THE GENETICS OF THE MIMETIC BUTTERFLY *PAPILIO MEMNON* L.

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[Plates 5 to 9]

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Papilio memnon is a swallowtail butterfly widely distributed in south-east Asia. The females are highly polymorphic and many of them are mimetic. The mode of inheritance of seventeen of the female forms is reported. In contradistinction to earlier work it has been shown that they are controlled by what appears to be a series of at least eleven autosomal alleles at one locus, sex-controlled to the female in effect. There is evidence, however, that the locus is complex, comprising at least three closely linked loci with occasional occurrence of crossing over between them. Two characters which are not polymorphic and one which may be polymorphic are controlled by genes unlinked to the complex locus (the super-gene).

In general, dominance is complete between sympatric forms but absent when they are allopatric. The resemblance between the mimetic forms of *P. memnon* and their models is greater in the gene-complex of a race in which the allelomorph occurs than in hybrids with a race in which it does not. Thus in no case is the resemblance better in the race cross, in ten cases there is no change and in thirty-five the mimicry is less good.

The genetic control of the polymorphism in *P. memnon* shows remarkable parallels with that in *P. dardanus* and provides further supporting evidence for Fisher's and Ford's view that mimicry evolved gradually by adjustment of the gene-complex as a result of natural selection favouring those wing patterns which most closely resembled the models. Furthermore, as in *P. dardanus*, the mimicry is controlled by what appears to be a super-gene, adding weight to the conclusion that the genetic control of the polymorphic Batesian mimicry has evolved gradually by the accumulation of closely linked allelomorphs in advantageous combinations. This contrasts with the genetic control of Müllerian mimicry as evidenced in the Heliconids.

In *P. memnon* the dominance relationships of the monomorphic tailed and tailless condition (excluding the form *achates*) indicate that dominance can be evolved even when the characters concerned are not polymorphic. In addition, the lower frequency of dominance between allopatric forms than between sympatric ones is strongly in favour of the view that dominance has evolved. Similar evidence has been found from breeding work in the Heliconids and in *P. dardanus*; however, the phenomenon is not confined to mimetic situations since there is also evidence for the evolution of dominance in other polymorphisms including industrial melanism.

I. Introduction

The theory of mimicry has received considerable support from field and laboratory work in recent years (see Brower, Brower & Collins 1963; Clarke & Sheppard 1962), and in the present paper we report some observations on *Papilio memnon* Linnaeus, the investigations being comparable with our earlier work on *P. dardanus* Brown.

Because of the highly polymorphic situation in *memnon*, it seemed to us that it would be very suitable for investigating the validity of our earlier conclusions on the evolution of mimicry in a species from a different area and mimicking entirely different groups of models.

P. memnon comprises a group of butterflies which extends from India and Ceylon in the west to the Philippines and the Moluccas in the east. To the north it flies as far as the south of Japan and to the south as far as Java (figure 1). The males are tailless, monomorphic and non-mimetic in all areas except in Palawan and the Celebes where they are tailed. In Japan the females are also monomorphic, tailless and non-mimetic (though unlike the males). *P. polymnestor* Cramer from Ceylon and India (a species very closely related to *P. memnon*) is also non-mimetic and here the females resemble the males more closely.

In other areas the females of *P. memnon* are either mimetic, or if non-mimetic forms occur, the species is polymorphic. The tailed individuals resemble various forms of *Parides coon* (Fabricius), *Pachlioptera aristolochiae* (Fabricius) or *P. polyphontes* (Boisduval), and the tailless ones are either non-mimetic or mimic other unpalatable aristolochian swallowtails where these occur. The resemblance in the colour patterns between model and mimic is often quite striking. However, the mimic shows a tendency to be larger than the model, as it does in *P. dardanus*. It is interesting to note that *P. memnon* has consistently failed to evolve the red markings on the body so characteristic of the models. Those on the abdomen of many models are represented by red on the inner margin of the hindwing of the mimic. Many of the models have either red, yellow or white on the thorax. This is mimicked in *P. memnon* by triangular coloured patches at the base of the forewing. Thus in most of the mimics these triangular patches are red, corresponding to red marks on the thorax of the model, but in *anceus* (plate 5, *l*) they are brilliant white and in *achates* from Java (plate 5, *d*) they are usually yellow, in both cases corresponding to similar patches on the thorax of the models. In some models red is absent and then the red triangular patches of *memnon* are often reduced or absent, as they are in the non-mimetic males of this species.

The various forms which we have investigated, their localities and their frequencies and models where known, are described below. Figures 2 to 7 give the distribution of the mimetic and non-mimetic forms we have studied together with that of their models. The nomenclature used in this paper is that given by Munroe (1961).

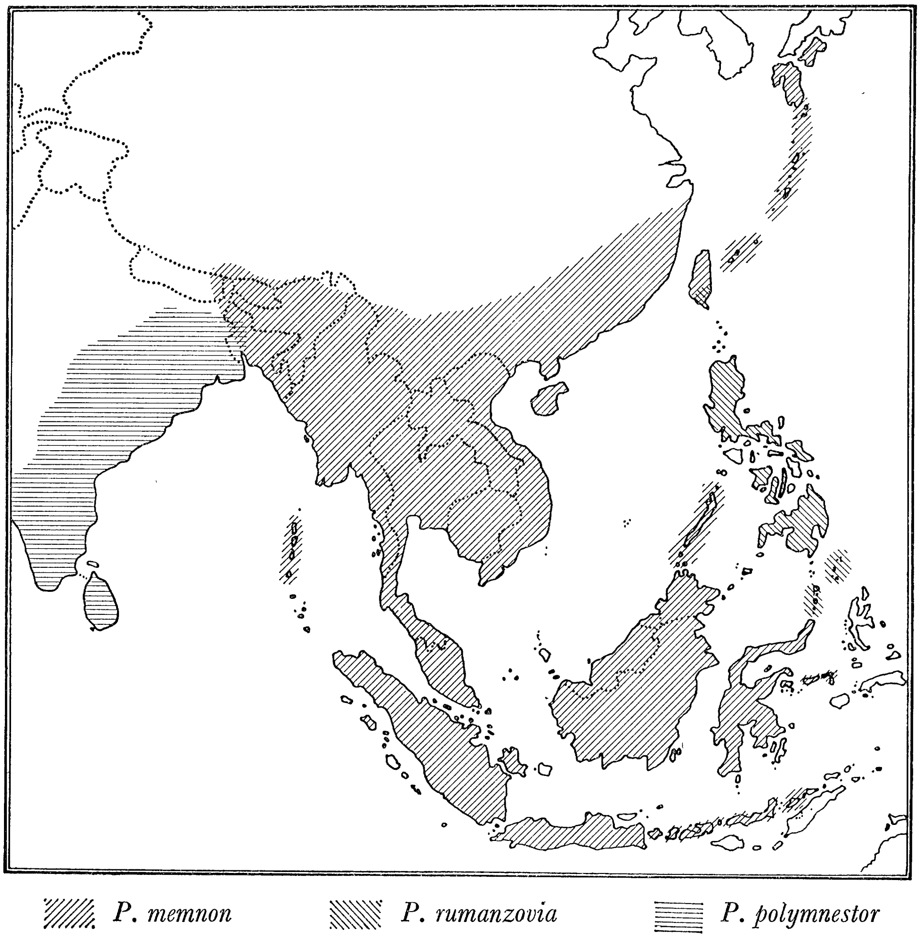


FIGURE 1. Sketch map showing distribution of three species of the *memnon* group of *Papilio*.

II. MATERIALS AND METHODS

Eggs, larvae or pupae or the living butterflies of *P. memnon* and of the allied species *P. polymnestor parinda* and *P. rumanzovia* Eschscholtz have been sent to us by air mail from various localities. When living butterflies have been sent, they have been put into Polythene envelopes with their wings folded back, and packed in expanded polystyrene ice-cream boxes which are light and provide good insulation against extremes of heat or cold. The *memnon* we have used in our work have come from Thailand, Kuala Lumpur, Singapore, Hong Kong, Java, Japan, northern Borneo, Palawan (Philippines) and Taiwan (Formosa). The *P. polymnestor parinda* came from Ceylon and the *P. rumanzovia* from the Philippines. Random samples, where they have been obtained, consisted of collections of wild caught butterflies or larvae (see table 1). We compared our bred material, and also the information on the distribution of some of the forms we obtained, with museum specimens and the

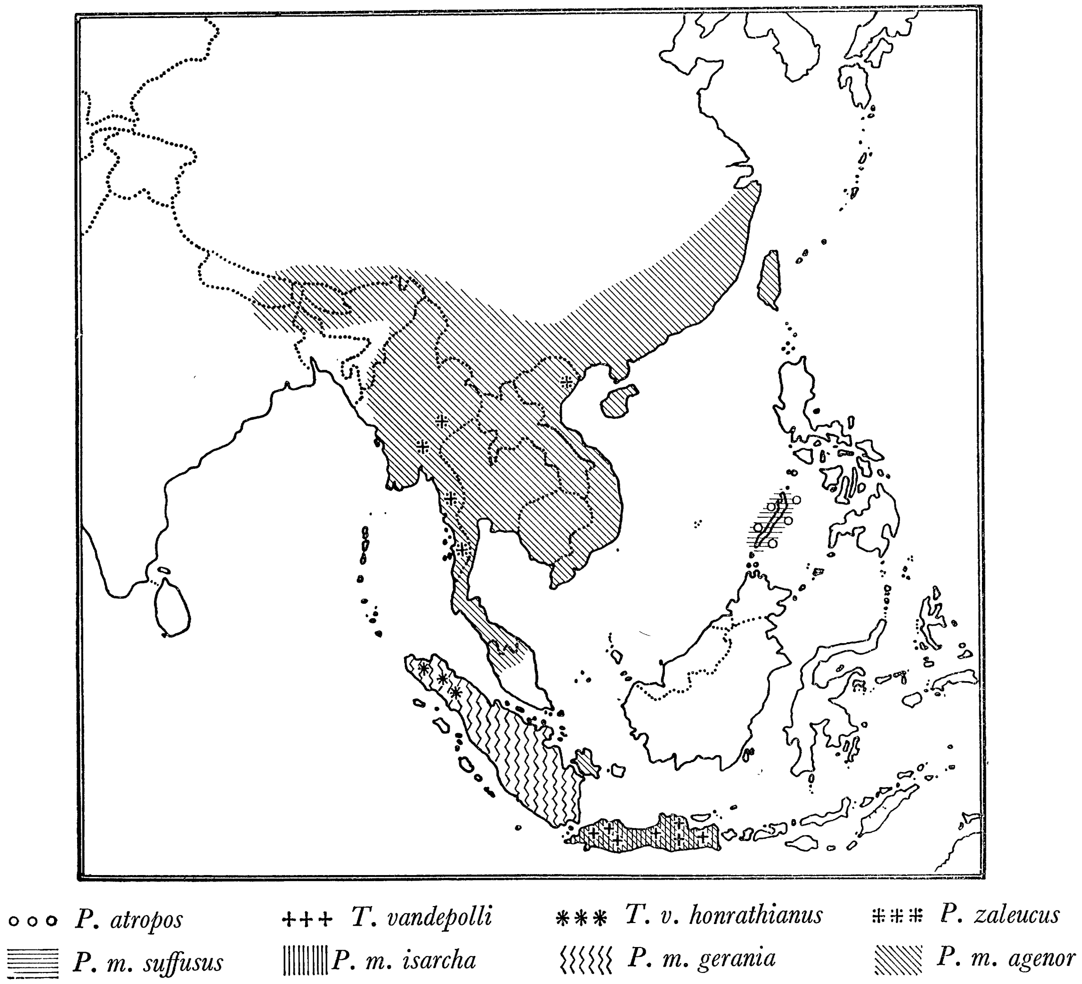


FIGURE 2. Sketch map shows the distribution of the models *P. atropos*, *T. vandepolli*, *T. v. honrathianus* and *P. zaleucus* and their respective mimics, f. *suffusus*, f. *isarcha*, f. *gerania* and f. *agenor*. The mimic is found only within the range of distribution of the model except for *agenor* and possibly *gerania*. *Agenor* is non-mimetic in most areas but may be a mimic where *P. zaleucus* is found.

TABLE 1. *P. MEMNON*. DISTRIBUTION OF THE FEMALE FORMS: RANDOM SAMPLES

locality	random samples	female forms (%)
Hong Kong (I.W.B.T.)	10 *achates*	23·3
	33 *agenor*	76·7
Thailand (Wang Takrai, 100 miles N.E. of Bangkok) (Limprasutr)	21 *achates*	70·0
	9 *agenor*	30·0
Kuala Lumpur (Corbet & Pendlebury, 1956) (taken by Corbet)	10 *achates*	47·6
	9 *esperi*	42·8
	2 *butlerianus*	9·5
Palawan (Philippines) (I.W.B.T. and P.M.S.)	11 *zephyria*	40·7
	16 *suffusus*	59·3
Ranau (Northern Borneo) (Conway)	3 *venusia*	20·0
	10 *laomedon*	66·7
	2 *anura*	13·3

descriptions given in various standard works (Rothschild 1895; Seitz 1908; Corbet & Pendlebury 1956).

On arrival in this country, the insects were reared in heated greenhouses and the food plant was usually *Citrus* though the larvae will eat *Choisya ternata.* All matings in the laboratory were carried out by the hand-pairing technique (Clarke & Sheppard 1956) and the breeding procedure was similar to that used for *P. dardanus.*

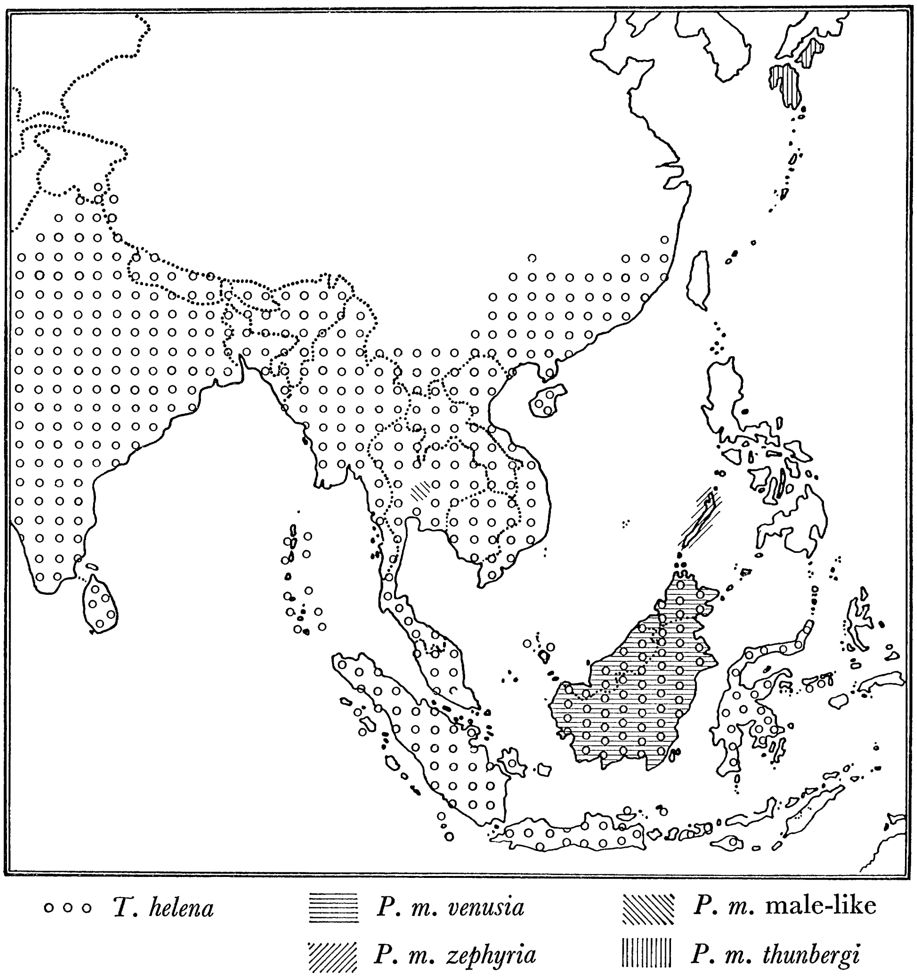


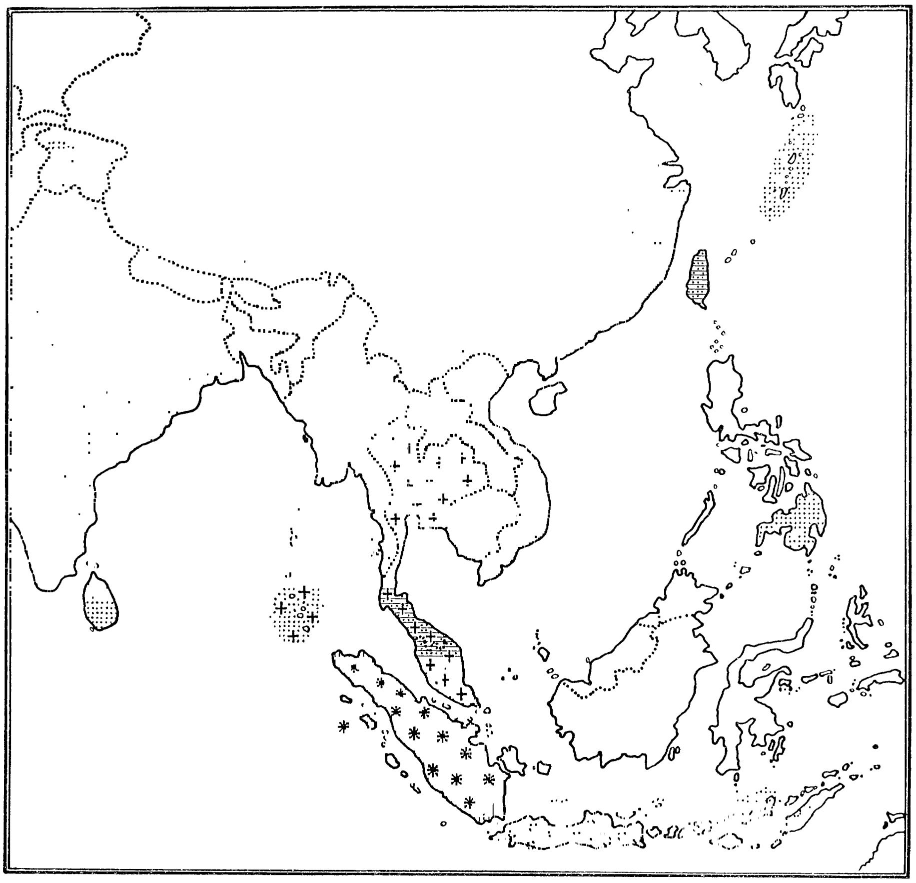
Figure 3. Sketch map showing the distribution of *T. helena* and its mimic f. *venusia.* The mimic is found only within the range of distribution of the model. It is important to note that f. *zephyria,* controlled by the same major gene as *venusia,* has a different pattern and is found outside the range of the model. The presence of the male-like form in Thailand and the distribution of f. *thunbergi* are also indicated.

III. Description of the female forms used in our work

(For frequencies see table 1)

1. *P. memnon* f. *achates* (plate 5 and figure 4)

Typically the insect has dark forewings, with a red triangular mark at the base. It has dark hindwings with a number of white spots in the cell and round it (called in this paper the 'window'). It also has red at the anal angle of the hindwing which may extend on to the margin of the wings. It has a characteristic swallow tail on the hindwings and the body is yellow laterally with a black dorsal stripe. It mimics *P. coon* and *P. aristolochiae* (plate 5 *a*, *b*, *c* and figure 4). There are modifications in the different areas where it occurs, the most important from the present point of view being in the size and distribution of the white spots on the hindwing forming the 'window'. Thus in Hong Kong there are two forms; in one, which we are calling *distantianus* (plate 5*e*), the white spot in the cell is large and those outside the cell do not extend far towards the margin of the wing. The other, *alcanor* (plate 5*f*), has little or no white in the cell and the white spots outside it extend much further towards the margin, the pattern thus approaching that of *agenor* (see below).



+ + + *P. coon* (red form)
∗∗∗ *P. coon* (orange form)
o o o *P. coon* (yellow form)
▦ *P. aristolochiae* (white form)
|||| *P. m. achates* (orange form)
▧ *P. m. achates* (yellow form)
▤ *P. m. achates* (red forms)

FIGURE 4. Sketch map shows the distribution of the red form of *P. coon* and that of the white form of *P. aristolochiae*, together with their mimic, f. *achates*. The range of the orange form of *P. coon* and of the yellow one and their respective mimics (the orange and the yellow f. *achates*) are also given. As with most other mimics, they are confined to areas within the range of their models.

Moreover, there are other variable characters. The yellow body is suffused with black in Hong Kong, in the Andamans and also in the Sikkim area. The pale marks on the hindwing border are more yellow in Thailand than in Hong Kong, where red predominates, and in the Andamans they are extended to form a border and are strikingly redder than in Hong Kong. In Taiwan these spots are absent and in Java (plate 5*d*) they are yellow, as are the basal triangles on the forewing. The colour of the spots on the hindwing follows the local variation of the models. In spite of these differences, the insect essentially looks the same from wherever we have investigated it and we have therefore, except where it has been necessary to distinguish between *distantianus* and *alcanor*, called it *achates*.

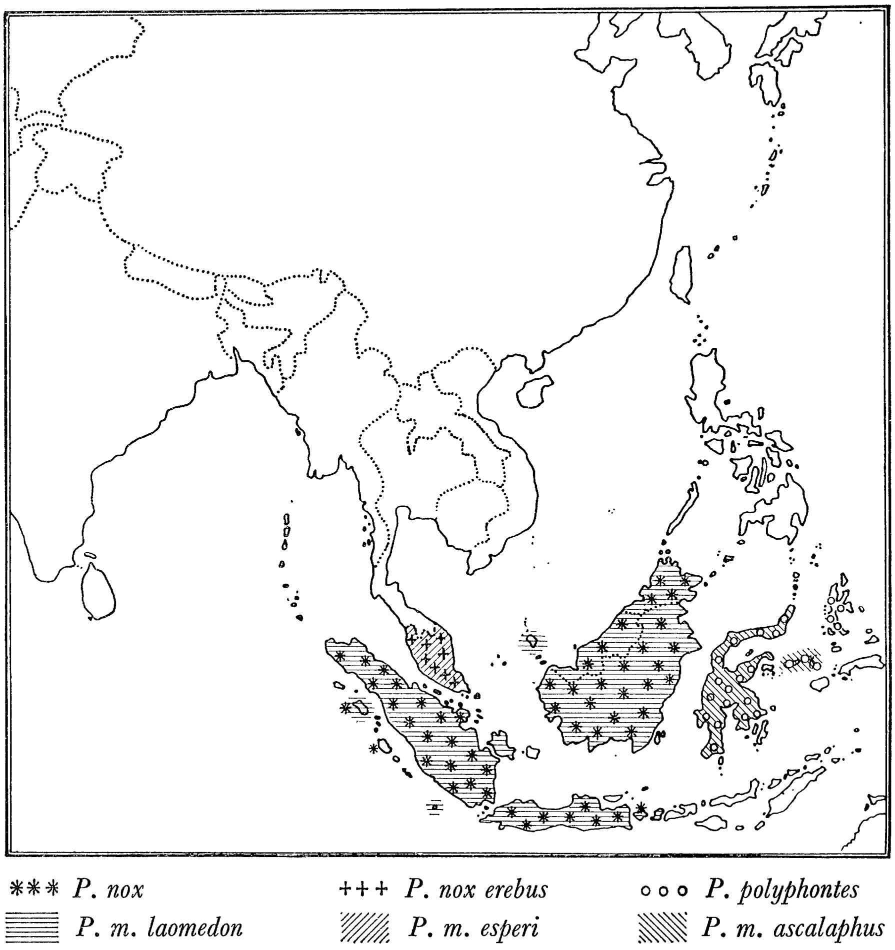


FIGURE 5. Sketch map shows the distribution of *P. polyphontes* and its mimic f. *ascalaphus* as well as the distribution of the variable model *P. nox* and its corresponding mimics.

In the Malay Peninsula both the model (*P. nox* ssp. *erebus*) and the mimic (*P. memnon* f. *esperi*) always have a clear subapical forewing patch. Elsewhere *nox* varies from district to district and often has two sympatric forms of female, one with a light subapical patch on the forewing and one without. This variation is followed by the mimic. In Borneo the female of *nox* is brown, and one form (*noctis*) has a double row of dark spots on the hindwing margin and is a very good model for the Borneo *laomedon*. Throughout Borneo both types of female occur in both *nox* and *laomedon*, and in both species the clearest forewing patches are seen in insects from the south. Another female form of *P. memnon*, f. *gyrtia*, from Banjermasin in southern Borneo, has a patch almost as white as that of *esperi*, and *nox* from that area (*banjermasinus*) also has a very white patch.

In Java and Sumatra the two types of forewing also occur in *nox* and in *memnon*, in Java the mimic being f. *laomedon* (variable, as in Borneo) and in Sumatra f. *trochila* and f. *erebinus* (both *laomedon*-like with variable *esperi*-like patches and treated as *laomedon* in the figure.) The ground colour of the model also varies from area to area, being blue-black in the Malay Peninsula for instance, and this too is closely followed by the mimics.

2. f. ***agenor*** (plate 9*d* and figure 2)

The forewing is similar to that of *achates* although more variable, particularly with respect to the paleness of the ground colour in Hong Kong (see p. 68). The hindwing is black with elongated white spots between the veins distal to the end of the cell (again referred to in this paper as the 'window') to near the hindwing margin. There is a submarginal row of black spots variable in size and the margin itself is either black or grey with black dots at the end of the nervures. There is a variable amount of red at the anal angle of the hindwing. The body is black. The form is tailless, usually non-mimetic and we have investigated it from Hong Kong, Thailand and Taiwan where it flies with *achates*. In Java it is also present (Jacobson 1909, 1910). *Agenor* is essentially the same in all these localities though the black hindwing border is interrupted by a row of yellow spots in Thailand which are reduced or not present in Hong Kong and Taiwan. Furthermore, in Java the hindwing is suffused with yellow.

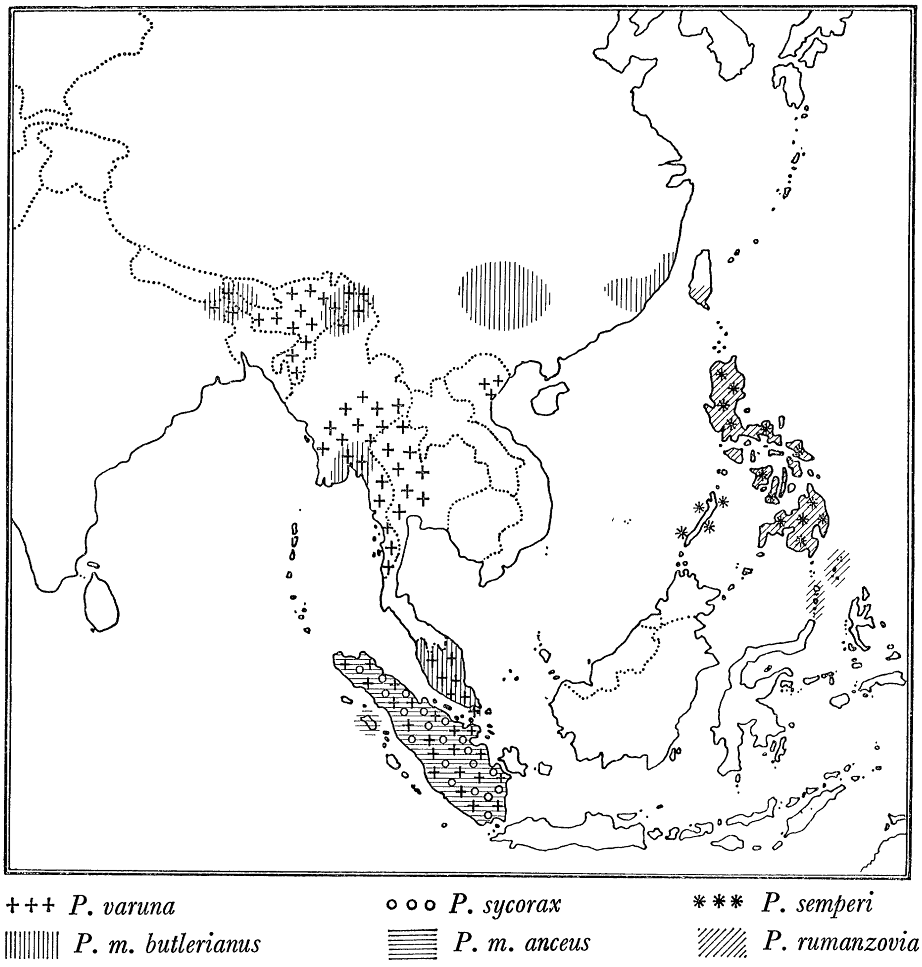


FIGURE 6. Sketch map shows the distribution of *P. varuna*, *P. sycorax* amd *P. semperi* and their corresponding mimics f. *butlerianus*, f. *anceus* and *P. rumanzovia* f. *semperinus*. F. *semperinus* has a range that extends outside that of its model but at least in Taiwan is a great rarity. F. *butlerianus* is mainly confined within the distribution of its model but is also reported from areas in South China where the model is not known to occur.

3. f. *thunbergi* (plate 9*c*,*f* and figure 3)

The female resembles a very dark *agenor* but the 'window' is much reduced in size, the white spots being farther from the end of the cell and the black marginal border and the black veins broader. Thus the black invades the spots from all directions. The body also is black. The forewing is either very black or in some specimens has a whiteish patch in the region of the inner margin of the forewing, extending upwards to about nervure 2, as in *butlerianus* (see below). In Japan *P. memnon* is at the edge of its range and f. *thunbergi* occurs only in the southern islands. The female is monomorphic, non-mimetic and tailless, but may be polymorphic with respect to the patch of white on the forewing.

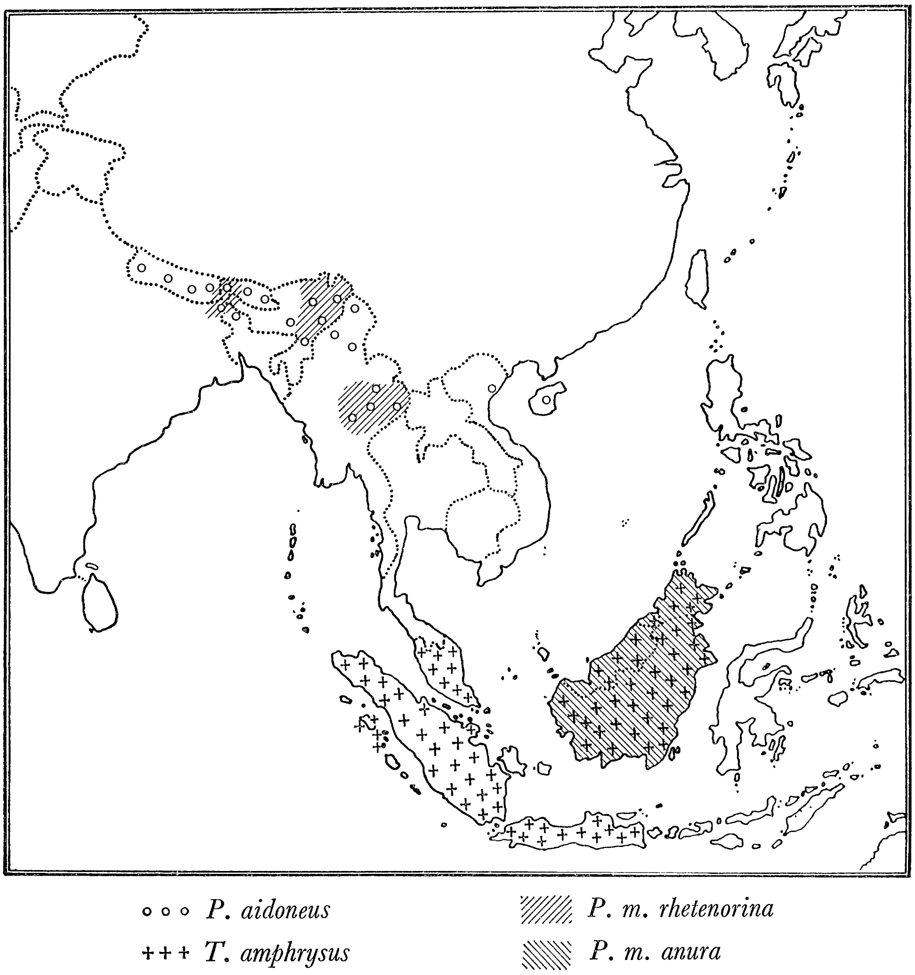


Figure 7. Sketch map shows the distribution of *P. aidoneus* and *T. amphrysus* and their respective mimics f. *rhetenorina* and f. *anura*. Again, the mimics are confined to within the range of their models. In Borneo, besides *T. amphrysus flavicollis*, *T. mirandus*, *T. andromache andromache* and *T. a. makropokensis* also act as models.

4. f. *esperi* (plate 6*f* and figure 5)

The forewings are like those of *achates* (but tend to be darker) except that there is a large white subapical patch which varies in size. The hindwings are black and liberally suffused with blue scales, being very similar to the males. The red at the anal angle of the hindwing is reduced (compared with *butlerianus*) or absent. The form is tailless and the body black. It occurs in the Malay Peninsula and is a mimic of the local subspecies of *Parides nox* (Swainson) (plate 6*c* and figure 5).

5. f. ***butlerianus*** (plate 6*e* and figure 6)

This form closely resembles *esperi* except that it has no white subapical patch, but it does have a white area in the region of the inner margin of the forewing extending upwards to about nervure 2. The intensity of the white varies and it has a less distinct outline than the patch of *esperi*. The hindwings closely resemble those of *esperi* but have more red at the anal angle. The body is black. The form occurs from North India to Malacca and mimics *Parides varuna* (White) (plate 6*b* and figure 6).

6. f. ***venusia*** (plate 5*j* and figure 3)

The forewings are similar to *achates* except that they are paleish grey becoming black only at the base. The hindwings are pale yellow becoming darker towards the hindwing border. There is a small area of black at the base of the hindwing, the veins are black with a small black dot at their distal ends and there is a submarginal row of black spots between the veins. It is tailless. The body is yellow as in *achates* with a dorsal black stripe. The form occurs in northern Borneo and is a mimic of *Troides helena* (Linnaeus) (plate 5*g* and figure 3).

7. f. ***zephyria*** (plate 8*b* and figure 3)

The forewings are a pale grey with a distinct black patch at the base. The distribution of pigment on the hindwings is very similar to that of *venusia* except that the pale yellow area is white and the more distal dark yellow is replaced by pale yellow. The submarginal black spots tend to combine to form a black band and the body of the insect is black with a yellowish tip to the abdomen. It has tails. It flies in Palawan (Philippines) and is non-mimetic.

8. f. ***anura*** (plate 5*k* and figure 7)

The forewings are as in f. *venusia*. The hindwings are tailless, black at the base merging to grey, with yellow spots in the cell and just distal to it, merging to orange yellow away from the cell, the distribution of these being very similar to that in *achates* (*distantianus*). The veins are black and between them there is a submarginal row of black spots. The body is yellow with a dorsal black stripe. (The insect resembles a tailless *achates* though it is much more orange.) It flies in northern Borneo and is a mimic of *Troides amphrysus* (Cramer) (plate 5*h* and figure 7) and perhaps also of *T. mirandus* (Butler) and *T. andromache* (Staudinger), though it is a better mimic of the first, more common insect.

9. The male-like forms

(*a*) f. *suffusus* (plate 6*l* and figure 2)

The forewings are like those of *zephyria* (plate 8*b*) which flies with it. The hindwings are dark, being black at the base and becoming grey towards the margin. Between the veins there are two rows of black spots, the outer one being homologous to that present in *achates*. There are yellowish spots at the anal angle and between the veins on the hindwing border. There is also a faint scattering of blue scales on the hindwing. The body is black with a yellow anal tip. The insect is tailed and may be a mimic of *Pachlioptera atropos* (Staudinger) (plate 6*i* and figure 2) and of the black *P. aristolochiae*. It flies in Palawan (Philippines).

(*b*) f. *laomedon* (plate 6*k* and figure 5)

The forewings are greyish brown, becoming black at the base of the wing, with some variable white in the subapical area reminiscent of, but much less extreme than, the white in *esperi*. The hindwings are a similar greyish brown to the forewings, becoming black at the base. There are two rows of black dots between the veins (as in *suffusus*) with the inner row much reduced or absent. There are yellow spots on the border of the hindwing, particularly at the anal angle. The form is tailless and the body black. Some specimens have yellow scales on the last two segments of the abdomen. The insect is particularly variable in the shade of the ground colour, the size of the spots and distinctness of the subapical pale area. It flies in Java and in northern Borneo, mimicking the local forms of *P. nox* (plate 6*h* and figure 5).

(*c*) f. *rhetenorina* (plate 9*e* and figure 7)

This form resembles *laomedon* except that it has no white near the apex of the forewing and the ground colour of the insect is much darker. There is also blue scaling on the hindwing and the rows of black spots are absent. Of all the male-like female forms of *memnon*, this resembles the male more than any other but still has a pattern recognizably distinct

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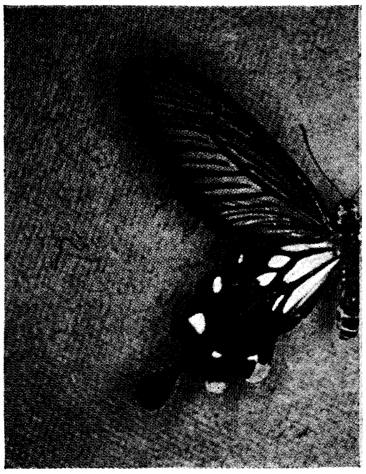
DESCRIPTION OF PLATE 5

Some models and the forms of *P. memnon* which mimic them. In the plate each mimic is placed below its appropriate model.

(*a*) *P. coon* ♀, yellow form from Java.
(*b*) *P. coon* ♀, red form from Malay Peninsula.
(*c*) *P. aristolochiae* ♂, white form.
(*d*) *P. m.* f. *achates*, yellow form from Java.
(*e*) *P. m.* f. *achates* (*distantianus*).
(*f*) *P. m.* f. *achates* (*alcanor*).
(*g*) *T. helena* ♀.
(*h*) *T. amphrysus* ♀.
(*i*) *P. sycorax* ♀.
(*j*) *P. m.* f. *venusia*.
(*k*) *P. m.* f. *anura*.
(*l*) *P. m.* f. *anceus*.

The plate demonstrates not only the general resemblance between model and mimic but also the way in which the details of the mimetic pattern follow those of the local model. For example, *achates* in (*d*) and (*e*) differ from one another in much the same way as *coon* in (*a*) and (*b*). Furthermore, the plate also shows that though the model and mimic are similar, the same overall effect is achieved in different ways. Thus the yellow on the thorax of *coon* (*a*) is mimicked by yellow at the base of the forewing in *achates* (*d*). Similarly, red on the thorax and abdomen of some of the other models is mimicked by red at the base of the forewing and the anal angle of the hindwing in the mimics. More strikingly, the brilliant white patch on the head and thorax of *P. sycorax* (*i*) is mimicked by a brilliant white patch at the base of the forewings in the mimic (*l*).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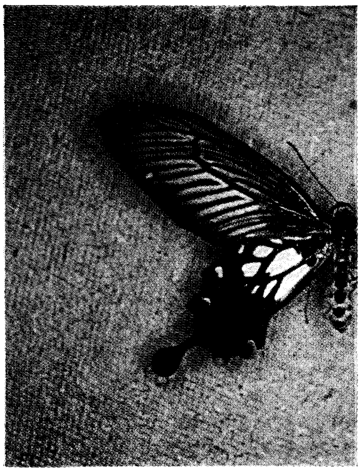
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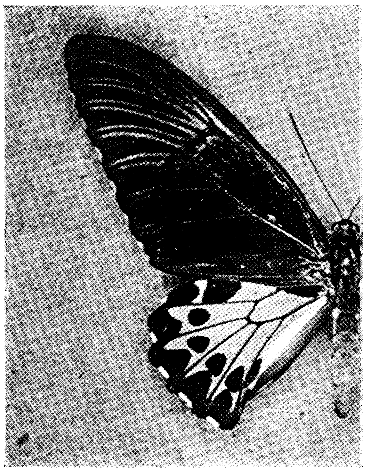
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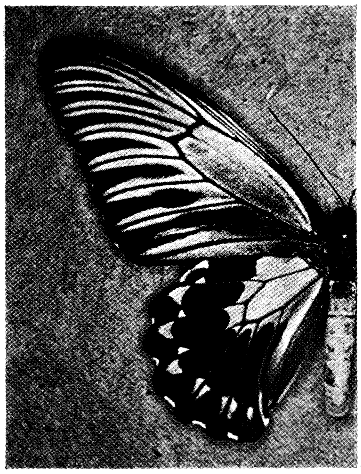
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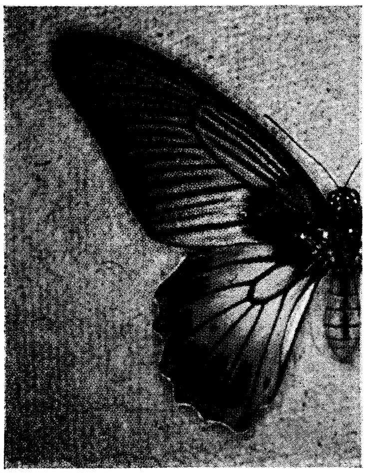
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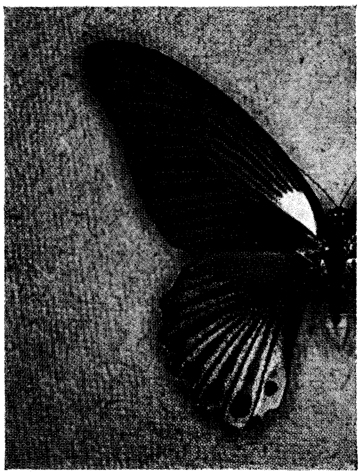
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DESCRIPTION OF PLATE 6

Some models and the forms of *P. memnon* which mimic them. In the plate each mimic is placed beneath its appropriate model.

P. rumanzovia (a mimic), a non-mimetic *P. memnon* male and a hybrid male, all treated on the underside with HCl, are also shown to demonstrate the chemical difference between the red pigment of *P. rumanzovia* and *P. memnon* (see p. 55).

(*a*) *P. semperi* (underside) ♂.

(*b*) *P. varuna* ♀.

(*c*) *P. nox* ♀ (Malay Peninsula).

(*d*) *P. rumanzovia* f. *semperinus* (underside). Note that the red body of the model is represented by a red stripe on the fore and hindwings of the mimic. The yellow spot is produced by the application of HCl.

(*e*) *P. m.* f. *butlerianus.*

(*f*) *P. m.* f. *esperi* (Malay Peninsula).

(*g*) *P. rumanzovia* × *P. memnon* male hybrid underside. Note that the application of HCl has produced only a slight alteration in the colour of the red pigment.

(*h*) *P. nox* ♀ (Borneo).

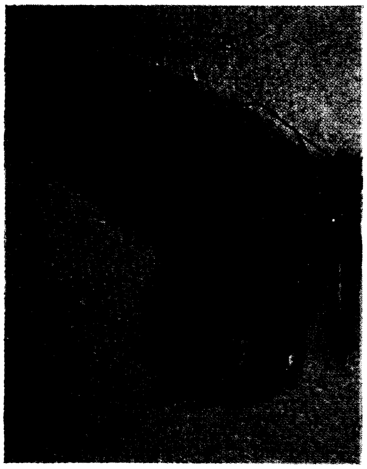
(*i*) *P. atropos* ♀.

(*j*) *P. memnon* ♂ underside. Note that the application of HCl has produced no change in the red pigment.

(*k*) *P. m.* f. *laomedon* (Borneo).

(*l*) *P. m.* f. *suffusus.*

The models and mimics illustrate the same general points about mimicry which are made in plate 5.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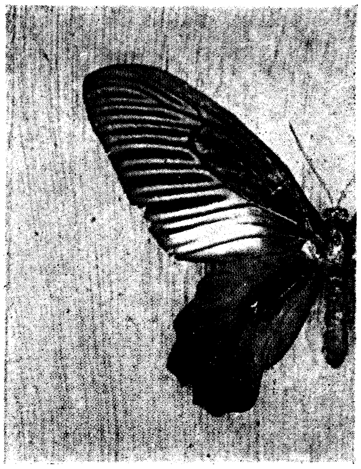
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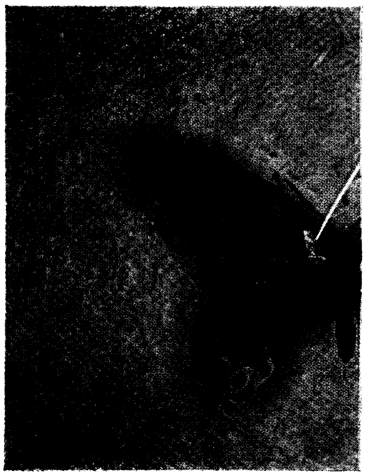
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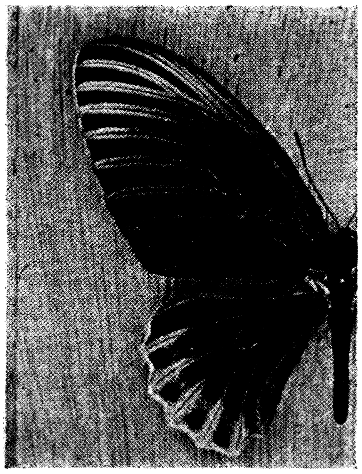
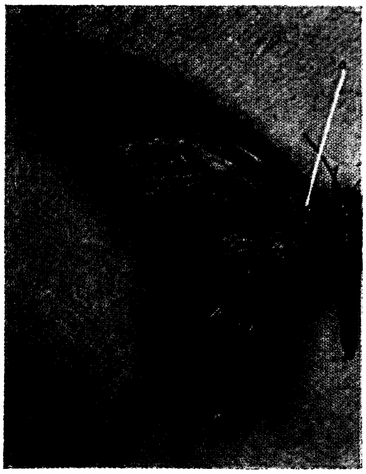
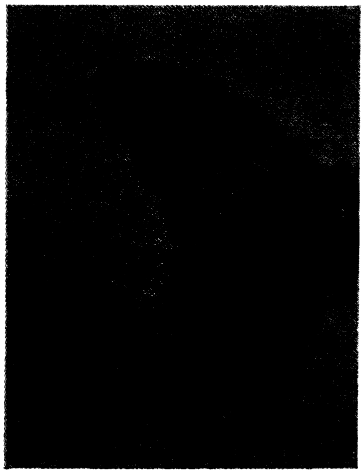

h


i


j


k


l

DESCRIPTION OF PLATE 7

P. polymnestor parinda from Ceylon and some of its female hybrids with *P. memnon*.

(*a*) *P. p. parinda* ♂.
(*b*) *P. p. parinda* ♀.
(*c*) *parinda—suffusus* F_1 hybrid.
(*d*) *zephyria—parinda* F_1 hybrid.
(*e*) *thunbergi—parinda* F_2 hybrid (homozygous male-like).
(*f*) *thunbergi—parinda* F_2 hybrid (heterozygous for *thunbergi* hindwing pattern).
(*g*) *agenor—parinda* F_2 hybrid (heterozygous for *agenor* pattern).
(*h*) *esperi—parinda* F_1 hybrid.
(*i*) *butlerianus—parinda* F_1 hybrid.
(*j*) *agenor—parinda* F_2 hybrid (homozygous for *agenor* pattern).
(*k*) *venusia—parinda* F_2 hybrid (heterozygous for *venusia*).
(*l*) *achates—parinda* F_1 hybrid.

a

b

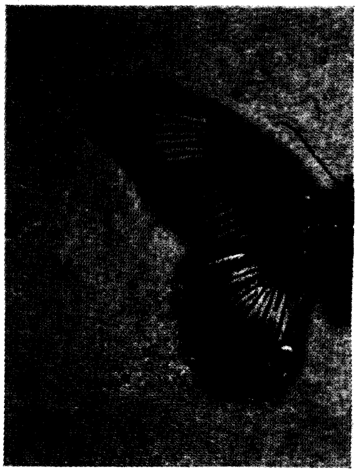
c

d

e

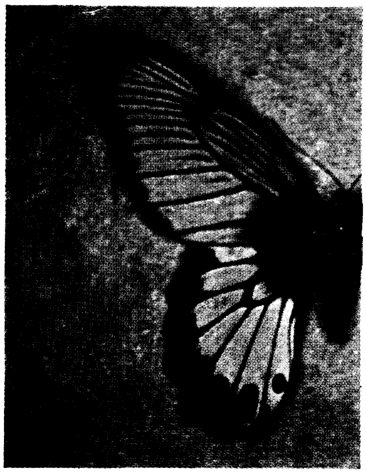
f

g



h

i



j

k

l

DESCRIPTION OF PLATE 8

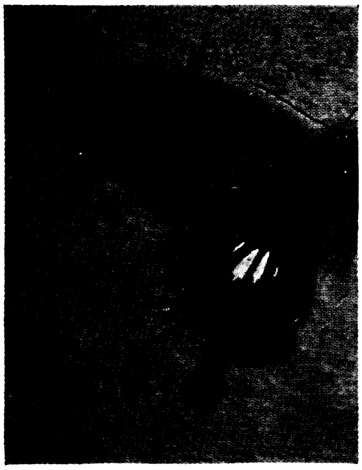
P. memnon from Palawan and some of the female hybrids with other races, (*a*) to (*j*). Two other female forms are also illustrated (*k*) and (*l*).

(*a*) *P. memnon* ♂ Palawan.
(*b*) *P. m.* f. *zephyria.*
(*c*) *agenor—suffusus* F_1.
(*d*) *achates* (*alcanor*) —*suffusus* F_1.
(*e*) *achates* (*distantianus*)—*suffusus* F_1.
(*f*) *achates* (*alcanor*)—*zephyria* F_1.
(*g*) *zephyria—agenor* (Thai) F_1.
(*h*) *achates* (*distantianus*)—*zephyria* F_1.
(*i*) *thunbergi—suffusus* F_1.
(*j*) *zephyria—laomedon*, obtained by back crossing a *zephyria—thunbergi* F_1 to a male homozygous for *laomedon* from Borneo. (Note the close resemblance to pure *venusia*, plate 5*j*).
(*k*) *anura—agenor* F_1.
(*l*) *P. m.* f. *gerania* (Sumatra).


a


b

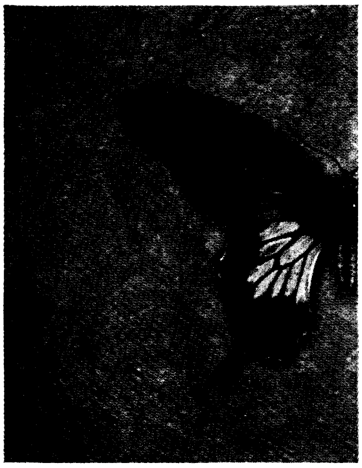

c


d

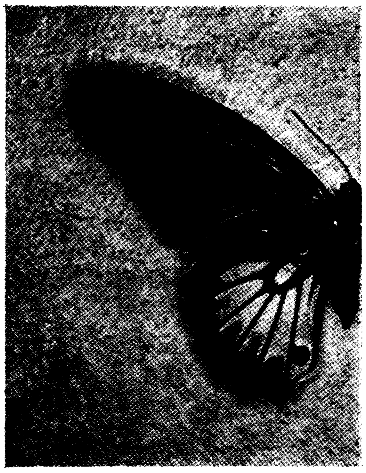

e


f


g


h


i


j


k


l

DESCRIPTION OF PLATE 9

Models, mimics and non-mimetic forms of *P. memnon*, together with some hybrids between various races.

(*a*) *P. zaleucus* ♀.

(*b*) *P. aidoneus* ♀.

(*c*) *P. m.* f. *thunbergi* (non-mimetic).

(*d*) *P. m.* f. *agenor*. This is usually non-mimetic but *zaleucus* may act as a model for it over a restricted area.

(*e*) *P. m.* f. *rhetenorina*, mimicking *P. aidoneus*.

(*f*) *P. m.* f. *thunbergi*. This variant has white on the forewing.

(*g*) *P. m.* f. '*titania*' from Hong Kong. This differs from the form found in Taiwan in that the hindwing pattern is that of *alcanor*, not *agenor* (see (*d*) above).

(*h*) *agenor*/*laomedon* heterozygote with dark forewings (the sib of (*i*)).

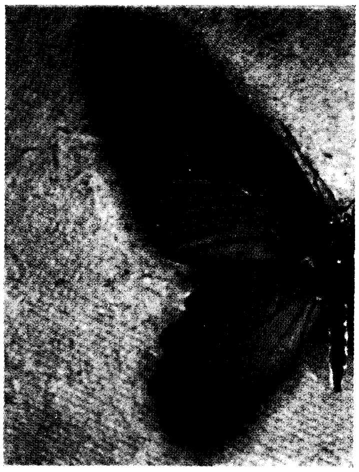
(*i*) *agenor*/*laomedon* heterozygote with light forewings (the sib of (*h*)). The brood segregated for light forewings (see pp. 68, 81).

(*j*) *achates* (*distantianus*)/*esperi* heterozygote showing the manifestation of the *esperi* forewing patch in the heterozygote.

(*k*) *agenor*—*esperi* F_1 hybrid. The *esperi* patch is reduced in intensity and the white *agenor* window on the hindwing much reduced in size.

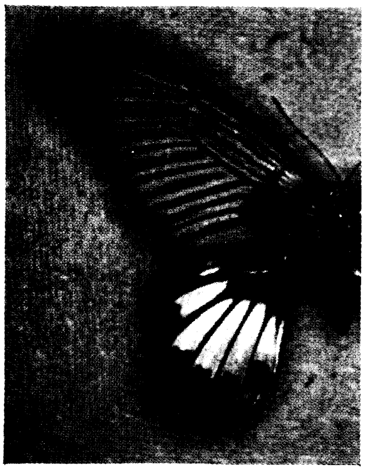
(*l*) *agenor*—*butlerianus* F_1 hybrid. The *butlerianus* patch is conspicuous but the *agenor* window is reduced in size.

a

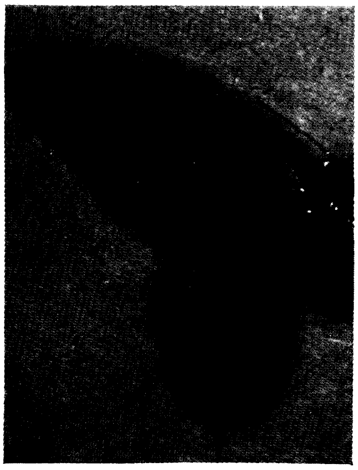


b

c



d

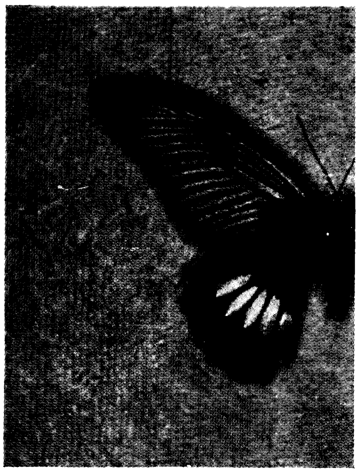


e

f

g

h



i

j

k

l

from it, particularly with respect to the comparative lack of blue scaling. It mimics *Parides aidoneus* (Doubleday) (plate 9*b* and figure 7). It flies in north India, Sikkim and Burma. We have evidence that it occasionally occurs in Thailand (broods 8329 and 8493, tables 4 and 6*a*), although we have never found a record of the insect having been caught there.

(*d*) *P. p. parinda*

This form is also male-like (see p. 60).

10. f. *titania* (plate 9*g*)

This form resembles a tailed *agenor* and flies as a great rarity (with the local *achates* and *agenor*) in Taiwan (Shirôzu 1960). It is probably non-mimetic. We have obtained one aberrant specimen from Hong Kong (see pp. 55, 64, 80).

11. f. *gerania* (plate 8*l* and figure 2)

The forewings are as in *esperi* but the white patch is less intense than in some specimens of *esperi*. The hindwings are black from the base to the distal end of the cell. The rest of the hindwing is white with black veins and a submarginal row of black patches between the veins. There are yellow spots at the anal angle of the hindwing. It is tailless, and the body is black with a yellow tip similar to but far more extreme than that of the females in Palawan. It flies in Sumatra but it has been reported occasionally in Singapore (Morrell 1960) from where we have obtained a single specimen. It resembles the hybrid between *esperi* and *agenor* (plate 9*k*).

12. *P. polymnestor parinda* from Ceylon (plate 7*a*, *b* and figure 1)

P. polymnestor (see p. 39) has a subspecies *parinda* which flies only in Ceylon. It is tailless, non-mimetic and black-bodied in both sexes. The males are black, with bright blue scaling on fore- and hindwings. The females, which are lighter than the males, are monomorphic though rather variable, with brownish forewings, the red basal spot being much reduced or absent. The hindwings are fawn, scattered liberally with blue scales. There are two rows of black patches between the veins on the hindwings homologous with those in f. *laomedon* females. The larva and pupa are indistinguishable from those of *P. memnon.*

13. *P. rumanzovia* f. *semperinus* (plate 6*d* and figure 1)

P. rumanzovia is a species closely related to *memnon.*

The forewing is dark with a large red basal spot. This is continued on the hindwing by a red band parallel with the inner margin. The rest of the hindwing above is black, with some blue scaling. The red longitudinal band is sometimes more or less whiteish and widened and where this is the case a number of submarginal black spots are also present between the veins. It is tailless and the body is black. It is a mimic of *Parides semperi* (Felder) (plate 6*a* and figure 6). The species flies in the Philippines, Siao, Sangir, Talaut and very rarely at the southern tip of Taiwan. In the model the brilliant red is on the body of the insect, not the forewings. The larva of *P. rumanzovia* is of the typical *Citrus* pattern (Clarke, Dickson & Sheppard 1963) and in general resembles that of *P. memnon.* It differs, however, in having a dorsal bar posteriorly joining the oblique stripes on the abdomen. The pupa is indistinguishable from that of *P. memnon.*

IV. Description of the male forms used in our work

The fore- and hindwings of the males are black, with blue scaling which varies in intensity and position from race to race. It is particularly intense in *P. polymnestor* (plate 7*a*) and almost absent in *thunbergi* from Japan. The red patch at the base of the forewing is either absent or very much reduced. The males are tailless except in Palawan (plate 8*a*) and the Celebes. In the males of *P. rumanzovia*, the upper surface of the wing is much like that of *P. memnon*, but it differs strikingly on the underside, having brilliant red or geranium pink markings on the fore- and hindwings similar to those of the female (plate 6*d*).

Table 2. Jacobson's broods

For clarity, we have numbered them 1 to 16, but Jacobson's original numbers and groups A, B and D are given in italics.

brood no.	mother	father	offspring	
			males	females
1 *A*	*achates no. 1* ancestry unknown	*no. 1* ancestry unknown	11	10 *agenor* (*isarcha*) 10 *achates*
2 *A*	*achates no. 5* (1)	*no. VI* (1) same as mating 3	3	1 *agenor* (*isarcha*) 4 *achates*
3 *A*	*achates no. 7* (1)	*no. VI* (1) same as mating 2	7	3 *agenor* (*isarcha*) 2 *achates*
4 *A*	*achates no. 8* (1)	*no. VIII* (5)	2	1 *achates*
5 *B*	*agenor* (*isarcha*) *no. 2* ancestry unknown	*no. II* ancestry unknown	32	17 *agenor* (*isarcha*) 19 *laomedon*
6 *B*	*laomedon no. 9* (5)	*no. VII* (1)	4	5 *agenor* (*isarcha*)
7 *B*	*laomedon no. 10* (5)	*no. IX* (5)	1	1 *laomedon*
8 *B*	*laomedon no. 11* (5)	*no. X* (5)	3	3 *laomedon*
9 *B*	*laomedon no. 12* (5)	*no. XI* (5)	3	11 *laomedon*
10 *B*	*agenor* (*isarcha*) *no. 16* (6)	*no. XVI* (2)	17	1 *agenor* (*isarcha*) 29 *achates*
11 *B*	*laomedon no. 17* (7)	*no. XVII* (4)	20	4 *laomedon* 8 *achates*
12 *B*	*laomedon no. 18* (8)	*no. XVIII* (4)	9	1 *laomedon* 3 *achates*
13 *B*	*laomedon no. 21* (11)	*no. XX* (12)	10	4 *laomedon*
14 *D*	*achates no. 4* ancestry unknown	*no. V* ancestry unknown	29	36 *achates*
15 *D*	*achates no. 15* (14)	*no. XV* (6)	10	8 *achates*
16 *D*	*achates no. 20* (15)	*no. XIX* (10)	14	4 *agenor* (*isarcha*) 15 *achates*

V. Previous investigations of the genetics of the female forms

The classical work on the breeding of *P. memnon* was done by Jacobson (1909, 1910) in Java, and the genetic analysis of his data was carried out afterwards, first by de Meijere (1910) and then by Baur (1911). In Java there are three female forms of *P. memnon*, f. *achates* (plate 5*d*) and two tailless forms, f. *agenor* (plate 9*d*) (called by Ford (1953) and also by Cockayne (1932) '*isarcha*') and f. *laomedon* (plate 6*k*). From 16 matings Jacobson (1909, 1910) obtained 376 insects of known parentage, and de Meijere (1910), using Jacobson's data, concluded that these broods are consistent with the female forms being controlled by single genes, sex-limited to the female and carried by the males, and that *achates* (*distantianus*) is dominant to the other forms, *agenor* being next in order of dominance and *laomedon* the bottom recessive. Baur (1911) made the alternative suggestion that there was a modifying gene (also sex-limited to the female and carried by the males) which needs to be present with *agenor* before *achates* can appear. The details of Jacobson's broods are set out in table 2. It will be seen below that we are in agreement with de Meijere's views but disagree with those of Baur.

Considering Jacobson's data from the point of view of sex-linkage, it is clear that neither the gene controlling the *achates* pattern nor that controlling the *agenor* pattern could be carried on the sex chromosomes. Thus, mating no. 1 shows that *agenor* is not Y-linked, since an *achates* female produced 10 *agenor* and 10 *achates* females. That *agenor* is not X-linked is shown by matings nos. 5, 7, 8 and 9. All the males from mating no. 5 would, if *agenor* were X-linked, be carrying *agenor* (since they had an *agenor* mother), and yet three of them, when mated to *laomedon*, failed to produce *agenor* among their female offspring. Mating no. 4 (in which *achates* appeared) shows that *achates* cannot be X-linked, since the father (from brood no. 5 which segregated 17 *agenor* and 19 *laomedon* females) could not have been carrying *achates*. Mating no. 11 shows that *achates* is not Y-linked since the form appeared in the offspring of a *laomedon* female in this brood.

Since *laomedon* is the bottom recessive, we cannot show from Jacobson's broods that the gene controlling this form is carried on an autosome, but it can be studied in race crosses (see below).

VI. Present study

1. *Autosomal inheritance of the major genes* (see table 3*a* for all broods)

(*a*) *Male-like* (plates 6*k*, *l*; 7*b*; 9*e*)

The gene controlling this group of forms is neither X- nor Y-linked. Thus brood 7600 shows that it cannot be Y-linked since recognizable *agenor*/male-like* heterozygotes appeared in the offspring of a female from Hong Kong which could not have carried the allelomorph controlling the male-like pattern. Brood 8624 shows that it cannot be X-linked since recognizable *agenor*/male-like heterozygotes appeared in the female offspring of a male from Hong Kong which could not have been carrying male-like.

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* Throughout the paper the separation of two form names by a solidus (/) indicates that an individual is heterozygous for these two forms. When the phenotype is being described and it is intermediate in appearance the form names are joined by a hyphen.

Table 3*a*. Autosomal inheritance of the female forms

In the tables the following conventions are used:

When the name of a form is given, the phenotype of the insect is indistinguishable from the normal appearance of that form. When the suffix 'like' is used, the phenotype is similar to the form but distinguishable from it. When two forms are given separated by a hyphen the phenotype is intermediate in appearance between the two forms.

Because the male-like form varies markedly from place to place, the regional form names have been used in all pure stock and F_1 hybrids, otherwise the term male-like has been given.

When the genotype rather than the phenotype is being indicated the form names concerned are separated by a solidus (/).

* In all these broods the male and female offspring were tailed, with the exception of brood 7744, in which a single male appeared to be tailless, and one was deformed.

			phenotype of offspring	
brood no.	mother	father	males	females
M29	*parinda* Ceylon	Japan	12	8 *thunbergi-parinda*
M335	*thunbergi* Japan	*parinda* Ceylon	7	7 *thunbergi-parinda*
6537	*rumanzovia* Philippines	Thailand	4	1 *achates-rumanzovia*
7148	*laomedon* North Borneo	Thailand	17	16 *agenor-laomedon*, all with hindwing orange
7230	*agenor* Hong Kong	Hong Kong	16	6 3 *agenor* 3 *achates*
*7262	*suffusus* Palawan	Thailand	33	37 17 *achates* 20 *agenor*-like
7263	*achates* Thailand	Japan	16	20 10 *achates* 10 *agenor*
7321	*agenor* Hong Kong	Kuala Lumpur	1	2 *agenor-butlerianus*
*7422	*agenor* 7302 (see table 4)	Palawan	0	1 *agenor*-male-like
7436	*achates* 7263	7289 cannot have been carrying *achates* (see table 4)	2	1 *achates*
*7443	*suffusus* Palawan	Palawan	1	2 *zephyria*
7532	*achates* Hong Kong	Kuala Lumpur	12	6 5 *achates-esperi* 1 *achates*
7597	*agenor* Hong Kong	North Borneo	21	13 *venusia*-like, all showed hindwing orange
7600	*agenor* Hong Kong	North Borneo	17	11 4 *agenor-laomedon* 7 *venusia*-like, all showed hindwing orange
*7744	*agenor*/male-like	Palawan	7	6 4 *agenor*-male-like 2 male-like
7833	pupae obtained from wild *achates* females from Hong Kong, may not be sibs		8	4 2 *agenor* 1 *achates* (*alcanor*) 1 *titania*
7879	*titania* 7833	7833	2	2 *titania*
7962	*agenor* Thailand	7879	1	3 1 *agenor* 2 *titania*

TABLE 3*a* (*cont.*)

			phenotype of offspring			
brood no.	mother	father	males	females		
8025	*agenor* 7962	7962	4	6 *agenor*		
8027	*titania* 7962	7962	0	2		1 *agenor* 1 *titania*
8246	*parinda* Ceylon	North Borneo	2	2 *parinda-laomedon*		
8264	*esperi* Singapore	North Borneo	2	3		2 *butlerianus-laomedon* 1 unscorable, deformed
8277	*venusia* North Borneo	*parinda* Ceylon	3	5		4 *parinda-laomedon* 1 *venusia-parinda*
8304	*laomedon* North Borneo	*parinda* Ceylon	8	4 *parinda-laomedon*		
8384	*butlerianus* Singapore	Hong Kong	8	8 *agenor-butlerianus*, all with pale forewings		
8457	*laomedon* (dark-winged) North Borneo	8384	42	55	21 dark forewings	12 *agenor*-male-like 9 *butlerianus*-male-like
					27 light forewings	12 *agenor*-male-like 15 *butlerianus*-male-like
					7 deformed unscorable for forewing	
8520	*esperi*/*parinda* (see table 6*a*) 8406	Thailand	19	13		6 *achates*-male-like 3 *agenor-esperi* 3 *agenor*-male-like 1 *achates-esperi*
8521	*esperi*/*parinda* (see table 6*a*) 8406	Thailand	12	5		1 *achates-esperi* 2 *agenor*-male-like 1 *achates*-male-like 1 *agenor-esperi*
*8598	*achates* (*alcanor*) Hong Kong	Palawan	18	27		8 *achates* (*alcanor*)-*zephyria* 9 *achates* (*alcanor*)-*suffusus* 4 *zephyria*-like 6 *agenor-suffusus*
*8624	*suffusus* Palawan	Hong Kong	15	11 *agenor-suffusus*		
*8640	*zephyria* Palawan	Thailand	7	9		3 *achates-zephyria* 1 *achates* 4 *zephyria*-like 1 *agenor-suffusus*
8835	*anura* North Borneo	North Borneo	13	8		7 *anura* 1 *laomedon*
8854	*anura* North Borneo	North Borneo	19	24		9 *anura* 15 *laomedon*

(*b*) f. *agenor* (plate 9*d*)

The gene controlling this form cannot be X- or Y-linked. Brood 7600 shows that it cannot be X-linked as recognizable *agenor*/male-like heterozygotes appeared in the offspring of a male from northern Borneo which could not have been carrying *agenor*. Brood 7148 shows that *agenor* cannot be Y-linked, as recognizable *agenor*/male-like heterozygotes appeared in the female offspring of a female from northern Borneo which could not have been carrying *agenor*.

(*c*) f. *achates* (plate 5*d*, *e*, *f*)

The locus controlling this form (including the presence of tails) cannot be X- or Y-linked. *Agenor* has been shown to be recessive to *achates* (de Meijere 1910; and see brood 7263, table 3*a*). The *agenor* mother of brood 7230 cannot therefore have been carrying the gene controlling *achates* on her Y chromosome. *Achates* appeared in her female offspring, so the gene controlling it cannot be Y-linked. *Achates* cannot be carried on the X chromosome, because it appeared in brood 7436 where the father could not have been carrying it.

(*d*) f. *zephyria* (plate 8*b*)

The gene controlling this form cannot be Y-linked. This is shown by brood 7443 where *zephyria* appeared in the offspring of a female of the male-like form. Moreover, it cannot be X-linked since a female *zephyria* mated to a male from Thailand, where the form does not occur, produced *zephyria*-like females among her offspring (brood 8640).

(*e*) f. *venusia* (plate 5*j*)

The gene controlling this form cannot be X- or Y-linked. Brood 7597 shows that *venusia* is not Y-linked since individuals clearly heterozygous for the gene appeared in the female offspring of a female from Hong Kong which could not have been carrying *venusia*. Brood 8277 demonstrates that *venusia* is not X-linked since a *venusia-parinda* female appeared in a brood with a *parinda* father which could not have carried the form.

(*f*) f. *anura* (plate 5*k*)

Brood 8854, in which an *anura* female produced female offspring segregating for *anura* and *laomedon*, shows that *anura* is not Y-linked. Brood 8835, in which an *anura* female produced 7 *anura* and 1 *laomedon* offspring, suggesting a 3:1 ratio, indicates that it is not X-linked either.

(*g*) f. *esperi* (plate 6*f*)

The gene controlling this form cannot be Y-linked since recognizable *achates-esperi* appeared in the female offspring of a female *achates* from Hong Kong which could not have carried *esperi* (brood 7532). Broods 8520 and 8521 show that *esperi* is not X-linked.

(*h*) f. *butlerianus* (plate 6*e*)

The gene controlling *butlerianus* is neither X- nor Y-linked. That it is not Y-linked is shown by brood 7321, since here recognizable *agenor/butlerianus* heterozygotes appeared in the female offspring of a female from Hong Kong which could not have been carrying *butlerianus*. Brood 8264 shows that *butlerianus* is not X-linked since it appeared in the female offspring of a male from northern Borneo which could not have been carrying the form.

(*i*) f. *thunbergi* (plate 9*c*, *f*)

The gene controlling *thunbergi* cannot be X- or Y-linked. Brood M 29 shows that it cannot be Y-linked, since *thunbergi-parinda* insects appeared in the female offspring of a *parinda* female which could not have been carrying *thunbergi*. Brood M 335 shows that *thunbergi* cannot be X-linked, since *thunbergi-parinda* insects appeared in the offspring of a male *parinda* which could not have been carrying *thunbergi*.

(*j*) f. *titania* (plate 9*g*)

The gene controlling f. *titania* cannot be Y-linked and is probably not X-linked. Brood 7962 shows that it is not Y-linked since it appeared in the offspring of an *agenor* mother. It is probably not X-linked, but we cannot guarantee that brood 7879 was not a mating between sibs. However, the likelihood of the male 7833 carrying the gene is extremely small, the insect coming from Hong Kong; it must be very rare there since we had no previous knowledge of the form occurring anywhere except in Taiwan.

(*k*) *The tailed condition in males and females from Palawan*

The gene controlling tails in both sexes in Palawan is neither X- nor Y-linked. This is demonstrated by brood 7262 since tails appeared both in all the male offspring and in all the *agenor*-like female offspring of a Palawan mother mated to a Thai father. The mother must have handed on the gene or genes for tails to her offspring of *both* sexes. This is shown again in broods 7422 and 7744 which are the reciprocal cross. One produced a tailed female and the other tailed insects of both sexes.

(*l*) *Yellow suffusion on the hindwings of Borneo material*

The characteristic yellow-orange of *anura*, *venusia* and *laomedon* is not Y-linked. This is shown by broods 7597 and 7600. Brood 7148 shows that this character cannot be X-linked since it appeared among the *agenor-laomedon* female progeny.

(*m*) *Pale ground colour of forewing of f.* agenor *in Hong Kong*

In brood 8384 a Hong Kong male was mated to a *butlerianus* female and the eight female offspring had pale forewings. A male from this brood crossed to a *laomedon* female (dark winged) from northern Borneo produced 27 females with light and 21 females with dark forewings (brood 8457). The gene responsible cannot be Y-linked since there was segregation among the female offspring.

(*n*) *P. polymnestor parinda* (plate 7*b*)

The distribution of black pigment is controlled by the allelomorph producing the male-like pattern and is therefore neither X- nor Y-linked (see broods 8246 and 8304). The other characters, notably the presence of buff in the female and blue scaling in the males and females, and the row of submarginal spots, appear to be multifactorially controlled, judged by the absence of clear-cut segregation in the F_2 and back-cross broods. The polygenes controlling blue scales, buff pigment and double band are not exclusively Y-linked nor X-linked, since insects in the F_1 (reciprocal) broods 8246 and 8304 both show these characters.

(*o*) *P. rumanzovia* (plate 6*d*)

Only two types of red pigment are found in the Papilionidae, called by Ford (1944) pigments A and B. They are readily distinguished, as type A is converted to a bright yellow shade by normal hydrochloric acid, whereas type B is not. Ford tested the red pigment of 107 species of *Papilio*, including that of the 15 species in the Memnon group which possess red markings, and in all but two the pigment is of type B, while that of all of the models of the mimetic forms of *P. memnon* is of type A. It is of great interest, however, that the two exceptions, *P. rumanzovia* and the closely allied species *Papilio deiphobus* Linnaeus, have the same pigment (type A) as their model, *P. semperi*. Brood 6537 shows that the difference in the chemical nature of the red pigment between *P. rumanzovia* and *P. memnon* cannot be X- or Y-linked, since a female *rumanzovia* transmitted the characteristic red pigment to her progeny of both sexes when mated to a Thai male. The progeny of this mating had both types of red pigment, the colour changing to a brownish yellow on the application of hydrochloric acid (plate 6*d*, *g*, *j* and table 3*b*).

TABLE 3*b*. COMPARISON OF THE COLOUR SCORES IN THE THREE CLASSES OF INSECT, USING THE COLOUR ATLAS OF VILLALOBOS & VILLALOBOS (1947) AND APPLYING THE ACID TO THE RED TRIANGULAR PATCH AT THE BASE OF THE FOREWING ON THE UNDERSIDE

genotype	'hue'	'lightness value'	'chromatic degree'
male *memnon* (treated and untreated with normal HCl)	page 3 S (scarlet)	8	10°
male *rumanzovia* (untreated)	page 2, RS (ruby/scarlet)	11	12°
male *rumanzovia* (treated)	page 9, OY (orange/yellow)	18	12°
male hybrid (brood 6537) (untreated)	page 4, SSO (scarlet/scarlet/orange)	11	10°
male hybrid (brood 6537) (treated)	page 6, OOS (orange/orange/scarlet)	14	8°

2. *Sex-controlled inheritance of pattern*

Since none of the genes controlling the female pattern are Y-linked and none of the characters they control appear in the male (with the exception of some male-like forms) the characters must be sex-controlled to the female, as de Meijere (1910) observed with respect to *agenor* and *achates*.

3. *Dominance relationships*

(*a*) *Dominance relationships of male-like* (plates 6*k*,*l*; 7*b*; 9*e*) *to other female forms*

(See table 4 for all broods.)

(i) *To* agenor (plate 9*d*)

Within races. We have no information, but Jacobson's breeding material showed that *agenor* in Java is fully dominant to the male-like form (*laomedon*) (de Meijere 1910).

Between races. The 16 female offspring of brood 7148 (using the subspecies from Thailand) were all similar and much more closely resembled f. *agenor* than f. *laomedon* from northern Borneo, but the *agenor* window on the hindwing was much reduced. The *agenor*/male-like heterozygotes in the reciprocal cross, using the Hong Kong subspecies, were similar but more variable and on average more intermediate (brood 7600). The back-cross broods to *agenor* (broods 7302, 7315 and 7326) and the F_2s (broods 7279 and 7289) segregated for *agenor* and heterozygous individuals. The back-cross to *laomedon* (brood 8327) segregated for male-like and heterozygous *agenor*-male-like individuals. These were intermediate in appearance between the two forms, but in second back-crosses to Borneo stock *agenor* was semi-recessive in a proportion of *agenor/laomedon* heterozygotes (broods 8957, 8958, 8960, 8961 and 8967; table 7*f*). *Agenor* from Hong Kong and Thailand is therefore semi-dominant in the F_1 to the male-like form from northern Borneo, the *agenor* showing greater dominance using Thailand material where the male-like form occurs. In one brood (8329) the *agenor* heterozygotes were indistinguishable from pure Thailand *agenor*.

Male-like (*suffusus*) from Palawan when crossed with *agenor* from Thailand produced a heterozygote more like *agenor* than *suffusus* but with a reduced window (brood 7262) and in the F_2 and back-cross broods, the *agenor*-like insects segregated for *agenor*-male-like and *agenor* (broods 7369, 7371, 7407, 7416 and 7859). When male-like (*suffusus*) was crossed with a heterozygous *achates* (*alcanor*)/*agenor* from Hong Kong (brood 8598) the *agenor* window was even more reduced (plate 8*c*) than in the Thai cross.

Agenor is therefore dominant to male-like in the Java race and semi-dominant in the three race crosses tested, the dominance being greatest in any cross involving the Thailand race. It is also semi-dominant to *parinda* (plate 7*g*, *j*) which is a male-like homozygote (see p. 60).

(ii) *To* achates (plate 5*d*, *e*, *f*)

Within races. Jacobson's data show that *achates* (plate 5*d*) is fully dominant to the male-like form in Java.

Between races. Broods 7262 and 8640 show *achates* (*distantianus*) (plate 5*e*) from Thailand to be dominant to male-like in the Palawan cross (plate 8*e*). On the other hand, *achates* (*alcanor*) (plate 5*f*) from Hong Kong (where the male-like form does not occur) produces an intermediate heterozygote in the Palawan cross (broods 8598 and 8636, plate 8*d*). In such individuals the white window can be reduced to two or a few white spots.

(iii) *To* venusia (plate 5*j*)

Within races. There are three female forms in northern Borneo, *anura*, *venusia* and *laomedon*, and there is full dominance between *venusia* and *laomedon.* Since in brood 8277 (table 3*a*) a *venusia* female, mated to *parinda* from Ceylon (where *venusia* is not found) produced a brood segregating for *venusia-parinda* and male-like, the *venusia* must have been carrying the male-like form. Therefore *venusia* is dominant to male-like in Borneo (*anura* is known not to be its homozygote—see below).

Between races. The heterozygote between *venusia* and male-like (*parinda*) is similar to *venusia* but has paler forewings and the yellow on the hindwings is much reduced, particularly at the border where the orange-yellow is replaced by greyish yellow (plate 7*k*). The dominance is unknown since we have not seen the homozygote.

(iv) *To* anura (plate 5*k*)

Within races. Brood 8835 is a mating between an *anura* and a wild male. It produced seven *anura* and one *laomedon*, suggesting a 3:1 ratio and therefore that *anura* is dominant.

The brood also shows that *anura* is not the homozygote for *venusia*, because it produced a *laomedon*.

TABLE 4. DOMINANCE RELATIONSHIPS OF MALE-LIKE TO OTHER FEMALE FORMS

			phenotype of offspring	
brood no.	mother	father	males	females
7148	*laomedon* North Borneo	Thailand	17	16 *agenor-laomedon*, all showed Borneo orange
7262	*suffusus* Palawan	Thailand (*achates*/*agenor*)	33	37 17 *achates* 20 *agenor*-like
7279	*agenor*/*laomedon* 7148	7148	4	2 1 *agenor*-male-like with orange 1 *agenor*-male-like without orange
7289	*agenor*/*laomedon* 7148	7148	5	3 1 *agenor*-male-like with orange 2 *agenor* without orange
7302	*agenor* Hong Kong	7148	0	5 1 unscorable, deformed 2 *agenor*-male-like with orange 1 *agenor* with orange 1 *agenor* without orange
7315	*agenor* Hong Kong	7148	8	3 1 *agenor* with orange 1 *agenor* without orange 1 *agenor*-male-like without orange
7326	*agenor* Hong Kong	7148	5	4 1 unscorable, deformed 2 *agenor*-male-like no orange 1 *agenor* no orange
7369	*agenor*-like 7262	Palawan	5	4 2 *agenor*-male-like 2 male-like
7371	*agenor*-like 7262	7262	1	3 1 unscorable, deformed 1 *agenor*-male-like 1 male-like
7376	*agenor*-like 7262	Kuala Lumpur (ex *esperi* mother)	1	1 *esperi*-male-like
7407	*agenor*-like 7262	7289	0	1 *agenor*
7416	*agenor*-like 7262	7262	9	4 1 male-like 1 *agenor*-male-like 2 *agenor*, deformed, unscorable for heterozygosity
7600	*agenor* Hong Kong	North Borneo (*venusia*/*laomedon*)	17	11 4 *agenor-laomedon* 7 *venusia*-like All 11 females had orange
7656	*laomedon* North Borneo	(*agenor*/*butlerianus*) 7593 (see table 5)	6	1 *butlerianus*-male-like
7857	*agenor*/male-like 7744 (see table 3*a*)	Japan	1	9 3 *agenor* 6 *thunbergi*-male-like
7859	*agenor*/male-like 7744 (see table 3*a*)	7744	2	9 3 *agenor*-male-like 1 *agenor* 5 male-like
7967	*thunbergi*/male-like 7857	7859	1	1 male-like
8202	*agenor* (Hong Kong × Thai)	North Borneo	1	0

Table 4 (*cont.*)

			phenotype of offspring		
brood no.	mother	father	males	females	
8246	*parinda* Ceylon	North Borneo	2	2	*parinda-laomedon*
8264	*esperi* Singapore	North Borneo	2	3	2 *butlerianus-laomedon* 1 unscorable, deformed
8304	*laomedon* North Borneo	*parinda* Ceylon	8	4	*parinda-laomedon*
8327	*laomedon* North Borneo	8202	4	4	1 *agenor*-male-like with marked spread of orange 1 *agenor*-male-like with slight spread of orange 2 male-like
8329	*venusia* North Borneo	Thailand	4	7	1 male-like 2 *agenor* 4 *venusia*-like
8598	*achates* (*alcanor*) Hong Kong	Palawan	18	27	8 *achates* (*alcanor*)-*zephyria* 9 *achates* (*alcanor*)-*suffusus* 4 *zephyria*-like 6 *agenor-suffusus*
8624	*suffusus* Palawan	Hong Kong	15	11	*agenor-suffusus*
8636	*achates* (*alcanor*) Hong Kong	Palawan	7	5	2 *achates* (*alcanor*)-*suffusus* 3 *agenor-suffusus*
8640	*zephyria* Palawan	Thailand	7	9	3 *achates-zephyria* 1 *achates*-like 4 *zephyria*-like 1 *agenor-suffusus*
8665	*thunbergi* Japan	Palawan	30	17	*thunbergi-suffusus*
8679	*zephyria* Palawan	*parinda* Ceylon	5	4	2 *zephyria-parinda* 2 *parinda-suffusus*
8835	*anura* North Borneo	North Borneo	13	8	7 *anura* 1 *laomedon*

(v) *To* zephyria (plate 8*b*)

Within races. Since there are only two forms in Palawan, one of them must be fully dominant to the other. Brood 8679 shows that *zephyria* is dominant to male-like in Palawan since a female *zephyria* mated to a male *parinda* produced two recognizable *parinda-suffusus* (plate 7*c*) and two recognizable *zephyria-parinda* (plate 7*d*). The *zephyria* mother must therefore have been carrying *suffusus*.

Between races. Brood 8679 shows *parinda* to form a recognizable heterozygote with *zephyria*, *zephyria* being semi-dominant or dominant (the homozygote has not been seen).

(vi) *To* butlerianus (plate 6*e*)

Between races. Brood 7656 shows that the *butlerianus* white patch on the inner margin of the forewing is present in the heterozygote with male-like (*laomedon*) from northern Borneo and therefore it is not recessive. The expression of this patch is very variable in pure *butlerianus*; we therefore have no information as to whether it is fully dominant or only semi-dominant in the cross. Brood 8264 again shows this forewing patch in a heterozygote with male-like, and here the red anal spot which is present in *butlerianus* but not in male-like is present in the F_1, suggesting that it is dominant. The male-like form used was again *laomedon* from northern Borneo. It is worth noting that the expression of the apical forewing patch in *laomedon* from north Borneo is highly variable. *Butlerianus* is also not recessive with *parinda* (see plate 7*i*).

(vii) *To* esperi (plate 6*f*)

Between races. Brood 7376, in a triple race cross, shows that the subapical white forewing patch of *esperi* is present in the heterozygote with male-like and is therefore not recessive. It is also not recessive with *parinda* (plate 7*h*).

(viii) *To* thunbergi (plate 9*c*, *f*)

Between races. Broods 7857 and 8665 show that male-like sometimes forms a recognizable heterozygote when mated with *thunbergi*, the *thunbergi* pattern being semi-dominant (plate 8*i*). Ae (1966) has also produced such a recognizable heterozygote using male-like (f. *rhetenorina*) from Nepal. However, in some broods it is recessive or almost recessive (broods 8650 and 8777 table 7*d* and *e*).

(ix) *To* parinda (plate 7*b*)

Between races. Male-like (northern Borneo) when crossed with *parinda* forms a recognizable but variable hybrid though the insects are essentially male-like in their pattern. There is no window on the hindwing. In broods 8246 and 8304 the light apical patch present, though variable, in male-like (northern Borneo) was visible on the forewing upperside, and there was a sprinkling of the characteristically sky-blue *parinda* scales on the inner margin of the hindwings. Crosses using *suffusus* from Palawan gave essentially similar results (brood 8679, plate 7*c*) though the *laomedon* forewing pale patch was absent. The *parinda* subspecies of *polymnestor* is apparently homozygous for the male-like gene, as is shown by these broods. This is confirmed by the crosses with *thunbergi* (broods M 29 and M 335, table 3*a*) in which all the F_1 had a fawn '*thunbergi*-like' window and where the presence or absence of this window segregated in the F_2 (plate 7*e*, *f*). All these crosses also suggest that the other characters of *parinda* (the blue scaling, the rows of black spots between the veins on the hindwing, the fawn scaling on the hindwing and the size of the red basal patch on the forewing) are multifactorially controlled, as do the crosses of *parinda* with *venusia* and with *agenor* (see plate 7).

(*b*) *Dominance relationships of* agenor *to the other female forms*

(See table 5 for all broods.)

(i) *To* achates

Within races. Jacobson's data (table 2) has shown that in Java *achates* is fully dominant to *agenor* (de Meijere 1910). Our brood 7263 shows that *achates* (*distantianus*) is dominant in Thailand material. Here a typical *achates* female from that area was mated to a *thunbergi* male which cannot have been carrying *agenor*, and the offspring were 16 males, 10 *agenor*-

TABLE 5. DOMINANCE RELATIONSHIPS OF F. *AGENOR* TO OTHER FEMALE FORMS

			phenotype of offspring	
brood no.	mother	father	males	females
7262	*suffusus* Palawan	Thailand	33	37 17 *achates* 20 *agenor*-like
7263	*achates* Thailand	Japan	16	20 10 *achates* 10 *agenor*
7321	*agenor* Hong Kong	Kuala Lumpur	1	2 *agenor-butlerianus*
7369	*agenor*-like 7262	Palawan	5	4 2 *agenor*-male-like 2 male-like
7371	*agenor*-like 7262	7262	1	3 1 unscorable, deformed 1 *agenor*-male-like 1 male-like
7407	*agenor*-like 7262	7289 (see table 4)	0	1 *agenor*
7416	*agenor*-like 7262	7262	9	4 1 male-like 1 *agenor*-male-like 2 *agenor*, deformed unscorable for heterozygosity
7513	*achates* Hong Kong	Hong Kong	29	29 20 *achates* 9 *agenor*
7593	*agenor* Hong Kong	Kuala Lumpur (*achates*/*butlerianus*)	24	21 11 *achates* 10 *agenor-butlerianus*
7597	*agenor* Hong Kong	North Borneo	21	13 *venusia*-like, all showed hindwing orange
7600	*agenor* Hong Kong	North Borneo	17	11 4 *agenor-laomedon* 7 *venusia*-like, all showed hindwing orange
7619	*agenor* Hong Kong	Kuala Lumpur	3	5 *agenor-esperi*
7859	*agenor*-male-like 7744 (see table 3*a*)	7744	2	9 3 *agenor*-male-like 1 *agenor* 5 male-like
7879	*titania* 7833 (see table 3*a*)	7833	2	2 *titania*
7962	*agenor* Thailand	7879	1	3 1 *agenor* 2 *titania*
8288	*agenor* Hong Kong	Ceylon	3	0
8292	*parinda* Ceylon	Hong Kong	4	10 *agenor-parinda*
8370	*agenor*/*parinda* 8292	8288	20	16 4 male-like 7 *agenor*-like, dark (*agenor*/male-like) 4 *agenor*-like, pale, (*agenor*/*agenor*) 1 unscorable
8598	*achates* (*alcanor*) Hong Kong	Palawan	18	27 8 *achates* (*alcanor*)-*zephyria* 9 *achates* (*alcanor*)-*suffusus* 4 *zephyria*-like 6 *agenor-suffusus*
8838	*anura* North Borneo	Hong Kong	6	4 1 *anura-agenor* 3 *agenor-laomedon*
8842	*anura* North Borneo	Hong Kong	1	4 2 *anura-agenor* 2 *agenor-laomedon*
8889	*anura* North Borneo	Hong Kong	5	1 *anura-agenor*

like and 10 *achates* females, thus demonstrating that the mother was a heterozygote. In Hong Kong there are two major polymorphic forms, indicating that dominance is complete. We have direct evidence that *achates* (*alcanor*) is dominant to *agenor*, since in mating 8598 in which an *achates* (*alcanor*) female from Hong Kong was crossed with a male from Palawan, where *agenor* is not found, the offspring segregated for *agenor-suffusus*, showing that the *achates* must have been carrying *agenor*. There is suggestive evidence from brood 7513 that Hong Kong *achates* (*distantianus*) is also dominant to *agenor*, since such a female, mated to a Hong Kong male, produced 29 males, 20 *achates* and nine *agenor* females.

Between races. Brood 7593 shows that *achates* (*distantianus*) from Kuala Lumpur is dominant to *agenor* from Hong Kong. This brood, from a Kuala Lumpur male mated to an *agenor* from Hong Kong (which we know could not have been heterozygous for *achates*), segregated for typical *achates* (*distantianus*).

(ii) *To* venusia

Between races. Brood 7597 shows that *agenor* is recessive to *venusia*, or nearly so. Here the mother was *agenor* and the father wild from northern Borneo, and the offspring were 21 males and 13 females, all resembling *venusia* much more than *agenor*. The window was larger than in *agenor* and the yellow-orange hindwing markings in the border were evident, though not so striking as in *venusia*. The window also was less yellow than in *venusia* and the black hindwing border, on average, more pronounced.

(iii) *To* anura

Between races. Broods 8838 and 8842 both resulted from an *anura* female mated to a Hong Kong male homozygous for *agenor*. They segregated for *agenor-laomedon* and *anura-agenor*. The latter insects were almost identical in pattern with *achates* (*distantianus*) but lacked the hindwing tails (plate 8*k*). Thus they have lost the typical orange-yellow suffusion of *anura* and have a slightly larger hindwing window. *Anura* must therefore be dominant or semi-dominant to *agenor* in this cross (the relevant homozygote has not been produced). On the other hand, in mating 8889 when an *anura* female was mated to a Hong Kong male the hindwing window was larger than in broods 8838 and 8842. However, it is not so extensive as in *venusia*/*agenor* heterozygotes since the costal border of the hindwing is black.

(iv) *To* butlerianus

Between races. Broods 7321 and 7593 show that *butlerianus* forms a recognizable heterozygote with *agenor*, the relevant females having the *butlerianus* patch on the inner margin of the forewings (p. 47) and a slightly to very reduced window on the hindwings (plate 9*l*).

(v) *To* esperi

Between races. Brood 7619 shows that *agenor* forms a recognizable heterozygote with *esperi*. The hindwing window is present but very variable and often much reduced. The white subapical forewing patch of *esperi* is present but tends to be less extreme than in some *esperi* (plate 9*k*).

(vi) *To* thunbergi

Between races. F. *agenor* is dominant to f. *thunbergi.* We have shown that this is so in five different broods, sometimes using a heterozygous *achates* mother and sometimes an *agenor* homozygote. The details of one brood (7263) are shown in table 5. From these five F_1s we obtained eight F_2 or F_2 equivalent broods and these in all produced 48 males, 11 *agenor*-like and 20 *achates*-like females. Four of the broods are shown in table 6*a*. The tailless females were variable; some were darker than *agenor* but none typically *thunbergi*-like. The complete absence of typical *thunbergi* among the 11 non-*achates*-like females suggests that more than one gene is involved in the difference between the *thunbergi* and *agenor* patterns.

Because of the ambiguity of the results the experiment was repeated. A female *thunbergi* was mated to a male from Hong Kong. The F_1 offspring were all *agenor*-like, confirming the dominance of *agenor*. Three F_2 matings were made. These between them produced 49 female offspring. They ranged in appearance between *thunbergi*-like, with a rather large window on the hindwing to *agenor*-like with a rather small one. The phenotypes showed continuous variation and could not be divided into discrete classes. Thus the difference between *thunbergi* and *agenor* appears to be polygenic. Nevertheless, there is evidence (see below, pp. 64, 74) that the genetic control of the difference is more complex than it would appear to be from these broods.

(vii) *To* parinda

Between races. Agenor forms a recognizable hybrid with *parinda* (brood 8292) and the presence of the hindwing *agenor* window is not recessive. This window was variable in colour in the ten females of brood 8292, being fawn in seven, yellow in two and white in one. The double row of *parinda* spots is present on the hindwing, but the spots are reduced in size. In this it differs from the cross with *laomedon* (Borneo) in which the second row of spots is absent.

In the F_2 brood 8370, three distinct phenotypes appeared. There were four male-like insects, seven were *agenor*-like (similar to the F_1) and four were *agenor*-like with the window much enlarged (plate 7*g*, *j*), the pale area being almost as extensive as in *venusia.* These last had large white areas between the veins outside the cell on the forewings. This brood suggests that *agenor* is not fully dominant in this cross and that the very pale *agenor*-like insects were homozygous *agenor.*

That this is the correct interpretation is strongly supported by brood 8941 (table 7*e*). In this brood a male heterozygous for *agenor* and *laomedon* was mated to an *achates* from Taiwan. The brood segregated for *achates* and two types of *agenor*. Two of the insects were typical *agenor* on the hindwings and had a general suffusion of white between the veins on the forewings, reminiscent of, but not as extreme as, those of 8370. The other four *agenor* had a hindwing window typical of *agenor*/*laomedon* heterozygotes and a faint subapical forewing patch which also showed that they were heterozygous for *laomedon.*

That the two types of *agenor* are homozygotes and heterozygotes respectively is confirmed by the presence of a yellow tip to the abdomen in two, and possibly all three of the putative heterozygotes but not in the homozygotes (see p. 79).

Thus in this race cross also dominance between *agenor* and male-like is incomplete.

The striking difference, as far as the size of the window on the hindwing is concerned, between the *agenor* × *parinda* F_2 brood and the *thunbergi* × *parinda* F_2 broods (plate 7*f*) suggests that these two forms may differ in the main by a single major gene rather than polygenically (see above). However, the result could still be due to different modifiers.

If this be the case, the modifiers producing *agenor* must be dominant to those controlling *thunbergi*. Furthermore, the modifiers in *agenor* must be dominant to their allelomorphs in *parinda*, as must those of *thunbergi*. Only thus could one get the large window of *agenor* in the *agenor*/*parinda* F_1 or the small window of *thunbergi* in the *thunbergi*/*parinda* F_1 coupled with the dominance of *agenor* over *thunbergi*. The number of modifiers involved (if this is the correct interpretation) is likely to be large, since no insects in the *agenor*/*parinda* F_2 bore any marked resemblance to those in the *thunbergi*/*parinda* F_2.

(viii) *To* titania (plate 9*g*)

Within races. *Titania*, which differs from *agenor* in being tailed, occurs as a great rarity in Taiwan and we have no knowledge of the dominance relationships in this region. It is probably dominant to *agenor* in Hong Kong material, since a female *titania* (which had an *alcanor*-like window on the hindwing (plate 9*g*), mated to a wild male, produced two *titania* (brood 7879). The dominance is not, however, certain since we cannot be sure that the male was not related to the female. However, *titania* is excessively rare in Hong Kong, and we have evidence of only the one wild specimen being taken there.

Between races. In brood 7962 an *agenor* from Thailand mated to a male, the sib of the two *titania* females of brood 7879, produced a normal *agenor* and two *titania*. Thus in this race cross, *titania* is not recessive to *agenor*, and is probably fully dominant.

(ix) *To* zephyria

Between races. Brood 8598 shows that *zephyria* is dominant or almost dominant to *agenor*. The brood resulted from a cross between Palawan and Hong Kong material, thus all the insects must have been heterozygous for *achates* or *agenor*. There were four phenotypes, two of them recognizably *zephyria*; one was clearly *zephyria-achates* and therefore the other, looking like normal *zephyria*, must have been heterozygous for *agenor*. However, in brood 8640 (table 3*a*) the same heterozygotes using the Thai race produced a phenotype in which the black hindwing border was reduced to a row of spots (plate 8*g*).

(*c*) *Dominance relationships of f.* achates *to f.* esperi, *f.* butlerianus, *f.* thunbergi, *f.* zephyria, P. p. parinda *and to* P. rumanzovia *f.* semperinus

(See table 6*a* for all broods.)

(i) *To f.* esperi

Within races. In the Malay Peninsula there are only three female forms, without intermediates, and the dominance must therefore be complete. By analogy with other races (Thailand and Hong Kong) *achates* is presumably dominant to the other forms in the Malay Peninsula.

Between races. Brood 7532 shows that the *esperi* forewing patch is not recessive to the Hong Kong *achates* (*distantianus*) forewing pattern, being present, though not as clearly as in *esperi*. Exactly the same happens with the Thai cross (broods 8520 (plate 9*j*) and 8521). Thus the heterozygote *achates*/*esperi* is recognizable. Furthermore, in crosses with Hong Kong material, the hindwings are like those of *achates*, though with a reduced window, and with blue scales as in *esperi*.

TABLE 6*a*. DOMINANCE RELATIONSHIPS OF F. *ACHATES* TO F. *ESPERI*, F. *BUTLERIANUS*, F. *THUNBERGI*, F. *ZEPHYRIA*, *P. P. PARINDA* AND TO *P. RUMANZOVIA* F. *SEMPERINUS*

brood no.	mother	father	phenotype of offspring		
			males	females	
6537	*rumanzovia* Philippines	Thailand	4 (*memnon-rumanzovia*)	1	*achates-rumanzovia*
6738	*achates* 6649*	6637*	9	7	1 *agenor* 6 *achates*
6765	*achates* 6646*	6649*	7	7	2 *agenor* 5 *achates*
7380	*achates* 7263*	7263*	1	1	*achates*
7381	*achates* 7263*	7253*	12	6	*achates*
7532	*achates* Hong Kong	Kuala Lumpur	12	6	5 *achates-esperi* 1 *achates*
7575	*achates* Hong Kong	Kuala Lumpur	0	3	1 *achates*-like (*achates*/*butlerianus*) 2 *achates*
8406	*parinda* Ceylon	Singapore (*esperi*/*butlerianus*)	21	24	17 *butlerianus-parinda* 7 *esperi-parinda*
8492	*butlerianus*/*parinda* 8406	Thailand (*achates*/*agenor*) (same as 8520)	12	11	3 *achates*-male-like 3 *agenor-butlerianus* 1 *agenor*-male-like 4 *achates-butlerianus*
8493	*butlerianus*/*parinda* 8406	Thailand (*achates*/male-like)	3	2	1 *achates-butlerianus* 1 male-like (homozygous or *butlerianus*/male-like), It has a faint *butlerianus* patch on the underside
8520	*esperi*/*parinda* 8406	Thailand (*achates*/*agenor*) (same as 8492)	19	13	6 *achates*-male-like 3 *agenor-esperi* 3 *agenor*-male-like 1 *achates-esperi*
8521	*esperi*/*parinda* 8406	Thailand	12	5	1 *achates-esperi* 2 *agenor*-male-like 1 *achates*-male-like 1 *agenor-esperi*
8598	*achates* (*alcanor*) Hong Kong	Palawan	18	27	8 *achates* (*alcanor*)-*zephyria* 9 *achates* (*alcanor*)-*suffusus* 4 *zephyria*-like 6 *agenor-suffusus*
8690	*parinda* Ceylon	Thailand	15	11	6 *agenor-parinda* 5 *achates-parinda*

* All F_1 broods *achates* × *thunbergi*.

(ii) *To f.* butlerianus

Within races. See above as for *esperi.*

Between races. Brood 7575 shows that Hong Kong *achates* (*distantianus*) probably also forms a recognizable heterozygote with *butlerianus.* This was a mating between an *achates* from Hong Kong and a wild male from Kuala Lumpur which produced no males and three females. Two were 'normal' *achates* and one a probable *achates/butlerianus* heterozygote, the father having presumably been *achates* (Kuala Lumpur)/*butlerianus. Butlerianus* and *esperi* both have a great deal of blue scaling on the hindwings, and the probable *achates/butlerianus* heterozygote in brood 7575 was recognizable (even though the white apical forewing patch of *esperi* or that on the inner margin as in *butlerianus* was absent). It had blue scaling on the hindwings and a reduced window, and moreover the body was dark, having many black scales on the yellow. Another reason why we suppose this insect may be of genotype *achates/butlerianus* is that it differs from our usual *achates/esperi* (brood 7532). The supposition is strengthened by brood 8264 (table 3*a*) which shows that *esperi* is dominant to *butlerianus.* In hybrids the white patch characteristic of *butlerianus* can however sometimes appear in *achates.* Such manifesting heterozygotes were found in broods 8492 and 8493 involving a cross with *parinda.*

(iii) *To f.* thunbergi

Between races. Achates (*distantianus*) is dominant to *thunbergi* (see brood 7263, table 5), the F_1 producing typical *achates.* In the F_2 broods 6738, 6765, 7380 and 7381 the *achates*-like individuals were very variable, some having much more black on the hindwing than others, but there was no clear-cut segregation among them.

(iv) *To f.* zephyria

Between races. Zephyria and *achates* produce an intermediate heterozygote. In brood 8598 a female *achates* (*alcanor*) mated to a male from Palawan segregated for *zephyria* (see above). The recognizable heterozygotes had a yellow body as in *achates* and a hindwing window which is slightly reduced compared with *zephyria* but larger than in *achates* (plate 8*f*). The tails on the hindwing were very long, but all F_1 hybrids involving Palawan have tails. In brood 8640 (table 3*a*) the corresponding *distantianus* heterozygotes were similar to those in brood 8598 except that the hindwing window was slightly more reduced (plate 8*h*).

(v) *To* P. p. parinda

Between races. Brood 8690, a mating between a *parinda* female and a wild Thai male, produced *achates*-like insects. These had the hindwing window, the yellow body and the tails characteristic of *achates* (plate 7*l*). The insects only differed from *achates* in the multifactorial characters which manifest themselves in all *parinda* F_1 hybrids.

(vi) *To* P. rumanzovia *f.* semperinus (plate 6*d*)

Between races. In brood 6537 the only female hybrid had to be extracted from its pupa case and did not grow. However, it was possible to determine that she had longish tails and much less red on both upper and underside than *rumanzovia.* She probably had the *achates* type of window on the hindwing but it is impossible to be sure of this. The body colour was not scorable. The presence of tails therefore is not recessive in this cross.

(*d*) *Dominance relationships of f.* venusia *to f.* anura *and to* P. p. parinda

(See table 6*b*.)

(i) *To f.* anura

Within races. There are three distinct forms in northern Borneo, f. *venusia*, f. *anura* and f. *laomedon* (see above) and since none of these is the heterozygote between the other two it would appear as if there were complete dominance. However, the female parent of brood 8920 (derived from a *venusia* and a male from a brood segregating for *anura*), although resembling *venusia*, had a rather broader black submarginal border on the hindwing than is typical of this form. This female, mated to a Hong Kong male homozygous for *agenor*, produced a brood segregating for *venusia-agenor* and *anura-agenor* only demonstrating that the female was heterozygous *anura*/*venusia*. A sister with a more typical black hindwing margin mated to a *parinda* produced a brood (8933) segregating for insects heterozygous for *venusia* and homozygous for male-like. Thus the data suggest that at least a proportion of *venusia*/*anura* heterozygotes may be recognizable although some *venusia* known not to be heterozygous for *anura* have a border almost as extreme as that of the mother of 8920. Thus the dominance of *venusia* over *anura* is almost complete and there may be full dominance since it could legitimately be argued that the difference between the two sisters (parents of 8920 and 8933) was due to factors other than the presence of *anura* in one of them.

TABLE 6*b*. DOMINANCE RELATIONSHIPS OF F. *VENUSIA* TO F. *ANURA* AND TO *P. P. PARINDA*

			phenotype of offspring		
brood no.	mother	father	males	females	
8835	*anura* North Borneo	North Borneo	13	8	7 *anura* 1 *laomedon*
8855	*venusia* North Borneo	North Borneo	30	23	16 *venusia* 7 *laomedon*
8869	*venusia* 8855	8835	1	3	1 *laomedon* 2 *venusia*
8920	*venusia* 8869	Hong Kong	30	19	8 *venusia-agenor* 11 *anura-agenor*
8933	*venusia* 8869	*parinda* Ceylon	19	12	6 *parinda-laomedon* 6 *venusia-parinda*

(ii) *To* P. p. parinda

Between races. In brood 8277 (table 3*a*) a *venusia* female from northern Borneo was mated to a male *parinda*. The brood segregated male-like and *venusia-parinda*, the *venusia-parinda* female having a pale fawn hindwing window extending over the whole wing, with only one submarginal row of spots, as in *venusia*. The forewing was like that of *venusia*. There was very little orange, and no blue *parinda* scales were present. The fawn colour was that of *parinda*. *Venusia* is therefore not recessive as regards the size of the window, and the absence of the inner row of submarginal spots appears to be dominant to its presence.

(*e*) *Dominance relationship of f.* butlerianus *to f.* esperi

Within races. *Butlerianus* is recessive to *esperi*. This is shown by brood 8264 (table 3*a*) where a female *esperi* mated to a male from northern Borneo which could not have carried *butlerianus*, produced offspring with a *butlerianus* forewing patch. The *esperi* mother must therefore have been carrying *butlerianus*.

(*f*) *Dominance of the yellow suffusion on the hindwings of females in Borneo*

Between races. The hindwings of the female form *venusia* are suffused with yellow, and this suffusion is also present to a less marked degree in *anura* and in *laomedon*. In the F_1s with the Thai and Hong Kong races the hybrids possess the suffusion, though its extent is less and the colour varies between the Borneo yellow and an orange-red more like the anal spot in Hong Kong and Thailand. Thus the suffusion is semi-dominant in both these race crosses. In the back-cross to pure Hong Kong material (broods 7302, 7315 and 7326, table 4) and in the F_2s (broods 7279 and 7289, table 4) there was clear-cut segregation, indicating that the character is controlled by a single major gene, the heterozygotes showing the typical yellow to orange-yellow of the F_1. In the back-cross to *laomedon* of an F_1 *agenor* female mated to a Borneo male (brood 8327, table 4) two *agenor*-like females emerged, one very yellow on the hindwing (probably homozygous for the character) and one much less so, probably the heterozygote.

(*g*) *Dominance of pale forewing in Hong Kong f.* agenor

As has been seen (p. 55) a cross between a Hong Kong male and a *butlerianus* female from Singapore produced all light forewinged females (brood 8384, table 3*a*) and the female offspring segregated in a 1:1 ratio when a male 8384 was crossed with a dark-winged female *laomedon* from northern Borneo (brood 8457, table 7 (*i*), plate 9*h*, *i*). Thus the character pale forewings is not recessive. Since it is extremely variable in Hong Kong material, we cannot be sure that it is fully dominant.

(*h*) *Dominance of the tailed condition from Palawan* (plates 6*l*; 8*a*, *b*)

Butterflies vary in size and this will affect their absolute tail length. Therefore in order to compare the tail length of Palawan insects with tailless butterflies from elsewhere, tail length has been adjusted to take into account the size of the butterfly's hindwing. This has been done in the same way as described previously for *P. dardanus* (Clarke & Sheppard 1960*a*). In *memnon* an average wing length of 35·68 mm was used and thus each tail length was adjusted by multiplying its length by the coefficient 35·68/wing length.

The mean tail length of pure Palawan material was 11·54 mm with a variance of 0·90. The tailless races had a mean value of 1·49 mm and a variance of 0·16. The F_1 material had a mean of 8·34 and a variance of 5·41. Thus the F_1 was intermediate in tail length between the two parental stocks and showed a very great increase in variance. This suggested that dominance was incomplete. However, it could be argued that although tail length had been reduced dominance was still present. Consequently matings were carried out to produce back crosses both to tailless stock and to the Palawan race as well as F_2 individuals in order to obtain both heterozygotes and homozygotes. The distribution of

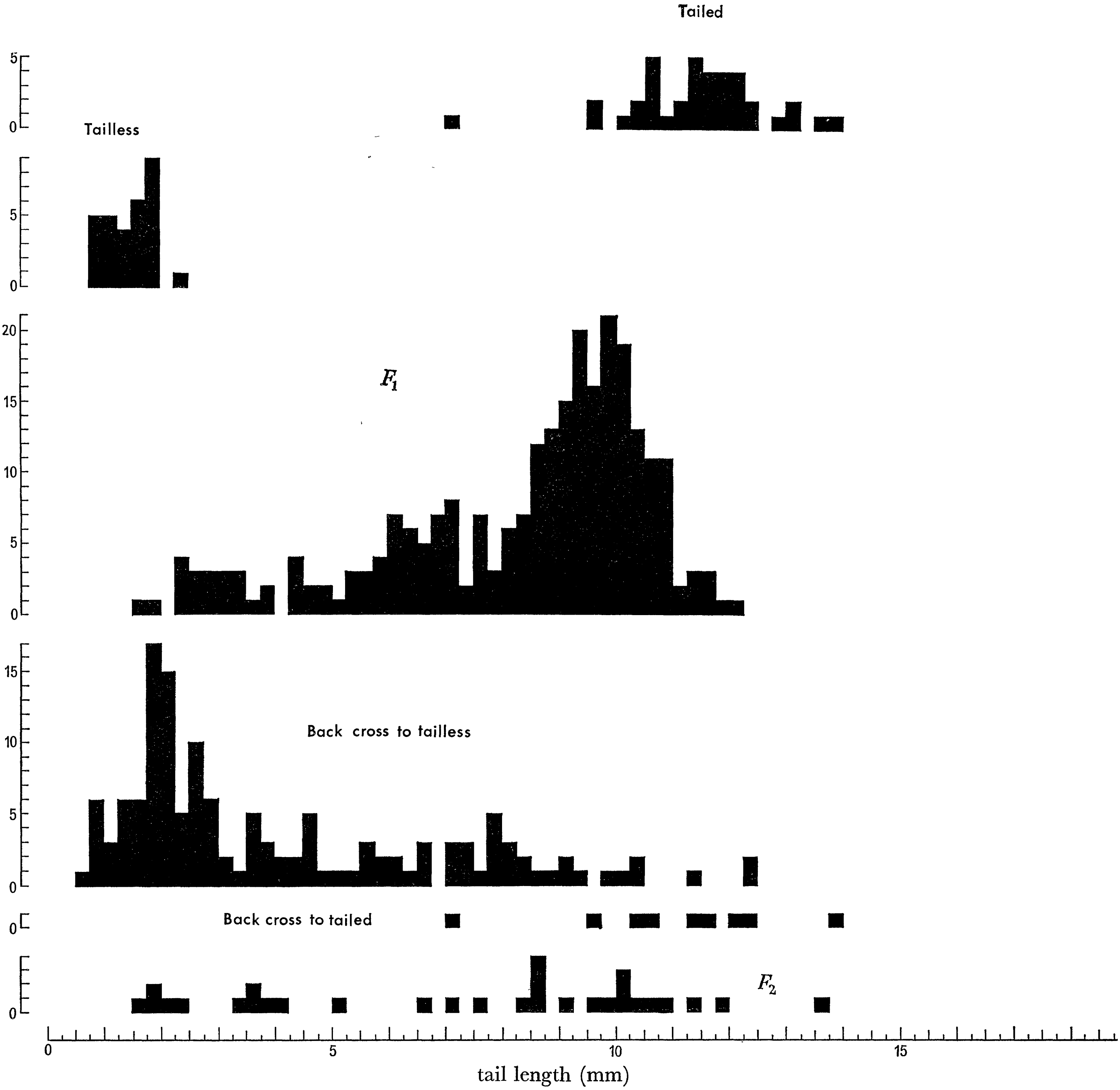

FIGURE 8. Histograms showing the length of the tails in the 'tailless' races (excluding f. *achates*), the tailed Palawan race, the F_1, the F_2 and the back crosses both to the tailed and the 'tailless' races. The variance in the crosses is far greater than in the parental races which makes it difficult to decide unequivocally which insects are tailed and which tailless. In the back-cross to the tailless race we have taken the dividing line as 3·50 mm (see text).

In the F_2 generation one insect stands out from the others in that it has an adjusted tail length of more than 19·5 mm. The unadjusted tail length was 11·75 mm, which is not exceptional for insects in the F_2 generation. The butterfly was only unusual in being small compared with most insects which have such a long tail.

adjusted tail length in all these, together with the parental and F_1 stocks, are given in figure 8.

The back-cross to tailless stock produced no clear segregation into tailed and tailless individuals, despite the fact that the pure races are quite distinct. However, from the evident mode at about 2 mm and the suggestion of an antimode at about 3·50 it was decided to use 3·50 mm as the dividing line between tailed and tailless. Judging by the distribution in the F_1 (figure 8) this should cause a misclassification of tailed individuals as tailless in approximately 7 % of cases. The dividing line of 3·50 mm has the merit of being the point at which insects looked tailed rather than tailless. This dividing line gave a ratio of 60 tailed to 78 tailless in the back-cross, a value not significantly different from the expected 1:1. Within broods the distinction between tailed and tailless was usually quite clear, but tends to be obscured in the combined figures because of variability in mean tail length between broods (see below).

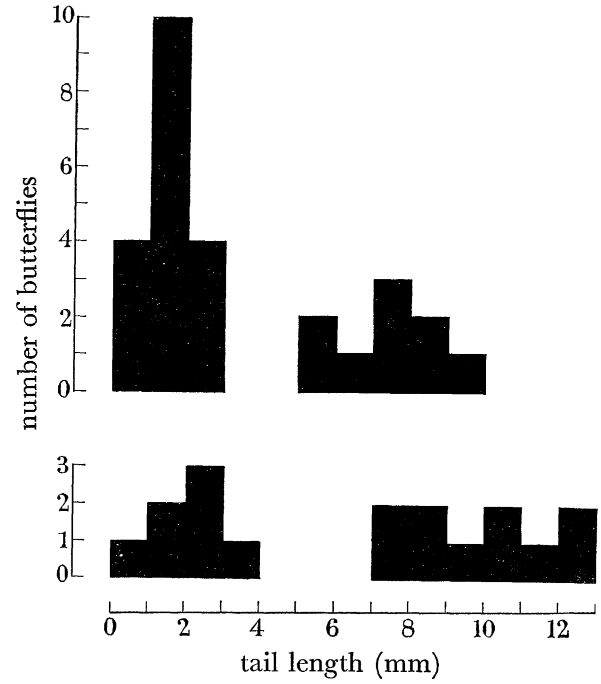

Figure 9. Histograms showing the length of the tails in the offspring of the back cross of the longest tailed individuals to tailless ones. The upper figure shows the offspring of a female with an adjusted tail length of 11·32 mm, the lower one those from a female with an adjusted tail length of 9·14 mm. In both broods there is a marked antimode indicating the presence of two qualitatively distinct classes, 'tailed' and 'tailless'.

Such misclassification as does occur is likely to be greatest among the offspring of parents where the tailed parent had a relatively short tail. Therefore, if one examines the offspring of a long-tailed parent, the segregation should be relatively clear if a single major gene is segregating. This proves to be the case (figure 9) where the offspring of the two parents with the longest tails are classified for tail length and segregate into two classes in a ratio not significantly different from 1:1.

Thus the tailed condition is apparently determined by a single gene with modifiers markedly affecting the actual length. As a result of these modifiers, the distinction between the heterozygotes and both homozygotes frequently disappears. Thus dominance is absent, in some individuals the tailless and in others the tailed condition being dominant, as will be seen in the back-cross to pure Palawan and the F_2 (figure 8). However, in the majority of insects the heterozygotes have an intermediate value.

Despite the fact that the mean tail length is greater in the pure Palawan race than in the F_1 ($t_{75} = 14{\cdot}03, P < 0{\cdot}001$) the variance in the latter is significantly greater ($P < 0{\cdot}001$). This could either be due to instability in development (environmental causes) or to the introduction of modifiers from the tailless parents. That the variance is due to modifiers is suggested:

(1) By the fact that the mean tail length of the tailed individuals in the back crosses to tailless races is further reduced ($t_{316} = 4{\cdot}76$, $P < 0{\cdot}001$) but the variance remains very similar to that found in the F_1.

(2) By the increased tail length ($t_{79} = 4{\cdot}98$, $P < 0{\cdot}001$) of the 'tailless' butterflies coupled with an increase in variance ($P < 0{\cdot}05$) over the pure tailless stocks. These two findings could not both be due to misclassification of tailed and tailless individuals. It therefore appears that modifiers decreasing tail length have been introduced from the tailless stocks and modifiers increasing tail length from the Palawan material, these modifiers also having some effect on wing shape even in homozygotes for the allelomorph determining the tailless condition.

That the variance of tail length and the modification of dominance is due to modifiers is confirmed by the regression of mean tail length of tailed offspring, in the back-cross, on the tail length of the tailed parent. The regression is highly significant ($t_9 = 3{\cdot}82$, $P < 0{\cdot}01$). The heritability of the modification of tail length estimated from the regression is 0·87. Thus most of the variability in these back-cross individuals, and by implication the F_1 generation is due to additive genetic variance and little can be due to environmental effects.

(*i*) *Hybrids between* P. memnon *and other species*

(i) *With* Papilio protenor demetrius

P. protenor is a *Citrus*-feeding *Papilio* which occurs in many parts of Asia; it is usually tailless but in Japan the race *P. protenor demetrius* is tailed in both sexes. The cross was obtained between a female *P. p. demetrius* and a male *P. memnon thunbergi*. Two male and one female offspring were produced, all of which had short tails (mean 5·2 mm variance 0·24) and the insects in general were very similar to *protenor*. The red basal patches on the forewing of the female were absent (as in *protenor*) and the hindwings lacked the white scaling typical of f. *thunbergi*. There was, however, some red scaling near the anal angle of the hindwing extending further laterally than that in *protenor* and occupying an area where there is white scaling in *thunbergi*. Thus the presence of white scaling in the hindwing is recessive or almost recessive.

The presence of tails in males and females is almost recessive, though not quite, since males and females had short tails. This contrasts with the results of Ae (1964) who produced no females in the same species cross. He describes the males as tailless, but judging from his photographs they have just detectable tails. S. A. Ae (personal communication) obtained very short tails in a male from a subsequent brood.

(ii) *With* Papilio aegeus.

P. aegeus is a *Citrus*-feeding *Papilio*, in which the adult is tailless. It occurs in New Guinea (where the female is polymorphic) and in Australia as far south as Sydney. From the cross of female *aegeus* × male *memnon* 31 males and no females were obtained. In these crosses males from Borneo, Palawan and Hong Kong were used. The *memnon* pattern was dominant to that of *aegeus* except that the red at the base of the wings on the underside, characteristic of *memnon*, was absent. Only in the crosses with the tailed Palawan race were the hybrid offspring tailed. However, the tails were far shorter than in F_1 crosses within *memnon* itself, the average length being 3·5 mm, variance 0·71. Thus the semi-recessiveness of the character presence of tails resembled that in the *protenor* crosses.

(iii) *With* Papilio helenus

Ae (1964) has produced hybrids between *P. memnon* f. *thunbergi* and *P. helenus*, obtaining only males. These were somewhat intermediate in appearance but the presence of the red patch at the base of the forewings characteristic of *memnon* was recessive, as was the white patch on the hindwings characteristic of *helenus*. The hybrids were tailed but the tails appeared to be shorter than in *helenus*, suggesting that there is no dominance.

In the present investigation a similar cross has been made which produced one female offspring only. This was deformed, but was tailed and had a white patch on the hindwing and a yellowish grey body. The red patch at the base of the forewing was absent except for two or three scales on the underside. It was clearly heterozygous for f. *achates* and the white area on the hindwing was characteristic of the *alcanor*/male-like heterozygote of *P. memnon* (see p. 57). Nevertheless, since the male *memnon* was from Thailand the female must be heterozygous for *distantianus*, indicating that this character is less dominant in the species cross.

4. *Allelomorphism and linkage*

(See table 7 for all broods.)

Baur (1911) analysing Jacobson's data, suggested, in contrast to de Meijere (see p. 51) that f. *achates* (*distantianus*) was controlled by two genes, the pattern only appearing in individuals carrying both the allelomorph for *agenor* and a gene modifying the *agenor* pattern to that of *achates* at an independent locus. Since in the southern part of the Malay Peninsula *achates* (*distantianus*) occurs and *agenor* does not, it is unnecessary for the gene controlling the *agenor* pattern to be present before *achates* can appear and the hypothesis of Baur falls to the ground. Furthermore, the hypothesis that *agenor* is present but its effect not expressed because of epistasis is also disproved by our breeding results.

It is not in fact clear why Baur formulated his hypothesis because Jacobson's data themselves tend to discredit it. For example broods 11 and 12 (table 2) from males carrying *achates* mated to *laomedon* females, failed to produce *agenor* among the five non-*achates* female offspring. Again, one of the males of brood 12 was also shown not to be carrying *achates* or *agenor* (brood 13, table 2).

Jacobson's data give no information on the allelomorphism of these three Java forms, but our breeding results do so in the forms which we studied and again disprove Baur's hypothesis.

(*a*) *Allelomorphism of f.* agenor *and f.* butlerianus

The informative broods are given in table 7 (*a*) and of these brood 8457 is the largest. Here a female *laomedon* (from a northern Borneo pupa) was mated to a male which was the offspring of an F_1 between a *butlerianus* female from Singapore and a male from Hong Kong (brood 8384). Since *butlerianus* is a homozygote and all the female offspring of the F_1 were clearly *butlerianus-agenor* in phenotype, this male must be a double heterozygote. The offspring resulting from this double back cross were 22 *butlerianus*-male-like and 24 *agenor*-male-like females (the latter with slightly reduced windows). In one of the *butlerianus*-male-like females the white patch characteristic of *butlerianus* could only be faintly detected on the under surface of the forewing. There were also nine individuals unscorable for either one or other of the characters because of deformity. The absence of the four phenotypic classes expected on independent assortment gives strong evidence of linkage and suggests allelomorphism. If the one insect in which the *butlerianus* character is much reduced, is in fact carrying the gene for this character, then the brood is consistent with allelomorphism, but otherwise there is only very close linkage. The other broods support the allelic hypothesis since there are no crossover classes among the 26 scorable insects.

(*b*) *Allelomorphism of f.* butlerianus *and f.* esperi

Brood 8406 (table 7 (*b*)) resulted from a cross between a *parinda* female (genotypically male-like) and a male which was the offspring of a wild *butlerianus* female from Singapore. It produced two classes of insects, 17 with the *butlerianus*-like patch and seven with the *esperi*-like patch (plate 7*h*, *i*). Since *butlerianus* is recessive to *esperi* (see p. 68) the male must have been heterozygous *esperi*. Both kinds of female were crossed to wild Thai stock, where neither *butlerianus* nor *esperi* is found, and in broods 8520 and 8521 an *esperi*/*parinda* female was used. Among the females heterozygous for *agenor* there were five not manifesting the *esperi* patch and therefore capable of demonstrating the presence of the *butlerianus* character. In fact none of these had the characteristic white patch, showing that the female parent was not heterozygous for *butlerianus*, and that therefore *butlerianus* and *esperi* are either allelic or closely linked. Though the *butlerianus* patch does not appear among the *achates* in broods 8520 and 8521 (see above), we have not used its absence in these insects in support of the hypothesis of allelomorphism. Furthermore, we have not included information from broods 8504 and 8507 since in these, which involved Hong Kong stock, the forewings in the *agenor* are so variable that we cannot score them unequivocally for either *butlerianus* or *esperi*.

The alternative hypothesis, that *butlerianus* does not express itself in these Thai hybrids in the presence of *agenor*, can be rejected since it segregates satisfactorily in the crosses using the *butlerianus* /*parinda* females—that is, it appeared in the *agenor*-like insects of broods 8492, 8497 and 8503 (table 7 (*b*)). It also manifested in the *achates* (*distantianus*) insects in the first two of these broods but not in the third (the fourth produced no *achates*).

(*c*) *Allelomorphism of f.* achates *and f.* agenor

In broods 8390 and 8407 (table 7 (*c*)) the same wild male from Thailand was mated to an *agenor* heterozygous for male-like (*laomedon*) and to a *butlerianus* from Singapore respectively. Brood 8390 produced 20 *achates* (*distantianus*) and nine *agenor*-like insects, and brood 8407 produced 12 *achates* and five *agenor*-like. If the Thai male had been heterozygous for male-like, one would have expected more than four male-like females among the combined progeny of the two broods, whereas in fact there were none. Even in brood 8407 there is a significant deficiency of male-like females on the hypothesis that the male was heterozygous for the gene concerned. Thus, if *achates* and *agenor* are not controlled by allelomorphs, the *achates* females in broods 8390 and 8407 should be at least heterozygous for *agenor*. Two of these females were crossed to a *butlerianus*/male-like heterozygous male and to a wild male from northern Borneo (known to be homozygous male-like) respectively. The two broods (8468 and 8489) between them produced eight non-*achates* offspring, none of which were *agenor*; neither did *agenor* appear in brood 8627. Thus the data are strongly in favour of *achates* (*distantianus*) and *agenor* being allelomorphs or closely linked.

In brood 8598 a female *achates* (*alcanor*) from Hong Kong was mated to a wild male from Palawan. The offspring segregated into four distinct phenotypic classes. These F_1 individuals were back-crossed to male-like forms, mostly to pure *parinda*. Of those segregating for *achates* (*alcanor*), or with an *achates* parent (broods 8699, 8702, 8706, 8716 and 8722) none has produced *agenor* and this deficiency is significant ($P = 0{\cdot}5^{14}$). This shows that the genes responsible are either allelomorphic or closely linked. It follows therefore that *achates* (*distantianus*) and *achates* (*alcanor*) are also allelomorphic or closely linked, as was anticipated from their both being tailed and having yellow bodies.

(*d*) *Allelomorphism of f.* achates *and f.* thunbergi

Broods 8635, 8650 and 8651 (table 7 (*d*)) give some information on the relationship between *achates* and *thunbergi*. The mother of 8635 was an *achates*/*thunbergi* F_1 female mated to a wild Palawan male, and produced one *thunbergi*-like female. The mother of 8650 was male-like and the father an *achates*/*thunbergi* heterozygote (having derived *achates* from one parent and *thunbergi* from the other). The brood produced four males, and of the females three were *achates*-male-like, three *thunbergi*-male-like and one possibly male-like but having a few scales of white on the underside of the hindwing. Brood 8651 had an *achates*/*thunbergi* mother (the forms having been inherited from different parents) and a Palawan father. The mating produced four *achates*-like and three *thunbergi*-male-like females, as well as three *zephyria*-like insects and one *achates-zephyria*. The insects in these broods which have received male-like from one parent can be combined, which gives seven *achates*-like, seven *thunbergi*-male-like and one which appears superficially male-like.

The data agree with the hypothesis that *achates* and *thunbergi* are not allelomorphic but are linked, there being a deficiency of male-like individuals among the non-*achates* insects ($P < 0{\cdot}05$). However, the *thunbergi*-male-like insects are immensely variable and some have an extremely small area of white on the hindwings, sometimes being reduced to one small patch. It is therefore more than probable that the single male-like insect is not a cross-over but is really carrying the gene for *thunbergi*, and that dominance has been reversed owing to

TABLE 7. LINKAGE RELATIONSHIPS OF THE VARIOUS FEMALE FORMS

			phenotype of offspring		
brood no.	mother	father	males	females	
		Section (*a*)			
8384	*butlerianus* Singapore	Hong Kong	8	8	*agenor-butlerianus* (all with pale forewings)
8456	*agenor/butlerianus* 8384	North Borneo (same as 8480)	14	5	2 *butlerianus*-male-like 3 *agenor*-male-like
8457	*laomedon* North Borneo	8384	42	55	24 *agenor*-male-like 22 *butlerianus*-male-like 9 unscorable, deformed
8458	*agenor/butlerianus* 8384	North Borneo (same as 8461 and 8478)	11	2	1 *agenor*-male-like 1 *butlerianus*-male-like
8459	*agenor/butlerianus* (F_1 hybrid)	North Borneo	21	7	3 *butlerianus*-male-like 2 *agenor*-male-like 1 *agenor* (unscorable on forewings) 1 unscorable, deformed
8461	*agenor/butlerianus* 8384	North Borneo (same as 8458 and 8478)	12	2	*agenor*-male-like
8467	*agenor/butlerianus* (F_1 hybrid)	North Borneo	8	2	*agenor*-male-like
8478	*agenor/butlerianus* (F_1 hybrid)	North Borneo (same as 8458 and 8461)	6	2	1 *agenor*-male-like 1 *butlerianus*-male-like
8480	*agenor/butlerianus* 8407 (see section *c*)	North Borneo (same as 8456)	8	8	4 *agenor*-male-like 4 *butlerianus*-male-like
		Section (*b*)			
8406	*parinda* Ceylon	Singapore	21	24	17 *butlerianus-parinda* 7 *esperi-parinda*
8492	*butlerianus/parinda* 8406	Thailand (same as 8520)	12	11	3 *achates*-male-like 3 *agenor-butlerianus* 1 *agenor*-male-like 4 *achates-butlerianus*
8493	*butlerianus/parinda* 8406	Thailand	3	2	1 *achates*-like 1 male-like (homozygous or *butlerianus*/male-like. It has a faint *butlerianus* patch on the underside).
8497	*butlerianus/parinda* 8406	Thailand	9	9	3 *achates*-male-like 2 *agenor-butlerianus* 1 *agenor*-male-like 2 *achates*-like 1 *achates-butlerianus*
8503	*butlerianus/parinda* 8406	Thailand	9	8	4 *agenor*-male-like 2 *agenor-butlerianus* 2 unscorable, deformed
8504	*agenor* Hong Kong	8406	10	4	*agenor*-like
8507	*achates* Hong Kong	8406	17	10	5 *achates*-male-like 1 *achates-esperi* 4 *agenor*-like

TABLE 7 (*cont.*)

			phenotype of offspring		
brood no.	mother	father	males	females	
8520	*esperi*/*parinda* 8406	Thailand (*achates*/*agenor*) (same as 8492)	19	13	6 *achates*-male-like 3 *agenor-esperi* 3 *agenor*-male-like 1 *achates-esperi*
8521	*esperi*/*parinda* 8406	Thailand	12	5	1 *achates-esperi* 2 *agenor*-male-like 1 *achates*-male-like 1 *agenor-esperi*
		Section (*c*)			
8390	*agenor*-like (*agenor*/*laomedon*)	Thailand (same as 8407)	16	30	20 *achates* 9 *agenor*-like 1 unscorable, deformed
8407	*butlerianus* Singapore	Thailand (same as 8390)	13	17	3 *agenor-butlerianus* 1 *agenor* (without *butlerianus* patch) 1 *agenor* (unscorable for *butlerianus* patch) 12 *achates*
8468	*achates* 8390	*butlerianus*/male-like	5	6	2 *achates* 4 male-like
8489	*achates* 8407	North Borneo	15	9	5 *achates*-like 4 male-like
8598	*achates* (*alcanor*) Hong Kong	Palawan	18	27	8 *achates* (*alcanor*)-*zephyria* 9 *achates* (*alcanor*)-*suffusus* 4 *zephyria*-like 6 *agenor-suffusus*
8627	*achates*-male-like 8507	Palawan	2	2	male-like
8636	*achates* (*alcanor*) Hong Kong	Palawan	7	5	2 *achates* (*alcanor*)-*suffusus* 3 *agenor-suffusus*
8699	*alcanor*/*suffusus* 8598	*parinda* Ceylon	0	2	1 *achates* (*alcanor*)-male-like 1 male-like
8702	*parinda* Ceylon	8598 (same as 8706)	5	10	4 *achates* (*alcanor*)-male-like 6 male-like
8706	*parinda* Ceylon	8598 (same as 8702)	14	8	4 *achates* (*alcanor*)-male-like 4 male-like
8716	*alcanor*/*suffusus* 8598	*parinda* Ceylon	4	2	male-like
8722	*alcanor*/*suffusus* 8598	*parinda* Ceylon	1	1	male-like
		Section (*d*)			
8471	*thunbergi* Japan	*butlerianus*/male-like	20	18	8 *thunbergi*-male-like 10 *thunbergi-butlerianus*
8541	*achates* (*alcanor*) Taiwan	Japan	15	12	7 *agenor* 4 *achates* (*alcanor*) 1 unscorable, deformed
8554	male-like 8468	8471	20	21	11 *thunbergi*-male-like 10 male-like
8559	*achates* 8468	Japan	5	1	*achates*
8635	*achates* (*alcanor*) 8541	Palawan	0	1	*thunbergi*-like

TABLE 7 (*cont.*)

			phenotype of offspring		
brood no.	mother	father	males	females	
8650	male-like 8554	8541	4	7	3 *thunbergi*-male-like 3 *achates*-male-like 1 male-like (a few white scales)
8651	*achates* 8559	Palawan	4	11	3 *zephyria*-like 4 *achates*-like 3 *thunbergi*-male-like 1 *achates-zephyria*
Section (*e*)					
8598	*achates* (*alcanor*) Hong Kong	Palawan	18	27	8 *achates* (*alcanor*)-*zephyria* 9 *achates* (*alcanor*)-*suffusus* 4 *zephyria*-like 6 *agenor-suffusus*
8651	*achates*/*thunbergi* 8541	Palawan	4	11	3 *zephyria-like* 4 *achates*-like 3 *thunbergi*-male-like 1 *achates-zephyria*
8730	*parinda* Ceylon	8598 (same as 8737)	3	1	*agenor*-male-like
8737	*parinda* Ceylon	8598 (same as 8730)	2	7	3 *agenor*-like 4 *zephyria*-like
8747	*achates* (*alcanor*)/*zephyria* 8598	*parinda* Ceylon	0	2	*achates* (*alcanor*)-male-like
8777	*zephyria*/*thunbergi* 8651	North Borneo	17	10	7 *zephyria*-male-like† 3 *thunbergi*-male-like
8923	*laomedon* Borneo	*agenor*/*laomedon* (same as 8941)	35	21	10 *agenor*-male-like‡ 11 male-like‡
8941	*achates* Taiwan	*agenor*/*laomedon* (same as 8923)	8	8	2 *achates* 2 *agenor* 4 *agenor*-male-like§
Section (*f*)					
8924	*laomedon* North Borneo	*laomedon*/*agenor* F_1 hybrid North Borneo × Hong Kong	24	10	6 male-like 4 *agenor*-male-like
8957	male-like 8924	8920 (see table 6*b*)	38	18	9 *anura*-like 9 *agenor*-male-like
8958	male-like 8923	8920	7	12	4 *anura*-like 8 *agenor*-male-like
8960	male-like 8924	8920	15	18	7 *venusia*-like 11 *agenor*-male-like
8961	male-like 8923	8920	18	13	7 *anura*-like 6 *agenor*-male-like
8962	male-like 8923	8920	30	9	5 *anura*-like 4 *agenor*-male-like
8967	male-like 8924	8920	20	19	12 *venusia*-like 7 *agenor*-male-like

† The hindwing pattern of these looked like that of *venusia* or *venusia*/*agenor* heterozygotes. However, the body was black with the yellow tuft typical of *zephyria*.

‡ Eight of the male-like and possibly one of the *agenor*-male-like females had a yellow tip to the abdomen.

§ Three and possibly all four of these females had a yellow tip to the abdomen.

Table 7 (*cont.*)

			phenotype of offspring		
brood no.	mother	father	males	females	
		Section (*g*)			
7833	Pupae obtained from wild *achates* females from Hong Kong. May not be sibs		8	4	2 *agenor* 1 *achates* (*alcanor*) 1 *titania*
7879	*titania* 7833	7833	2	2 *titania*	
7962	*agenor* Thailand	7879	1	3	1 *agenor* 2 *titania*
8027	*titania* 7962	7962	0	2	1 *agenor* 1 *titania*
		Section (*h*)			
7279	*agenor*/*laomedon* 7148	7148 (see table 4)	4	2	1 *agenor*-male-like with orange 1 *agenor*-male-like without orange neither scorable for heterozygosity of *agenor* pattern
7289	*agenor*/*laomedon* 7148	7148	5	3	1 *agenor*-male-like with orange 2 *agenor* without orange
7302	*agenor* Hong Kong	7148	0	5	2 *agenor*-male-like with orange 1 *agenor* with orange 1 *agenor* without orange 1 unscorable, deformed
7315	*agenor* Hong Kong	7148	8	3	1 *agenor* with orange 1 *agenor* without orange 1 *agenor*-male-like without orange
7326	*agenor* Hong Kong	7148	5	4	2 *agenor*-male-like without orange 1 *agenor* without orange 1 unscorable, deformed
8327	*laomedon* North Borneo	8202 (see table 4)	4	4	1 *agenor*-male-like with marked spread of orange 1 *agenor*-male-like with slight spread of orange 2 male-like
		Section (*i*)			
8457	*laomedon* (dark-winged) North Borneo	8384 (see section *a*)	42	55	21 dark forewings: 12 with *agenor* window 9 without *agenor* window 27 light forewings: 12 with *agenor* window 15 without *agenor* window 7 deformed, unscorable for forewing

the segregation of modifiers. This view is strengthened by the presence of a few white scales on the hindwing of this insect, a character not associated with the normal male-like phenotype. If this second interpretation be true, then *achates and thunbergi* are probably allelic.

(*e*) *Allelomorphism of f.* zephyria, *f.* agenor, *f.* thunbergi *and f.* laomedon

In brood 8747 an *achates* (*alcanor*)/*zephyria* female (8598) was mated to a *parinda* male which must, therefore, have been homozygous for the allelomorph producing the male-like pattern. This brood produced two recognizable *achates*/male-like heterozygotes. In broods 8730 and 8737 two *parinda* females were mated to the same male from 8598 and produced between them four *agenor*-like and four *zephyria*-like females. Thus the male must have been heterozygous for *zephyria* and *agenor*. The three broods are therefore double back-crosses and in the absence of linkage between *zephyria* on the one hand and *achates* and *agenor* on the other (*achates* and *agenor* being known to be allelomorphic, or very closely linked), would be expected to give a ratio of 2 *zephyria* to 1 *achates* or *agenor* to 1 male-like. Thus there is a significant deficiency ($P < 0{\cdot}02$) of male-likes among the six non-*zephyria* insects, demonstrating that the locus controlling *zephyria* is closely linked or allelomorphic with that (or those) controlling *agenor* and *achates*. Since all the *zephyria*-like females had yellow at the tip of the abdomen and none of the *agenor*-like did, the gene controlling the large window of *zephyria* must also control the yellow tip on the abdomen characteristic of the Palawan females (or be linked to the locus concerned).

In brood 8777 a *zephyria*-like female from brood 8651 (obtained by mating an *achates* heterozygous for *thunbergi* to a Palawan male, and therefore heterozygous for both *zephyria* and *thunbergi* was back-crossed to a male homozygous for *laomedon*, of pure Borneo stock. The three non-*zephyria* offspring were *thunbergi*-male-like, supporting the view that *thunbergi* and *zephyria* are allelic or closely linked, and that *thunbergi* and *achates* are also allelomorphic (see p. 74) since *achates* and *zephyria* are known to be controlled by the same locus, or by closely linked loci.

The *zephyria*-like insects all had the characteristic yellow tip to the abdomen, whereas the *thunbergi*-male-like ones did not, confirming that the gene controlling the *zephyria* pattern also controls the yellow on the abdomen (or is closely linked).

That the latter hypothesis is the correct one is suggested by another Borneo race cross this time not involving the *zephyria* pattern (table 7 (*e*)). Here brood 8923 resulted from a pure Borneo female f. *laomedon* without yellow at the tip of the abdomen, mated to a male heterozygous for *agenor* and *laomedon*. The offspring were ten *agenor*, all but one having a black tip to the abdomen. This one insect had a suggestion of yellow scales. There were also 11 *laomedon*, eight with the yellow tip and three apparently without. Thus there is strong evidence for linkage between the presence or absence of a yellow tip to the abdomen and wing pattern.

That the association is not due to the suppression of the yellow tip by the gene controlling the *agenor* pattern is demonstrated by brood 8941 (which had the same male parent) in which there were six *agenor*, two homozygous for *agenor* and four heterozygous for *laomedon* (see p. 63). Three and possibly four of the latter had a yellow tip to the abdomen which was absent in the homozygotes.

Brood 8777 gives evidence on the relationship between *zephyria* and *venusia*. The pattern of the hindwings of the *zephyria*-like insects in this brood was indistinguishable from that of *venusia* with respect to the size of the pale areas and the reduction of the black hindwing border to a row of black spots. The orange colour was variable but sometimes as intense as that in *venusia* (plate 8*j*). The fact that the allelomorph controlling *zephyria* in a gene-complex half of which is derived from pure Borneo stock, produces a pattern indistinguishable from *venusia* suggests that the allelomorphs are the same and the differences in pattern due to the rest of the gene-complex. The hypothesis that the *venusia* allelomorph was introduced from the Borneo stock can be refuted for two reasons: (1) the fact that none appeared among the 11 sisters of the father (all being *laomedon*, the recessive) and (2) the fact that none of the 8777 females had the yellow body of *venusia*.

(*f*) *Allelomorphism of f.* venusia, *f.* anura *and f.* achates

Brood 8855 segregated for *venusia* and *laomedon* and was not carrying *anura*. Brood 8835 segregated *anura* and *laomedon* and was not carrying *venusia*. The female parent of 8920 (table 6 (*b*)) (see p. 67) was derived from a cross between these broods. The male parent of brood 8920 was pure Hong Kong and was homozygous for *agenor*. The offspring segregated 11 *anura-agenor* and eight *venusia-agenor*. The absence of *agenor*-male-like heterozygotes shows that *venusia* and *anura* are allelomorphic or very closely linked.

We have no breeding data which would enable us to detect linkage between *achates* and either *venusia* or *anura* directly. However, that *venusia* and *anura* are allelomorphic to *achates* is conclusively demonstrated by the offspring of 13 broods in which individuals heterozygous for *venusia*/*agenor* and *anura*/*agenor*, mated to male-like, produced no male-like in 101 females (see table 7 (*f*) for the largest broods). This demonstrates that *agenor* is allelomorphic to the other two forms which itself is allelomorphic to *achates*.

(*g*) *f.* titania *and its linkage relationship with f.* achates

F. *titania*, with the wing pattern of *agenor* but the presence of long tails, is reported as a great rarity from Taiwan where the usual forms are *achates* and *agenor*. A single specimen somewhat similar to this form appeared among the imagines emerging from wild pupae sent to us from Hong Kong. This insect had a black body but the tails and white window of *achates* (*alcanor*) (plate 9*g*). The tailed condition behaved as a dominant, sex-controlled character in a race cross (table 7 (*g*)), as does the tailed condition of *achates* in all crosses. Since no similar specimen is known to us from Hong Kong, and it is unlikely that it had migrated or been imported from Taiwan, we assume that this is again a rare 'mutant' form and not part of the normal polymorphism. In view of the presence of *achates* in Hong Kong it seems to us likely that this 'mutant' has arisen as a result of a crossover and that the characters forming the *achates* pattern are controlled by a super-gene. On this hypothesis the crossover has separated the allelomorph determining the body colour from those controlling the tailed condition and the *achates* pattern on the hindwing. This view is strengthened by the appearance of forms in other regions. For example, in Borneo, *venusia* has the typical body coloration of *achates* but no tails and an entirely different hindwing pattern. *Anura*, on the other hand, has the hindwing window and the yellow body of *achates* but no tails. If our interpretation is correct, the allelomorph controlling body colour


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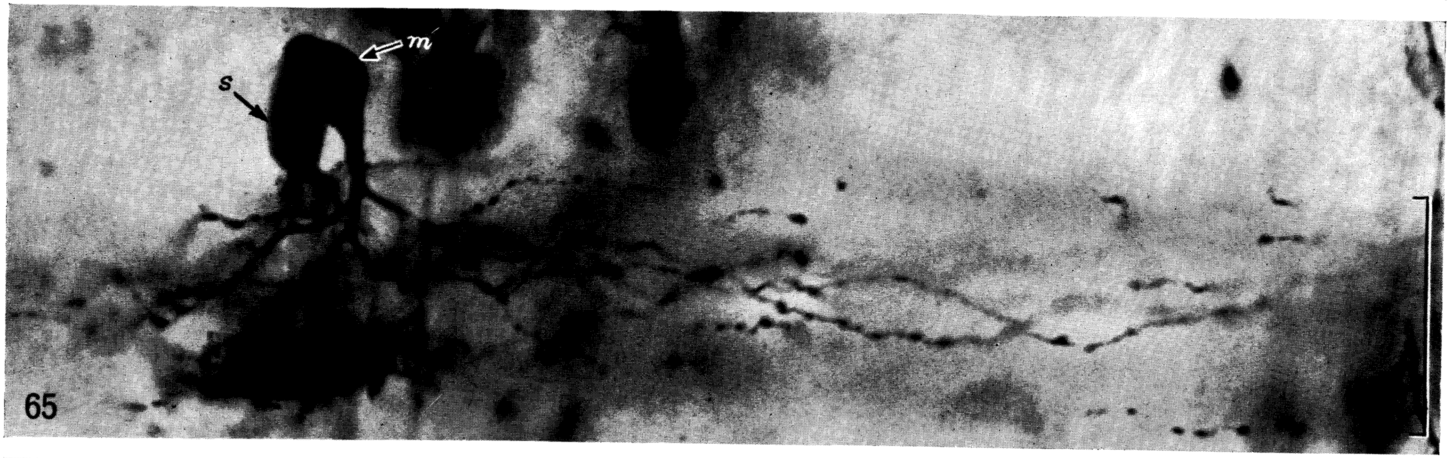
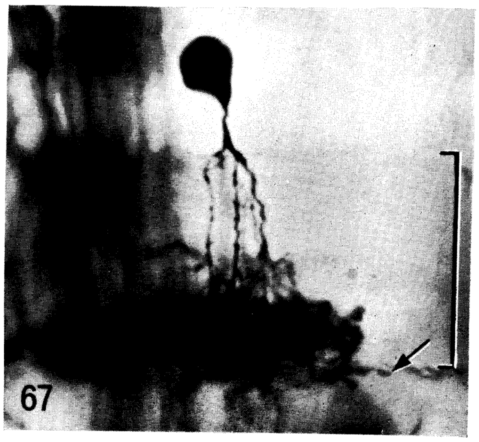
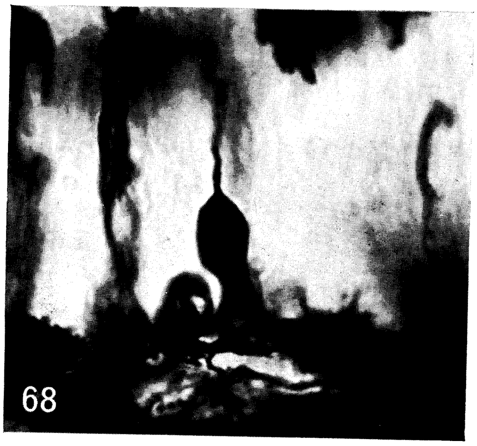
64


65


66


67


68

Furthermore, the monomorphic tailed condition found in the Palawan insects, but not in those from the other areas studied (excepting *achates*), is controlled also by a single locus unlinked to the multiple allelomorphic series or super-gene determining the main polymorphism. We have no information on whether it is linked to the locus controlling the presence or absence of a suffusion of yellow on the hindwing or that affecting the colour of the forewing.

Table 8

Closely linked loci within the super-gene

The locus denoted by T controls the presence or absence of tails. T determines their presence and t their absence, the presence being dominant. The locus W controls the pattern on the wings, W^d controlling that of *distantianus*, W^{al} *alcanor*, W *agenor*, W^v *venusia*, W^t *thunbergi* (may $= W$), w^b *butlerianus*, w^e *esperi*, w male-like, and w^l *laomedon*.

The locus B controls the colour of the abdomen, B^Y yellow abdomen (with a dorsal and ventral black stripe), b^y black abdomen with a yellow tip, and b black abdomen.

Unlinked loci

Two loci are unlinked to the super-gene, P and Y. P is not sex-controlled in effect and determines the presence or absence of tails, p^T determining their presence in both males and females, and p^t their absence.

The locus Y determines the presence or absence of a yellow suffusion on the hindwings, Y controlling the presence of the suffusion.

form	super-gene	super-genes recessive in effect	other major genes
achates (*distantianus*)	$T\ W^d\ B^Y$	$t\ W\ b,\ t\ w^e\ b,\ t\ w^b\ b$	$p^t\ p^t\ y\ y$
achates (*distantianus yellow*)	$T\ W^d\ B^Y$	$t\ W\ b,\ t\ w^l\ b$	$p^t\ p^t\ Y\ Y$
achates (*alcanor*)	$T\ W^{al}\ B^Y$	$t\ W\ b$	$p^t\ p^t\ y\ y$
titania (Taiwan)	$T\ W\ b$		$p^t\ p^t\ y\ y$
titania (Hong Kong)	$T\ W^{al}\ b$	$t\ W\ b$	$p^t\ p^t\ y\ y$
agenor	$t\ W\ b$		$p^t\ p^t\ y\ y$
agenor (yellow)	$t\ W\ b$	$t\ w^l\ b$	$p^t\ p^t\ Y\ Y$
thunbergi	$t\ W^t\ b$		$p^t\ p^t\ y\ y$
butlerianus	$t\ w^b\ b$		$p^t\ p^t\ y\ y$
esperi	$t\ w^e\ b$	$t\ w^b\ b$	$p^t\ p^t\ y\ y$
parinda	$t\ w\ b$		$p^t\ p^t\ y\ y$
laomedon	$t\ w^l\ b$		$p^t\ p^t\ Y\ Y$
laomedon	$t\ w^l\ b^y$		$p^t\ p^t\ Y\ Y$
anura	$t\ W^d\ B^Y$	$t\ w^l\ b$	$p^t\ p^t\ Y\ Y$
venusia	$t\ W^v\ B^Y$	$t\ w^l\ b,\ t\ W^d\ B^Y*$	$p^t\ p^t\ Y\ Y$
zephyria	$t\ W^v\ b^y$	$t\ w\ b^y$	$p^T\ p^T\ y\ y$
suffusus	$t\ w\ b^y$		$p^T\ p^T\ y\ y$

* at least some of the heterozygotes may be recognizable.

VII. Discussion

Previous investigation into the genetic control of mimicry in *P. dardanus* revealed that the polymorphic characters were controlled by one locus, or by a closely linked group of loci and that one non-polymorphic character, the presence or absence of tails on the hindwing, was controlled at an independent one. It was further found that dominance was frequently absent between characters controlled by allelomorphs whose distributions were allopatric, but present when they were sympatric. It was also shown that the mimetic patterns were made up of rather few basic elements in different combinations. From these results it was concluded that the explanation of the evolution of mimicry suggested by Fisher and Ford (Ford 1953) was correct. They maintained that in the initial stages of the evolution of mimicry a mutant becomes established which gives a sufficient resemblance to the model to be advantageous, and that this is gradually improved by the selection of modifiers which alter the effect produced by the mutant. We (Clarke & Sheppard 1960*a*, *b*, *c*) pointed out that the results from *P. dardanus* supported the view that when a new mutant arises for the first time, dominance may be absent and that as a result of disruptive selection dominance is evolved, since there are initially three phenotypes, only two of which are optimal. Furthermore, the control of all the mimetic patterns by what appeared to be a multiple allelomorphic series suggested to us that during the evolution of this complex mimetic situation in *P. dardanus*, a super-gene had evolved along the lines suggested by Sheppard (1953) and by Mather (1955). Subsequent investigation of *P. dardanus* (unpublished) has strengthened this view since one form, f. *salaami*, then only known to be formed as a heterozygote between two allelomorphs controlling other patterns (Clarke & Sheppard 1959) has since been shown also to be controlled by a single gene, suggesting that the latter condition has arisen as a cross-over within the super-gene.

The present investigation in *P. memnon* was designed to throw light on all these points by using a mimetic species from a different faunal region in which the accepted view (Baur 1911; Fryer 1913; Punnett 1915; Cockayne 1932; Goldschmidt 1945; Ford 1953; and Clarke & Sheppard 1960*b*) was that (in contradistinction to *P. dardanus*) more than one locus was involved in the control of the mimetic pattern.

1. *The evolution of mimicry*

The genetic investigation of mimicry in *P. memnon* has shown quite clearly that there is an allelomorphic series responsible for the various patterns of the wings and that the genes do not have the same effect in all gene-complexes. Thus the resemblance between the mimetic forms and their models is greater in the gene-complex of a race in which the allelomorph is found than in hybrids with a race in which it does not occur. In comparing the resemblance between model and mimic within races and in race crosses, the resemblance in the cross is better in 0 cases, as good in 10, and poorer in 35. This finding is entirely consistent with that in *P. dardanus* and adds great weight to Fisher's and Ford's view that mimicry evolved gradually by the adjustment of the whole gene-complex as the result of natural selection for a better resemblance between model and mimic. The comparison between *P. memnon* and *P. dardanus* with respect to the inheritance of the length of the tails on the wing corroborates this view. In *P. dardanus* there is evidence that in the tailed Madagascar race there is stabilizing selection in favour of the presence of long tails, whereas in Abyssinia there is disruptive selection favouring long tails in the male-like females, but discriminating against them in the mimetic forms, the models being tailless (Clarke & Sheppard 1962).

In *P. memnon* there are modifiers increasing tail length in the tailed Palawan race but decreasing it in the other races. Moreover, there is evidence of stabilizing selection since tail length has a low variance in pure races compared with F_1 hybrids. This indicates that the tailless races segregate for modifiers of tail length in a way that the tailed Palawan race does not, suggesting that there has been selection against segregation in the latter.

Within the tailless races there are mimetic forms (f. *achates*) which are tailed. The presence of this character is determined by an allelomorph sex-controlled in effect and part of the super-gene controlling the mimicry. The mean tail length of these forms is 12·82 mm with a variance of 2·40. The F_1 hybrid with the Palawan race has a mean tail length of 13·72 mm and a variance of 2·00. Thus the tail length of the F_1 is significantly greater than that of pure *achates* ($t_{85} = 3{\cdot}09$ $P < 0{\cdot}01$), but there is no increase in variance. However, in the back-cross to the tailless race, the mean tail length is 12·40 and the variance 6·48. There is therefore a significant increase in variance here ($P < 0{\cdot}05$). This finding again suggests that there is stabilizing selection reducing variance of tail length in the mimics. However, it is not certain whether much of the variance in the back-cross is not due to segregation for the gene determining the presence or absence of tails in the Palawan race.

2. *The evolution of dominance*

In *P. memnon*, as in *P. dardanus*, heterozygotes between allelomorphs taken from the same population show complete dominance more often than heterozygotes resulting from the crosses between allopatric genes. Thus, here again there is evidence that dominance is not an attribute of the allelomorphs themselves, but depends on the whole genetic constitution. The evidence gives direct support to the view that dominance is often evolved.

An examination of the tail length of a number of crosses between the monomorphic tailed race from Palawan and the 'tailless' races from elsewhere suggests that dominance has evolved, even in the absence of a polymorphism. The comparison between the Palawan stocks, the F_1 broods, the F_2 and the back-cross to Palawan insects shows that the 'tailless' condition is recessive in most butterflies of this back-cross. Thus, the data suggest that the condition must be recessive in the pure Palawan race, where the character can only be maintained as the result of recurrent mutation.

By contrast, a comparison between the F_1 and a back-cross to the 'tailless' races shows that the tailed condition is completely recessive in some insects. Moreover, the data also suggest that the greater the proportion of the gene-complex of the 'tailless' race that is present, the greater the frequency of these recessives. In the races where the allelomorph controlling the tailed condition is only maintained by recurrent mutation, this character tends to be recessive. Thus, in both 'monomorphic' areas the rarer condition, whichever it may be, is the more recessive. The absence of complete recessiveness in tailed individuals back-crossed to the tailless race may result from the presence of non-specific modifiers selected to maintain the dominance of the independently inherited tailed condition of *achates*.

Similar evidence has been obtained from *P. dardanus* (Clarke & Sheppard 1960*d*, 1963). All the females in Madagascar are non-mimetic and tailed (mean tail length 14·38 mm, variance 1·05) but all are tailless in South Africa. The tailed condition is more recessive in the first back-cross to the South African race (the mean of 3·30 mm is an over-estimate and the variance of 0·65 an under-estimate since tailed and tailless insects could not always be distinguished) than in the F_1 (mean 4·38 mm, variance 2·74), which is in agreement with the *memnon* results. No back-cross to the Madagascan race has yet been obtained but in the F_2 tailless appeared to be a recessive. There were two tailless individuals (1·50 mm) and four tailed ones (mean 13·64 mm, variance 4·55). The back-cross to the tailed Ethiopian race is not informative, since there is disruptive selection acting, owing to the presence of both mimetic and non-mimetic females (Clarke & Sheppard 1962).

The Madagascan race as well as being tailed is monomorphic for the male-like pattern, which does not occur in the largely mimetic South African race. The heterozygote in the F_1 between the yellow male-like form and the mimetic pattern is intermediate in appearance, as it is in the F_2. However, the male-like pattern is almost completely recessive in the first back-cross to the South African race, where the form does not occur. This contrasts markedly with the situation in Ethiopia where both types of pattern occur as a polymorphism and where the male-like pattern is completely dominant! Thus, here again there is evidence that the pattern maintained solely by recurrent mutation is the recessive even when it is a dominant elsewhere.

In *P. dardanus* the situation in Ethiopia is particularly relevant to the problem of the evolution of dominance in polymorphic situations as distinct from monomorphic ones. The allelomorphs producing the mimics f. *cenea* and f. *hippocoonides* were recessive to the male-like form of female in this race (Clarke & Sheppard 1960*d*), where all three occur. In contrast they produced intermediate heterozygotes in crosses between the South African race and the Madagascan race. The allelomorphs controlling *cenea* and *hippocoonides* are not found in Madagascar and that producing the male-like form is not found in South Africa. Thus, as pointed out above, there was complete dominance where the three allelomorphs involved are sympatric, but no dominance in F_1 crosses between races where the very same allelomorphs are allopatric. An entirely analogous situation has been found in *P. memnon*. Thus, there is complete dominance between the forms *achates* (*distantianus*), *esperi* and *butlerianus* in Malaya, where all three mimetic forms are found. However, in crosses involving both Hong Kong and Thailand material where *distantianus* is found but *esperi* and *butlerianus* are not, dominance often breaks down and *distantianus*/*esperi* and *distantianus*/*butlerianus* heterozygotes are recognizable. Similarly, the non-mimetic form *agenor* appears to be dominant or nearly so to the male-like form in Thailand stock and in F_1 hybrids with other races where the male-like form is found; in this respect it is important to note that the male-like form *is* found in Thailand. In contrast, *agenor* from Hong Kong, where male-like is not found, produces a more intermediate F_1 heterozygote with male-like in crosses with the very same races. Thus, there is good evidence that, as in *P. dardanus*, the presence of complete dominance and recessiveness within races is dependent on the particular gene-complex of the race itself.

There are two possible explanations of this phenomenon. One is that the dominance evolved gradually as the result of the selection for modifiers on the lines suggested by Fisher (1928); the other, that the particular allelomorph has been selected just because it was dominant in the particular gene-complex concerned from the beginning. This latter hypothesis is a slight modification of Haldane (1930, 1939), who suggested that more active genes which were dominant in all gene-complexes would replace those which would produce an intermediate heterozygote in the presence of a less active mutant, as the result of selection. As Ford (1930, 1931) has pointed out, the two hypotheses do not differ materially since the level at which a gene may be judged more or less active depends on the rest of the genetic constitution. Nevertheless, under one hypothesis dominance will be complete from the beginning; under the other, the heterozygote will gradually come to resemble one of the homozygotes as the result of the selection for modifiers. Which hypothesis is the correct one in any particular situation cannot be determined without an historical record of the progress of the evolution.

That an historical record is essential in distinguishing between the two hypotheses is well illustrated by industrial melanism in the moth *Biston betularia* (L). Kettlewell (1958) pointed out that the original melanic forms (*carbonaria*) were less extreme than known present-day heterozygotes for this dominant character. This suggests that the dominance of the black form has been evolved since 1848, when the first one was caught. He has shown recently (1965), however, that this cannot be due to selection of modifiers, since on out-crossing the present-day melanics from an industrial area to Cornish stock, where the black form is not found, dominance remains almost complete. Thus, a new gene dominant in effect has replaced, or nearly replaced, the original one which determined the presence of *carbonaria* in 1848. However, the dominance is dependent on the particular gene-complex of the British race since on out-crossing to North American stock, he also showed that dominance broke down and heterozygotes intermediate between *carbonaria* and the speckled form were produced. Furthermore, these heterozygotes were different in phenotype from the early British specimens. If the latter had not been available as an historic record, it would not have been possible to determine whether dominance had evolved by the selection of specific modifiers, as suggested by Fisher (1928), or as the result of selection for a gene already dominant in that particular gene-complex.

There is no record of the stages in the evolution of mimicry of *P. memnon* and *P. dardanus*, and therefore it is impossible to show unequivocally whether the dominance was evolved by the selection of dominant mutants or by the selection of modifiers. However, since several loci incorporated into a super-gene appear to be involved in the mimicry (see below) it is difficult to believe that the dominance has arisen by the selection of dominant mutants. Such a hypothesis would require that dominants had to be accumulated at each of the several loci in the super-gene and this would be a very lengthy process compared with that involved in the selection of modifiers. Therefore, one would expect the evolution of dominance to be completed by the selection of modifiers before any substantial progress had been made through the selection of dominant mutants.

3. *Mimicry and the evolution of a super-gene*

At the beginning of the present investigation, it was believed that the mimicry in *P. memnon* was controlled by epistatic interactions between unlinked loci. This is not the case and the mimicry is in fact controlled by what appears to be a multiple allelomorphic series, as in *P. dardanus*. However, in *P. memnon* there is even better evidence that the mimicry is really controlled by a super-gene, in which a number of different loci are aggregated. Thus, the super-gene controlling the *achates* pattern determines not only the presence of tails on the hindwing (that is the shape of the wing), but also body colour and wing pattern. Such a series of distinct characters is not likely to be controlled by a single locus determining the amino acid sequence of a single polypeptide chain. Furthermore, in *P. memnon*, we have better evidence that crossing over occurs within the super-gene itself. If our interpretation be correct, then the order of the loci controlling the various characters is such that the allelomorph determining wing pattern is between the other two (p. 80). The results strongly support the hypothesis of Sheppard (1953) and Mather (1955) that in a polymorphism with disruptive selection, such super-genes will evolve.

It is impossible to say whether the loci involved were originally on the same chromosome or have been moved as the result of selection for translocations. Whichever hypothesis be true, there will be selection for linkage because crossing-over and independent assortment will produce deleterious combinations of characters. In this connexion it is important to note that the presence of tails could have been evolved by the selection of a gene unlinked to those determining the other *achates* characters (wing pattern and body colour) had such a situation been favoured by natural selection. Tails are inherited independently of the super-gene in the Palawan race, where there is no polymorphism for the tailed condition. This again parallels the situation in *P. dardanus*, where the control of tails in the Madagascan and Ethiopian races is independent of the super-gene controlling colour pattern. The main difference is that in *P. memnon* there are two loci determining the presence or absence of tails, one sex-controlled and the other not, whereas in *P. dardanus* there is only one and that is sex-controlled. Thus, though the inheritance of tails is more complex in *P. memnon*, it resembles *P. dardanus* in that in both species the locus concerned specifically with mimicry is sex-controlled.

The conclusions on the mechanisms controlling the evolution of mimicry, of dominance and of super-genes, obtained from the study of *P. dardanus* are strikingly confirmed by the study of *P. memnon*. Moreover, it cannot be objected that the similarities of the results are due to the fact that in both cases a member of the genus *Papilio* has been studied. *Heliconius melpomene* (L.) and *Heliconius erato* (L.) are Müllerian mimics, whereas *P. dardanus* and *P. memnon* are Batesian. Nevertheless, there is genetic evidence for the gradual evolution of mimicry and the evolution of dominance in these heliconids since the mimetic forms differ at several loci and dominance is less common amongst allopatric than amongst sympatric forms. However, polymorphism in these species unlike that in *Papilio* is maintained by hybridization between adjacent monomorphic races. Consequently there is not likely to be disruptive selection favouring the evolution of super-genes, as there is in polymorphic species of *Papilio*. The genetic investigations of Turner & Crane (1962), Sheppard (1963), Emsley (1964), J. R. G. Turner (personal communication), and G. M. Emsley (personal communication), although giving some evidence of linkage, give none for the presence of a super-gene. In fact, strikingly different forms are controlled by several independent loci. Thus, super-genes are characteristic of polymorphic situations where there is disruptive selection favouring linkage between loci, and not of non-polymorphic differences, even when they are striking and involve mimicry.

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REFERENCES

Ae, S. A. 1964 Hybrids between *Papilio memnon* and *P. helenus* and between *P. memnon* and *P. protenor*. *J. Res. Lepid.* 3, 55–62.

Ae, S. A. 1966 A study of hybrids between Japanese and Himalayan *Papilio* butterflies. *Spec. Bull. Lep. Soc. Jap.* 2, 75–107.

Baur, E. 1911 *Einführung in die experimentelle Vererbungslehre*, pp. 155–159. Berlin: Verlag von Gebrüder Borntraeger.

Brower, L. P., Brower, J. VZ. & Collins, C. T. 1963 Experimental studies of mimicry. 7. Relative palatability and Müllerian mimicry among neotropical butterflies of the subfamily Heliconiinae. *Zoologica* **48**, 65–84.

Clarke, C. A. & Sheppard, P. M. 1956 Hand-pairing of butterflies. *Lepid. News* **10**, 47–53.

Clarke, C. A. & Sheppard, P. M. 1959 The genetics of *Papilio dardanus*, Brown. I. Race *cenea* from South Africa. *Genetics*, **44**, 1347–1358.

Clarke, C. A. & Sheppard, P. M. 1960*a* The evolution of dominance under disruptive selection. *Heredity* **14**, 73–87.

Clarke, C. A. & Sheppard, P. M. 1960*b* Super-genes and mimicry. *Heredity* **14**, 175–185.

Clarke, C. A. & Sheppard, P. M. 1960*c* The evolution of mimicry in the butterfly *Papilio dardanus*. *Heredity* **14**, 163–173.

Clarke, C. A. & Sheppard, P. M. 1960*d* The genetics of *Papilio dardanus*, Brown. III. Race *antinorii* from Abyssinia and race *meriones* from Madagascar. *Genetics* **45**, 683–698.

Clarke, C. A. & Sheppard, P. M. 1962 Disruptive selection and its effect on a metrical character in the butterfly *Papilio dardanus*. *Evolution* **16**, 214–226.

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., Dickson, C. G. C. & Sheppard, P. M. 1963 Larval color pattern in *Papilio demodocus*. *Evolution* **17**, 130–137.

Cockayne, E. A. 1932 A new explanation of the genetics of sex-limited inheritance in butterflies. *Entomologist* **65**, 169–176.

Corbet, A. S. & Pendlebury, H. M. 1956 *The butterflies of the Malay Peninsula*, 2nd ed. Edinburgh: Oliver and Boyd.

Emsley, G. M. 1964 The geographical distribution of the color-pattern components of *Heliconius erato* and *Heliconius melpomene* with genetical evidence for the systematic relationship between the two species. *Zoologica* **49**, 245–286.

Fisher, R. A. 1928 The possible modification of the response of the wild type to recurrent mutations. *Am. Nat.* **62**, 115–126.

Ford, E. B. 1930 The theory of dominance. *Am. Nat.* **64**, 560–566.

Ford, E. B. 1931 *Mendelism and evolution.* London: Methuen.

Ford, E. B. 1944 Studies on the chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 3. The red pigments of the Papilionidae. *Proc. R. Ent. Soc. Lond.* (A) **19**, 92–106.

Ford, E. B. 1953 The genetics of polymorphism in the Lepidoptera. *Advanc. Genet.* **5**, 43–87.

Fryer, J. C. F. 1913 An investigation by pedigree breeding into the polymorphism of *Papilio polytes*, Linn. *Phil. Trans.* B **204**, 227–254.

Goldschmidt, R. B. 1945 Mimetic polymorphism, a controversial chapter of Darwinism. *Quart. rev. biol.* **20**, 147–164, 205–230.

Haldane, J. B. S. 1930 A note on Fisher's theory of the origin of dominance, and on a correlation between dominance and linkage. *Am. Nat.* **64**, 87-90.

Haldane, J. B. S. 1939 The theory of the evolution of dominance. *J. Genet.* **37**, 365–374.

Jacobson, E. 1909 Beobachtungen über den Polymorphismus von *Papilio memnon* L. *Tijdschr. voor Entomolog.* **52**, 125–157.

Jacobson, E. 1910 Corrigenda zu Beobachtungen über den Polymorphismus von *Papilio memnon* L. *Tijdschr. voor Entomolog.* **53**, 195.

Kettlewell, H. B. D. 1958 A survey of the frequencies of *Biston betularia* (L.) (Lep.) and its melanic forms in Great Britain. *Heredity* **12**, 51–72.

Kettlewell, H. B. D. 1965 Insect survival and selection for pattern. *Science* **148**, 1290–1296.

Mather, K. 1955 Polymorphism as an outcome of disruptive selection. *Evolution* **9**, 52–61.

de Meijere, J. C. H. 1910 Über Jacobsons Züchtungsversuche bezüglich des Polymorphismus von *Papilio memnon* L. ♀ und über die Vererbung sekundärer Geschlechtsmerkmale. *Z. ind. Abst. u. Vererbungslehre* **3**, 161–181.

Morrell, R. 1960 *Papilio memnon agenor* L. in Singapore: some problems of mimicry. *Malayan Nature J.* **8**, 109–115.

Munroe, E. 1961 The classification of the Papilionidae (Lepidoptera). *The Canadian Entomologist.* (Suppl.) **17**, 1–51.

Punnett, R. C. 1915 *Mimicry in butterflies.* Cambridge University Press.

Rothschild, W. 1895 A revision of the Papilios of the Eastern Hemisphere, exclusive of Africa. *Novitates Zoologicae*, **2**, 167–465.

Seitz, A. 1908 *The macrolepidoptera of the world.* II. *Fauna Indoaustralica.* Stuttgart: Fritz Lehman Verlag.

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.

Shirôzu, T. 1960 *Butterfiies of Formosa in colour.* Japan: Hoikusha.

Turner, J. R. G. & Crane, J. 1962 The genetics of some polymorphic forms of the butterflies *Heliconius melopomene Linneaus* and *H. erato Linnaeus.* I. Major genes. *Zoologica* **47**, 141–152.

Villalobos-Dominguez, C. & Villalobos, J. 1947 *Colour atlas.* Buenos Aires: E. L. Ateneo.

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