109	<i>venusia</i> -like 9023	9023 (same as 9111)	14	13	12 <i>venusia</i> -like 1 <i>agenor</i> -like big window
9110	<i>agenor</i> -like 9023	9023	37	25	19 <i>agenor</i> -like 6 <i>laomedon</i> -like
9111	<i>agenor</i> -like 9023	9023 (same as 9109)	13	14	10 <i>venusia</i> -like 3 <i>agenor</i> large window 1 <i>agenor</i> small window with <i>laomedon</i> patch
9135	<i>achates</i> white shoulders 9039	9039	6	5	3 <i>achates</i> orange shoulders 2 <i>achates</i> white shoulders
9140	<i>agenor-laomedon</i> Java 9045	9045	13	11	10 <i>agenor</i> -like 1 male-like
9147C	<i>agenor</i> -like, big window, Hong Kong/Java 9024	<i>parinda</i> Ceylon	23	21	10 <i>agenor (isarcha)-parinda</i> 11 <i>agenor-parinda</i>
9147N	<i>thunbergi</i> Japan	9054	2	2	1 <i>thunbergi</i> -like 1 male-like
9161	<i>agenor</i> -like small window 9045	9045	6	7	4 <i>agenor</i> -like big window 2 <i>agenor</i> -like small window 1 male-like
9162	<i>agenor</i> -like big window 9045	9045	10	8	3 <i>anura</i> -like 4 <i>agenor</i> -like big window 1 <i>agenor</i> -like small window
9176	<i>agenor</i> 9101	Java 9039	17	17	1 <i>achates</i> red shoulders 9 <i>achates</i> orange-red shoulders 4 <i>agenor</i> -male-like 3 <i>agenor(isarcha)</i> -male-like
9179	<i>thunbergi/laomedon</i> 9054	Japan	10	19	8 <i>thunbergi</i> -like 3 <i>thunbergi-laomedon</i> 8 male-like
9186	<i>achates</i> red shoulders 9085	9102 (same as 9206)	13	13	<i>achates</i> red shoulders
9199	<i>achates</i> white shoulders 9096	9102	19	20	<i>achates</i> orange shoulders
9206	<i>achates</i> white shoulders 9096	9102 (same as 9186)	14	9	7 <i>achates</i> orange shoulders† 2 <i>achates</i> unscorable for shoulder colour

† Two were white distally.

brood no.	mother	father	phenotype of offspring	
			males	females
9272	<i>agenor</i> , small window, Java	Java 9135	7	5 <i>achates</i> orange shoulders
9477	<i>thunbergi</i> Japan	Thailand	17	20 11 <i>agenor-thunbergi</i> 4 <i>thunbergi-butlerianus</i> 5 <i>butlerianus</i> -like
9546	<i>butlerianus</i> -like 9477	9477 (same as 9551 and 9564)	9	9 2 <i>agenor</i> -like 2 <i>agenor-butlerianus</i> 5 <i>butlerianus</i> -like
9548	<i>butlerianus</i> -like 9477	9477	15	16 1 <i>thunbergi-butlerianus</i> 2 <i>butlerianus</i> 5 <i>butlerianus</i> -like 8 male-like†
9549	<i>butlerianus</i> -like 9477	9477	25	25 7 <i>agenor</i> -like 4 <i>agenor-butlerianus</i> 5 <i>thunbergi</i> -like 2 <i>thunbergi-butlerianus</i> 6 <i>butlerianus</i> -like 1 male-like†
9551	<i>thunbergi-butlerianus</i> 9477	9477 (same as 9546 and 9564)	13	7 1 <i>agenor</i> -like 3 <i>thunbergi</i> -like 3 <i>butlerianus</i> -like
9560	<i>agenor</i> -like 9477	9477	9	13 1 <i>agenor-thunbergi</i> 2 <i>agenor-butlerianus</i> 4 <i>thunbergi</i> -like 4 <i>thunbergi-butlerianus</i> 2 male-like†
9564	<i>thunbergi</i> Japan	9477 (same as 9546 and 9551)	11	10 7 <i>agenor</i> -like 3 <i>thunbergi</i> -like
9579	<i>thunbergi</i> Japan	Hong Kong	45	27 <i>agenor</i> -like
9583	<i>thunbergi</i> Japan	9477 (same as 9592)	33	25 5 <i>thunbergi</i> 7 <i>thunbergi</i> -like‡ 8 <i>thunbergi-butlerianus</i> 5 <i>butlerianus</i> -like
9592	<i>thunbergi</i> Japan	9477 (same as 9583)	45	45 11 <i>thunbergi</i> 8 <i>thunbergi</i> -like‡ 13 <i>thunbergi-butlerianus</i> 13 <i>butlerianus</i> -like
9671	<i>butlerianus</i> -like 9548	<i>parinda</i> Ceylon	16	11 6 <i>thunbergi-parinda</i> 5 <i>butlerianus-parinda</i> §
9672	male-like† 9548	<i>parinda</i> Ceylon	4	4 3 <i>butlerianus-parinda</i> § 1 unscorable
9682	male-like† 9548	<i>parinda</i> Ceylon	18	4 1 <i>thunbergi-parinda</i> 3 <i>butlerianus-parinda</i>
9690	<i>parinda</i> Ceylon	9579	11	9 6 <i>agenor-parinda</i> 3 <i>thunbergi-parinda</i>
9691	<i>agenor</i> -like 9564	<i>parinda</i> Ceylon	5	4 2 <i>agenor-parinda</i> 2 <i>thunbergi-parinda</i>
9709	<i>agenor</i> -like 9579	9579	0	2 1 <i>agenor</i> 1 <i>agenor</i> -like
9712	<i>agenor</i> -like 9579	9579	9	4 2 <i>agenor</i> 1 <i>agenor</i> -like 1 <i>thunbergi</i>
9713	<i>agenor</i> -like 9579	9579	25	30 6 <i>agenor</i> 16 <i>agenor</i> -like 8 <i>thunbergi</i>

† *Butlerianus* patch absent.

‡ They have a general suffusion of white on the forewing.

§ The *butlerianus* patch was absent in one.



brood no.	mother	father	phenotype of offspring	
			males	females
9717	<i>agenor</i> -like 9579	9579	9	11 5 <i>agenor</i> -like 5 <i>thunbergi</i> 1 unscorable
9752	<i>agenor</i> -like 9709	<i>parinda</i> Ceylon	7	7 4 <i>agenor-parinda</i> 3 <i>thunbergi-parinda</i>
9766	<i>thunbergi</i> 9713	<i>parinda</i> Ceylon	7	4 <i>thunbergi-parinda</i>
9771	<i>agenor</i> -like 9713	<i>parinda</i> Ceylon	3	1 <i>thunbergi-parinda</i>
9807	<i>anceus</i> N. Sumatra	Thailand (same as 9811)	21	14 9 <i>agenor-anceus</i> with black abdomen 4 <i>agenor-anceus</i> with end of abdomen yellow 1 unscorable
9811	<i>trochila</i> N. Sumatra	Thailand (same as 9807)	8	14 9 <i>agenor-trochila</i> (5 with yellow tip to abdomen 4 with all black abdomen) 5 <i>agenor-anceus</i> with yellow end to abdomen
9827	<i>agenor</i> 9713	N. Sumatra	7	7 <i>agenor-anceus</i>
9840	<i>achates</i> Thailand	N. Sumatra	16	6 3 <i>achates</i> -like 3 <i>agenor</i> -like with yellow end to abdomen
9920	<i>agenor</i> -like 9840	Thailand	1	4 <i>agenor</i> -like with yellow end to abdomen
9926	<i>trochila</i> N. Sumatra	N. Sumatra	16	7 4 <i>achates</i> red shoulders, full dorsal line 3 <i>trochila</i>
9930	<i>achates</i> N. Sumatra red-white shoulders	9811	10	5 1 <i>achates</i> -like, red shoulders, full dorsal line 2 <i>achates</i> -like, red-white shoulders, short dorsal line 1 <i>agenor-anceus</i> yellow end to abdomen 1 <i>anceus</i> -like
9965	<i>agenor-anceus</i> Thailand 9920	Thailand	13	6 2 <i>achates</i> -like, red shoulders, short dorsal line 2 <i>agenor</i> black abdomen 2 <i>agenor-anceus</i> yellow end to abdomen
9977	<i>trochila</i> N. Sumatra	Thailand	4	15 <i>achates</i>
9987	<i>agenor-anceus</i> 9930	9930	10	6 4 <i>agenor-anceus</i> 2 <i>anceus</i> -like
10018	<i>achates</i> red shoulders, full dorsal line 9926	Thailand	9	10 8 <i>achates</i> red shoulders, full dorsal line 2 <i>agenor-trochila</i>
10113	<i>achates</i> N. Sumatra, red-white shoulders full dorsal line	<i>parinda</i> Ceylon	4	2 1 <i>achates-parinda</i> 1 <i>anceus-parinda</i>
10127	<i>parinda</i> Ceylon	9977	13	11 5 <i>achates-parinda</i> 6 <i>trochila-parinda</i>
10128	<i>parinda</i> Ceylon	9977	6	5 2 <i>achates-parinda</i> 3 <i>trochila-parinda</i>
10132	<i>parinda</i> Ceylon	10018	24	17 8 <i>achates-parinda</i> 9 <i>trochila-parinda</i>
10160	<i>agenor-anceus</i> 9987	N. Sumatra	1	5 2 <i>agenor-trochila</i> 3 <i>trochila-anceus</i>
10251	<i>achates-parinda</i> 10127	<i>parinda</i> Ceylon	8	4 2 <i>achates-parinda</i> 2 <i>parinda</i> -like

brood no.	mother	father	phenotype of offspring	
			males	females
10267	<i>parinda</i> Ceylon	10132	13	11 3 <i>trochila-parinda</i> 8 male-like
10268	<i>achates</i> N. Sumatra	N. Sumatra (sib)	14	21 12 <i>achates</i> some with short dorsal line 9 <i>trochila</i> with big yellow end to abdomen
10275	<i>trochila-anceus</i> 10160	<i>parinda</i> Ceylon	9	16 6 <i>trochila-parinda</i> 10 <i>anceus-parinda</i>
10301	<i>achates</i> N. Sumatra	N. Sumatra	16	7 6 <i>achates</i> some with short dorsal line 1 <i>anceus</i>
10313	<i>achates</i> N. Sumatra	N. Sumatra	28	15 11 <i>achates</i> some with short dorsal line 4 <i>trochila</i>
10358	<i>achates-parinda</i> 10251	10275 (same as 10372)	19	17 6 <i>achates-anceus</i> 1 <i>achates-parinda</i> 6 <i>anceus-parinda</i> 4 <i>parinda</i> -like
10359	<i>trochila-parinda</i> 10275	<i>parinda</i> Ceylon	9	13 5 <i>trochila-parinda</i> 7 <i>parinda</i> -like 1 unscorable
10361	<i>anceus-parinda</i> 10275	Hong Kong	21	25 11 <i>agenor</i> -like 14 <i>agenor-anceus</i>
10367	<i>trochila-anceus</i> N. Sumatra 10268	Malaya	3	2 unscorable
10372	<i>agenor</i> Hong Kong	10275 (same as 10358)	16	6 2 <i>agenor-anceus</i> 4 <i>agenor-parinda</i>
10374	<i>trochila</i> , big yellow end to abdomen N. Sumatra 10268	<i>parinda</i> Ceylon	26	20 9 <i>trochila-parinda</i> 11 <i>anceus-parinda</i>
10383	<i>anceus-parinda</i> 10275	10275	10	9 3 <i>trochila-anceus</i> 3 <i>trochila-parinda</i> 3 <i>parinda</i> -like
10390	<i>trochila-parinda</i> 10275	<i>parinda</i> Ceylon	41	31 15 <i>trochila-parinda</i> 16 <i>parinda</i> -like
10393	<i>trochila</i> N. Sumatra	N. Sumatra	9	6 1 <i>achates-trochila</i> 3 <i>achates-anceus</i> 1 <i>trochila-anceus</i> 1 <i>anceus</i>
10416	<i>achates</i> , red-white shoulders, short dorsal line N. Sumatra	10267 (same as 10437)	18	14 8 <i>achates</i> 6 <i>anceus-parinda</i>
10417	<i>anceus</i> N. Sumatra	N. Sumatra	6	8 <i>achates</i> (see table 1)
10418	<i>achates</i> 10313	10313	12	13 <i>achates</i>
10437	<i>achates</i> , red shoulders, dorsal line not quite to end, N. Sumatra 10313	10267 (same as 10416)	11	12 <i>achates</i> -like
10439	<i>trochila</i> 10313	10313	8	8 4 <i>achates</i> 1 <i>trochila</i> 3 <i>anceus</i>
10458	<i>agenor-anceus</i> 10361	N. Borneo	1	1 <i>laomedon-anceus</i>
10470	<i>thunbergi</i> Japan	N. Sumatra 10393 (same as 10512)	7	1 <i>thunbergi-anceus</i>
10494	<i>trochila-anceus</i> N. Sumatra 10393	Malaya	13	11 3 <i>achates</i> 1 <i>achates-trochila</i> 1 <i>achates-anceus</i> 1 <i>butlerianus-trochila</i> 5 <i>butlerianus-anceus</i>
10506	<i>laomedon</i> N. Borneo	N. Borneo	10	4 <i>laomedon</i>
10510	<i>parinda</i> -like 10390	N. Sumatra	13	1 <i>anceus-parinda</i>

brood no.	mother	father	phenotype of offspring	
			males	females
10512	<i>parinda</i> -like 10383	10393	7	5 <i>anceus-parinda</i>
10513	<i>parinda</i> -like 10359	10367	13	14 7 <i>esperi-parinda</i> 7 <i>anceus-parinda</i>
10514	male-like 10390	<i>achates/anceus</i> N. Sumatra 10417	32	13 7 <i>achates-parinda</i> 6 <i>anceus-parinda</i>
10520	<i>anceus-parinda</i> 10416	<i>achates/anceus</i> N. Sumatra 10417	38	25 19 <i>achates</i> 2 <i>anceus</i> 4 <i>anceus-parinda</i>
10522	<i>trochila/anceus</i>	Singapore	8	3 1 <i>esperi</i> -like 1 <i>butlerianus-anceus</i> 1 <i>trochila</i> -like
10529	<i>anceus</i> N. Sumatra	<i>achates/anceus</i> N. Sumatra 10417	4	5 <i>achates-anceus</i>
10558	<i>achates</i> 10494	Borneo 10506	7	6 5 <i>achates</i> 1 <i>laomedon</i> -like
10564	<i>laomedon</i> 10506	10470	0	2 1 <i>thunbergi-laomedon</i> 1 <i>laomedon-anceus</i>
10573	<i>anceus-parinda</i> 10513	10506	9	5 4 <i>laomedon-parinda</i> 1 <i>anceus-parinda</i>
10574	<i>achates-parinda</i> 10514	<i>parinda</i> Ceylon	12	7 5 <i>achates-parinda</i> 2 <i>parinda</i> -like
10579	<i>esperi-parinda</i> 10513	10506	3	1 <i>esperi-laomedon</i>
10614	<i>esperi-parinda</i> 10513	<i>parinda</i> Ceylon	7	5 1 <i>esperi-parinda</i> 4 <i>parinda</i> -like
10616	<i>parinda</i> 10603	10494	2	2 <i>butlerianus-parinda</i>
10760	<i>anceus-parinda</i> 10510	Java	5	5 3 <i>achates-anceus</i> white shoulders 1 <i>agenor</i> -like 1 <i>agenor-anceus</i>
10764	<i>achates</i> Java orange shoulders	Java	15	14 10 <i>achates</i> orange shoulders 2 <i>achates</i> pale orange shoulders 1 <i>agenor</i> big window 1 <i>agenor-laomedon</i> (small window)
10765	<i>achates</i> Java orange shoulders	S. Sumatra	17	12 3 <i>achates</i> orange shoulders, full dorsal line 3 <i>achates</i> orange-white shoulders, full dorsal line 2 <i>achates</i> orange-white shoulders, short dorsal line 4 <i>agenor-anceus</i>
10805	<i>anceus</i> N. Sumatra	10765	30	25 23 <i>achates-anceus</i> white shoulders, short dorsal line 1 <i>achates</i> shoulders un- scorable, short dorsal line 1 <i>achates</i> shoulders and dorsal line unscorable
10806	<i>anceus</i> N. Sumatra	10765	4	4 1 <i>achates-anceus</i> white shoulders, short dorsal line 2 <i>anceus</i> 1 unscorable (not <i>achates</i> )
10815	<i>achates</i> 10764	10764	0	1 <i>agenor</i> small window
10821	<i>achates</i> orange shoulders 10765	Japan	4	4 2 <i>achates</i> red-orange shoulders, full dorsal line 2 <i>agenor</i> -like
10822	<i>achates</i> 10765 orange- white shoulders, short dorsal line	Japan	6	2 <i>thunbergi-anceus</i>

brood no.	mother	father	phenotype of offspring	
			males	females
10824	<i>achates</i> 10764 pale orange shoulders	Japan	2	2 1 <i>achates</i> red-orange shoulders, full dorsal line 1 <i>agenor</i> -like
10828	<i>agenor</i> 10764 small window	10764	17	12 7 <i>achates</i> orange shoulders 4 <i>agenor-laomedon</i> small window 1 <i>laomedon</i>
10836	<i>achates</i> 10765 orange shoulders, full dorsal line	S. Sumatra	5	4 2 <i>achates</i> orange shoulders, full dorsal line 2 <i>agenor-laomedon</i> small window
10838	<i>agenor-anceus</i> 10765	Japan	2	6 3 <i>agenor</i> -like 3 <i>thunbergi-anceus</i> †
10842	<i>achates</i> 10760 white shoulders, short dorsal line	Japan	9	10 4 <i>achates</i> -like orange-red shoulders, full dorsal line 6 <i>thunbergi-anceus</i> ‡
10847	<i>achates</i> 10760 white shoulders, short dorsal line	Japan	12	14 10 <i>achates</i> -like orange-red shoulders, full dorsal line 4 <i>thunbergi-anceus</i> §

† 1 with shoulders yellow distally.

‡ 3 with white and 1 with yellow shoulders distally.

§ 3 with white shoulders distally, 1 unscorable for shoulders.





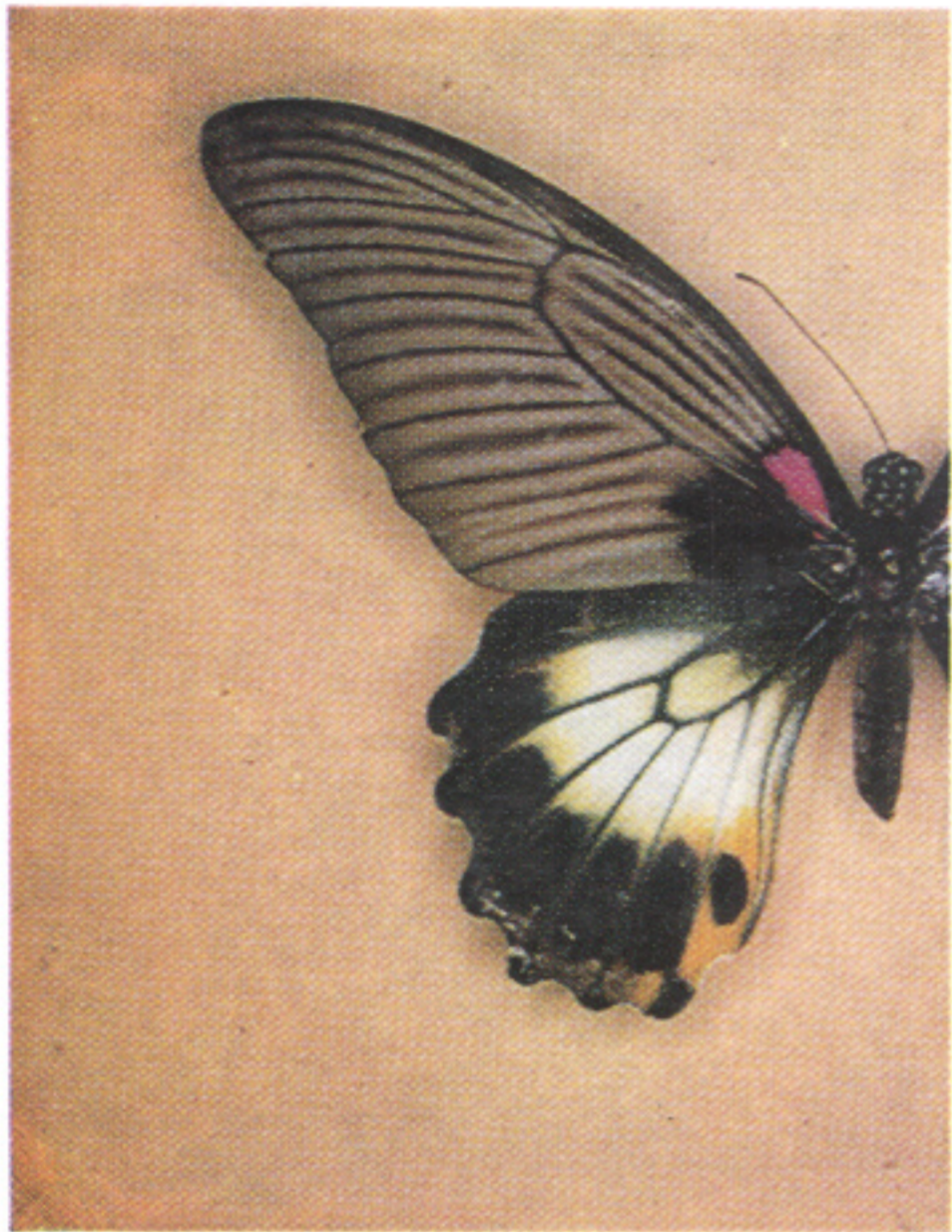
*a*



*b*



*c*



*d*



*e*



*f*



*g*



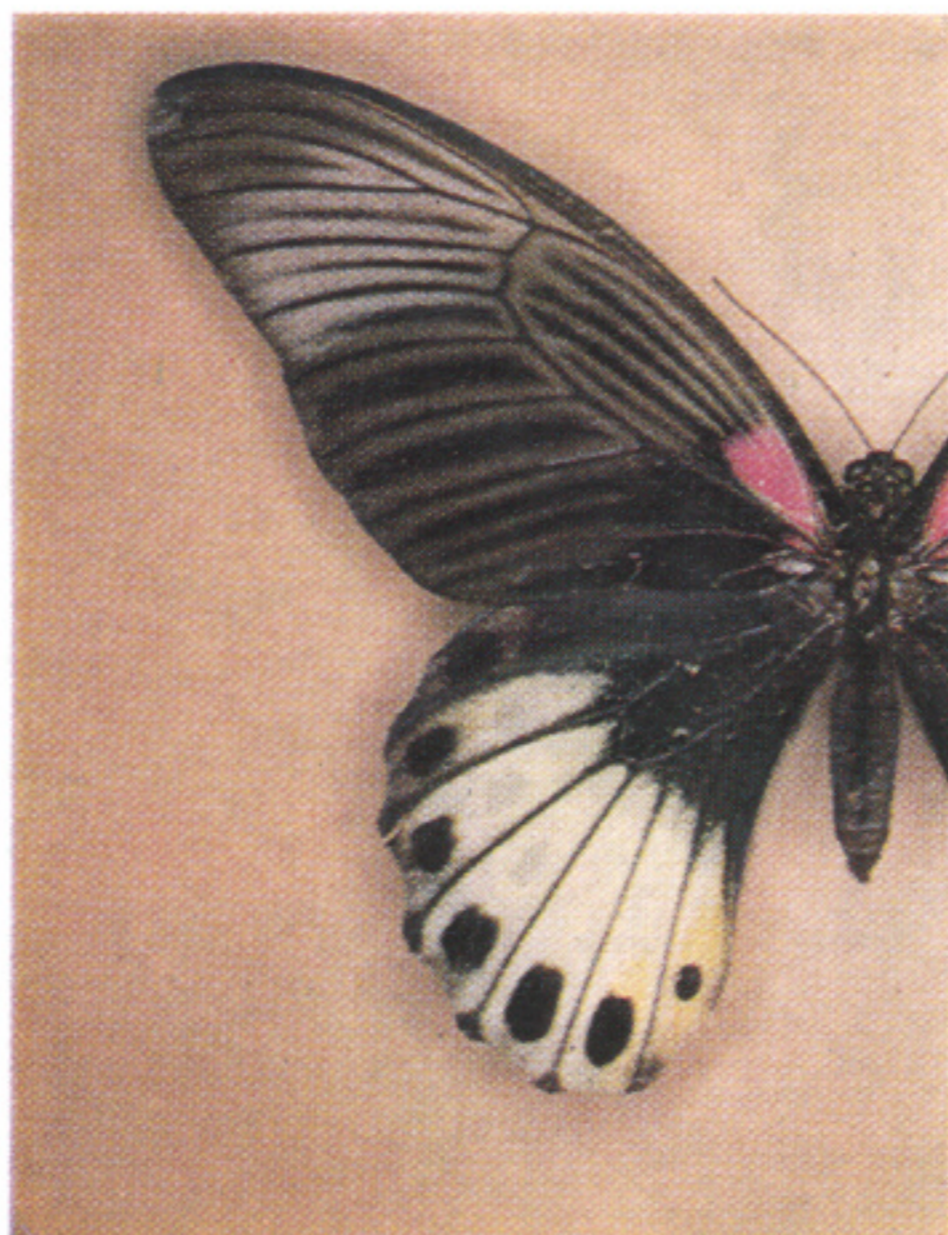
*h*



*i*



*j*



*k*



*l*

PLATE 1. For legend see facing page





*a*



*b*



*c*



*d*



*e*



*f*



*g*



*h*



*i*



*j*



*k*



*l*

PLATE 2. For legend see facing page





*a*



*b*



*c*



*d*



*e*



*f*



*g*



*h*



*i*



*j*



*k*



*l*

PLATE 3. For legend see facing page





*a*



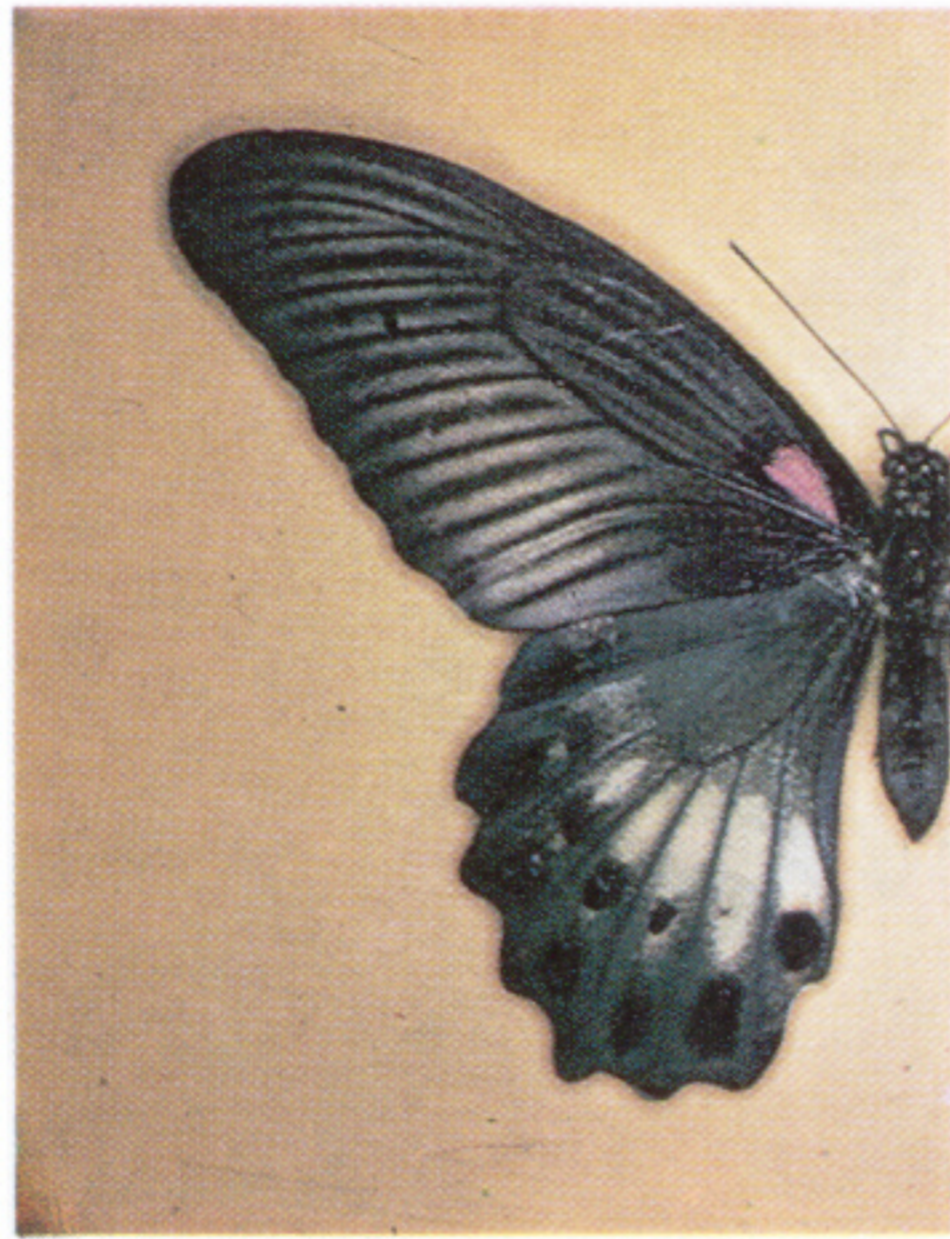
*b*



*c*



*d*



*e*



*f*



*g*



*h*



*i*



*j*



*k*



*l*

PLATE 4. For legend see facing page