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

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[Plates 40 to 42]

CONTENTS

Papilio polytes L. is a mimetic Swallowtail butterfly widely distributed in South East Asia. It has four female forms, three mimetic, and one non-mimetic resembling the monomorphic male in appearance. The various female forms are now shown to be controlled by allelomorphs at a single autosomal locus and not by independent genes as previously thought. The effects of the allelomorphs controlling the mimetic patterns are sex-limited to the female. There is some evidence that the locus is a complex one consisting of two or more tightly linked genes. As in previous investigations into mimicry in Swallowtails the dominance tends to be complete between sympatric forms.

The accuracy of the mimicry depends not only on the presence of the appropriate major genes but also on the rest of the gene complex. Thus within a race there is an integrated genetic system and on outcrossing this becomes disturbed, leading to poorer mimicry. The system of modifiers controlling the accuracy of the mimetic pattern is closely paralleled by that in *P. dardanus*. In particular, in *P. polytes* f. *theseus* appears to differ from f. *polytes* only as a result of the presence of a modifier system, as does f. *hippocoon* from f. *hippocoonides* in *P. dardanus*.

In *P. dardanus* from Ethiopia it was found that specific modifiers adjusting the tail length of mimetic females have been selected for, thus improving the mimicry. An analogous situation has been found in *P. polytes* although here the control is more effective in that the resulting difference in tail length between the mimetic and non-mimetic forms can be as much as 10 mm, whereas in *P. dardanus* it rarely exceeds 3 mm.

The great similarity in the genetic structure of *P. polytes* and *P. dardanus* (as well as *P. memnon*) strongly suggests that selection for a mimetic polymorphism results in the evolution of very similar genetic control mechanisms in different species – that is to say it is the nature of the selection rather than the species involved which determines the genetic architecture.

I. INTRODUCTION

The study of mimicry has made important contributions to our understanding of microevolution. Most of the early work was concerned with the distribution of models and mimics, but really to understand the processes acting on wild populations one has to conduct experiments in the field and laboratory and also analyse the situation genetically.

In our previous investigations (see Clarke & Sheppard 1963, 1971*a*; Clarke, Sheppard & Thornton 1968) we have concentrated on the genetic analysis of mimetic situations and the results have led us to conclude:

(1) That mimicry evolves gradually as the result of a modification of the effects of the mutant gene which first gave rise to the imperfect resemblance between the potentially mimetic species and its future model.

(2) That if the original mimetic form initially showed no dominance then dominance will evolve and the mimic will usually become dominant. If, however, the mimetic species is already polymorphic or becomes so because of immigration of mimetic forms then the mimic may become recessive (Clarke & Sheppard 1960*a*; Sheppard 1962).

(3) Since Batesian mimicry tends to promote polymorphism, the major genes controlling the mimicry must either have appropriate epistatic interactions which avoid the production of deleterious non-mimetic combinations of characters, or perhaps more often be aggregated into a tightly linked supergene. Such supergenes appear to be evolved by the bringing together of mutually advantageous genes not previously linked, by the selection of new mutants that are already linked to the locus controlling the mimicry, and by the production of duplications and their subsequent evolution by mutation and selection (Clarke & Sheppard 1960*c*).

The present study is an investigation into the distribution of the forms of the mimetic Swallowtail *Papilio polytes* L. and its models and the genetic control of the mimetic and non-mimetic forms. This species was chosen because the original genetic investigation (Fryer 1913) suggested that the various forms were controlled by epistatic interactions between unlinked genes rather than by supergenes of the type we had found in *Papilio dardanus* Brown and *Papilio memnon* L. (Clarke & Sheppard 1960*a*, 1971*a*; Clarke *et al.* 1968) on which we based our hypothesis of the processes involved in the evolution of Batesian mimicry.

II. MATERIALS AND METHODS

The geographical distribution of the models of *P. polytes* and the mimetic and non-mimetic forms of this species has been investigated by studying the material in the British Museum (Natural History) and the Hope Museum (Oxford) in conjunction with information in standard works, including Rothschild (1895) and Seitz (1908).

Living material has been sent to us by airmail from many localities in the manner previously described (Clarke *et al.* 1968). The chief collecting areas have been Ceylon, Japan, Hong Kong, Thailand, Malay Peninsula and Singapore, Sumatra, Java, Bali, Borneo and the Philippines. In some of these places one of us (P. M. S.) has himself collected.

The butterflies were bred in our heated greenhouses using the same methods and food plants as for *P. memnon* and *P. dardanus*. In addition, we kept two populations of known genotypes flying and breeding freely on *Citrus* in two additional greenhouses (Clarke & Sheppard 1971*b*).

III. DISTRIBUTION AND DESCRIPTION OF *P. POLYTES* WITH REFERENCE TO THE MODELS OF THE MIMETIC FORMS

The approximate geographical distribution of *P. polytes* is shown in figure 1, and within this area there are a number of subspecies whose locations are also indicated.

1. *The males*

Throughout the species the males are black with a bar of white on the hindwing (plate 41*b*), and there is a row of marginal white spots on the forewing. The details of both of these characters vary slightly from subspecies to subspecies. In all areas except in the extreme east of the distribution the hindwings have the tails characteristic of most Papilios. These are longest in India and Ceylon in the west and tend to become progressively shorter towards the east and south-east (table 1).

2. *The female forms*

There are a number of these which although genetically the same have been given different varietal names (see table 1) because they come from different subspecies. Here we are combining all phenotypically similar forms under one varietal name and this reduces the number of female names to four.

(*a*) f. **cyrus** (plate 41*a*)

This non-mimetic form very closely resembles the male in appearance but tends to have submarginal red marks distally on the hindwing which are reduced or absent in the male. We know of the presence of f. *cyrus* in almost every locality where the species is found (figure 2). In addition to its similarity in pattern to the male, the tail length also varies with locality in parallel with that of the male.

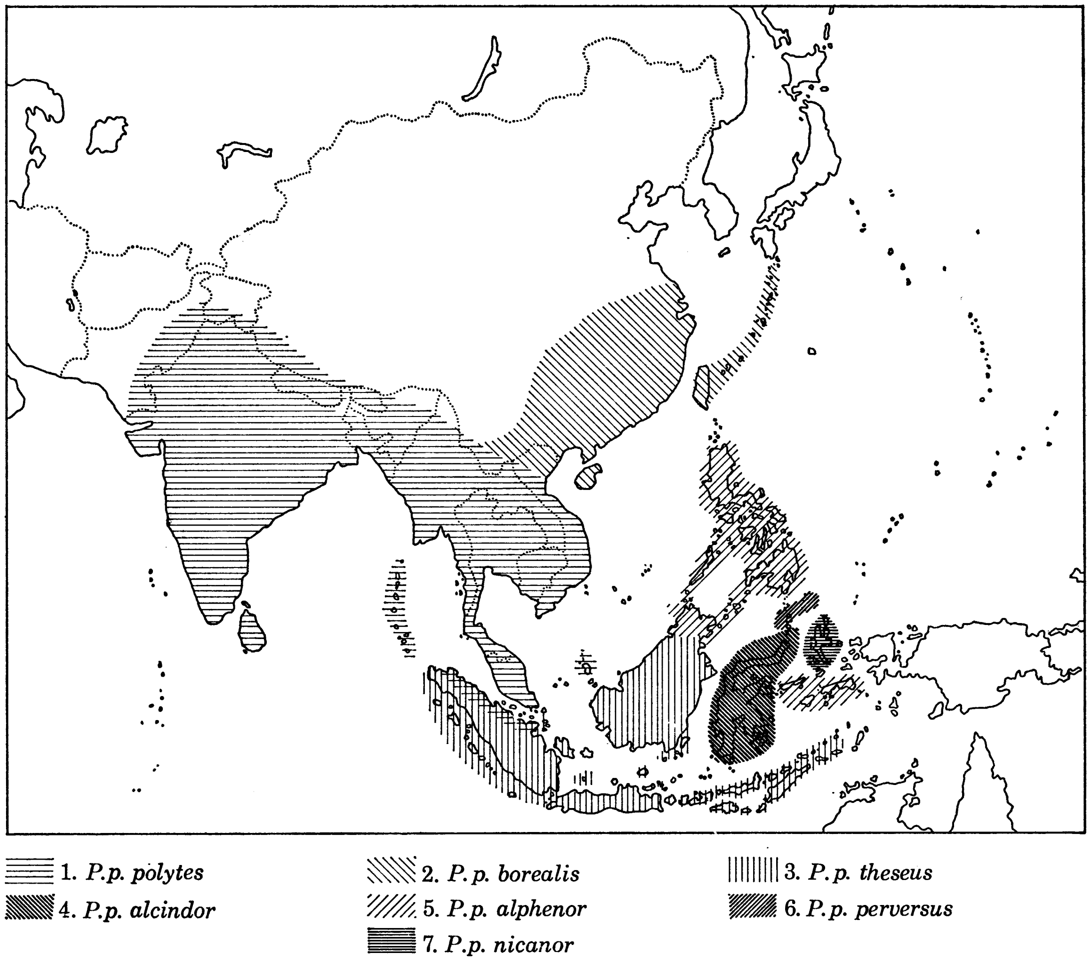

FIGURE 1. The distribution of the races of *P. polytes*.

(*b*) f. **polytes** (plate 40*d*)

The hindwing of this form, which usually has long tails, has a large white area in the centre which frequently extends into the distal end of the cell, a row of submarginal red lunules and a black spot surrounded by red at the anal angle. The background colour is black. The forewing is black proximally but there is a posteriorly narrowed paler central area traversed by black ribbed lines. The marginal white spots present in *cyrus* are reduced to mere vestiges in f. *polytes* and are bordered on the inside by a narrow dark band. This form, which is widespread, follows

TABLE 1. SUBSPECIES OF *PAPILIO POLYTES* WITH MEAN TAIL LENGTHS OF THE VARIOUS PHENOTYPES

	phenotype																		
	cyrus				*polytes*				*romulus*				*theseus*				males		
subspecies	form name	no. of indiv.	tail length mm	S.D.	form name	no. of indiv.	tail length mm	S.D.	form name	no. of indiv.	tail length mm	S.D.	form name	no. of indiv.	tail length mm	S.D.	no. of indiv.	tail length mm	S.D.
polytes	*cyrus*	45	8.61	±0.62	*polytes*	29	9.37	±0.59	*romulus*	11	9.08	±0.53	—	—	—	—	44	7.56	±0.76
borealis	*mandane*	18	8.66	±0.64	*borealis*	8	9.25	±0.86	—	—	—	—	—	—	—	—	28	7.85	±0.85
theseus	*virilis*	43	4.73	±1.12	*javanus* *polyphontes* *polytes*	46	8.54	±1.38	—	—	—	—	*theseus*	36	8.41	±1.14	126	4.41	±1.31
alcindor	—	—	—	—	*alcindor*	18	9.01	±0.53	—	—	—	—	—	—	—	—	15	4.64	±1.92
alphenor northern area	*horsfieldi*	71	2.05	±0.46	*alphenor*	29	9.53	±1.55	—	—	—	—	*elyros*	33	8.84	±1.18	138	1.65	±0.44
southern area	*horsfieldi*	7	2.06	±0.34	*ledebourius*	22	5.69	±3.07	—	—	—	—	—	—	—	—	10	1.71	±0.29
perversus	*martius*	2	1.70	±0.18	*atavus*	3	8.36	±0.86	—	—	—	—	—	—	—	—	6	1.46	±0.24
nicanor	*cyrus*-like (? *manzer* (Seitz))	4	2.18	±0.38	*nicanor*	19	1.93	±0.70	—	—	—	—	—	—	—	—	19	1.57	±0.27

The distribution of each subspecies is given in figure 1. Since *alphenor* is geographically divided by *perversus* and *nicanor* we have calculated mean tail lengths separately for the two regions.

very closely the geographic distribution of its appropriate model (figure 3). Over much of its range this is the variety of *Pachlioptera aristolochiae* (Fabricius) which has a white patch on the hindwings (plate 40*a*). In Celebes its model is *Pachlioptera polyphontes* (Boisduval) (plate 40*g*) which, like *aristolochiae*, has tails on the hindwings. East of Celebes and south of the Philippines the model is the tailless species *Pachlioptera polydorus* (L.) (plate 40*h*). In this area f. *polytes* has tails that are reduced or absent.

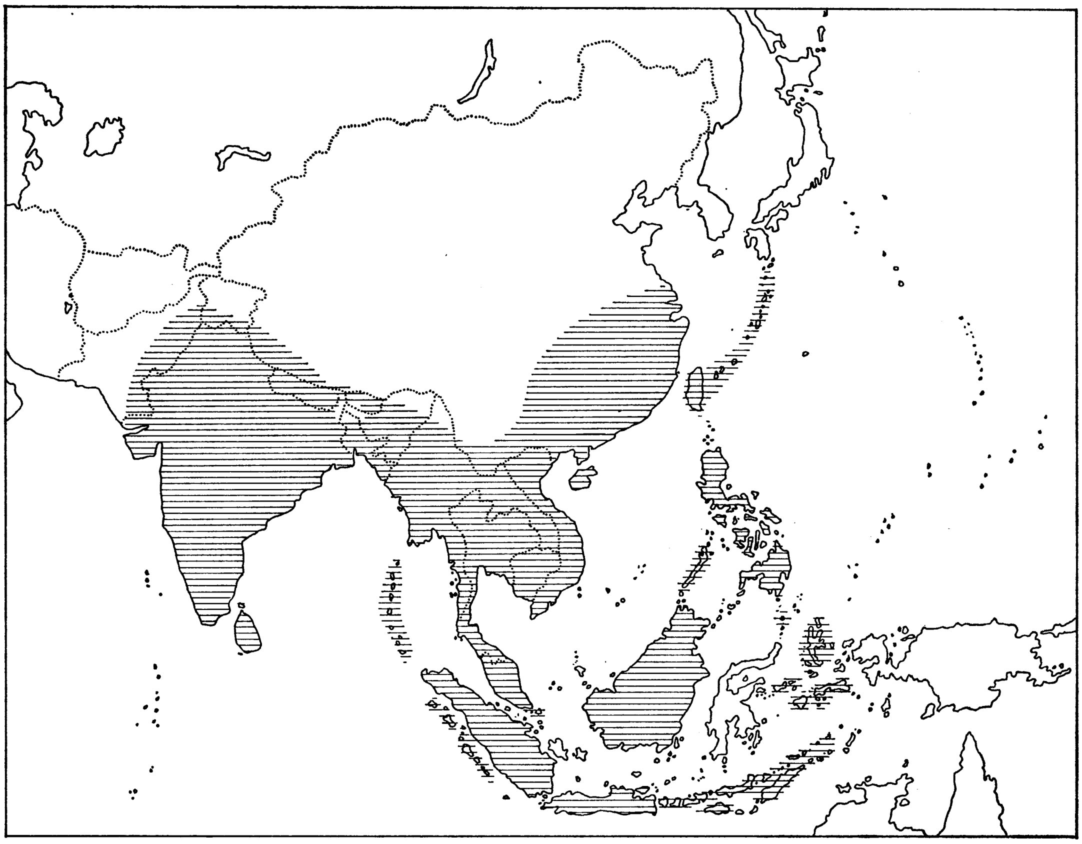

FIGURE 2. The distribution of *P. polytes* f. *cyrus*.

(*c*) f. **romulus** (plate 40*e*)

The hindwing of this form, which always has long tails, lacks the white area of f. *polytes* and the white band of f. *cyrus*. The size of the red submarginal lunules tends to be greater than in f. *polytes*, and the area of the white band of f. *cyrus* nearest to the anal margin of the wing is replaced by smaller red spots in f. *romulus*. In addition, there is sometimes a red spot at the distal end of the cell. The forewing of f. *romulus* has a black proximal area as in f. *polytes*, but the

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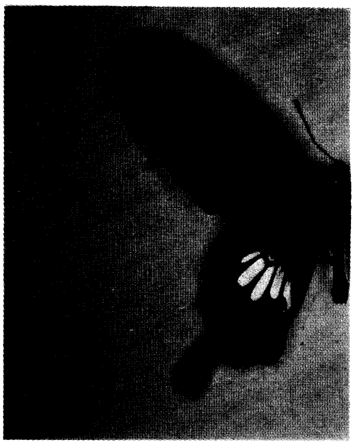
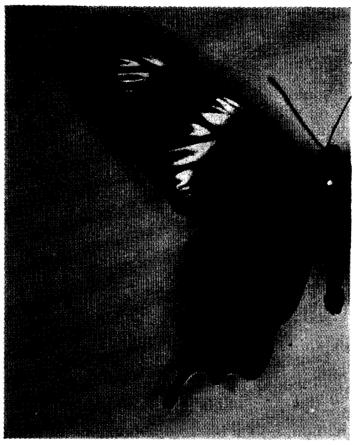
DESCRIPTION OF PLATE 40

(*a*) *Pachlioptera aristolochiae*, white form	(*g*) *Pachlioptera polyphontes*
(*b*) *P. hector*	(*h*) *P. polydorus*
(*c*) *P. aristolochiae*, black form	(*i*) *P. atropos*
(*d*) *Papilio polytes* f. *polytes*	(*j*) *Papilio polytes* f. *polytes*, Philippines
(*e*) *P. p.* f. *romulus*	(*k*) *Pachlioptera annae*
(*f*) *P. p.* f. *theseus*	(*l*) *P. mariae*



a



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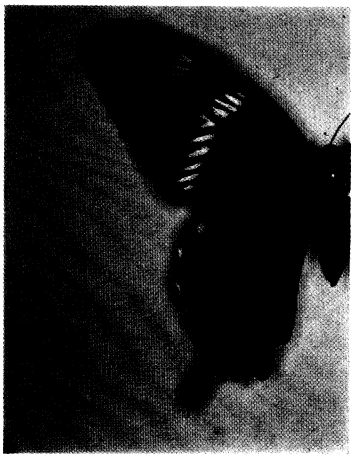

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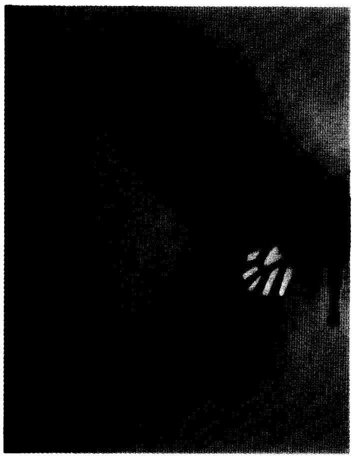
f



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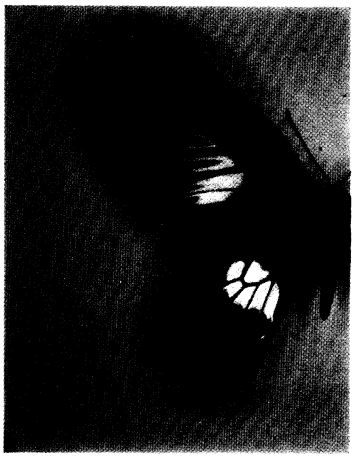
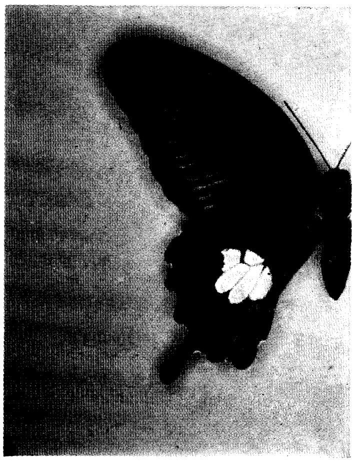


h

i



j

k

l

submarginal black border of that form is broader. The ground colour of the reduced pale central area is white both proximally and distally in the subapical area but darker than in f. *polytes* elsewhere. This gives the impression of a long and a short irregular white band lying diagonally across the forewing, giving a very good imitation of the model *Pachlioptera hector* (plate 40*b*). The hindwing also mimics well that of the model except that the red is less intense and the red abdomen of the model is imitated by a red area at the inner margin of the hindwing in the mimic.

The strictly limited distribution of this model and its mimic is given in figure 4.

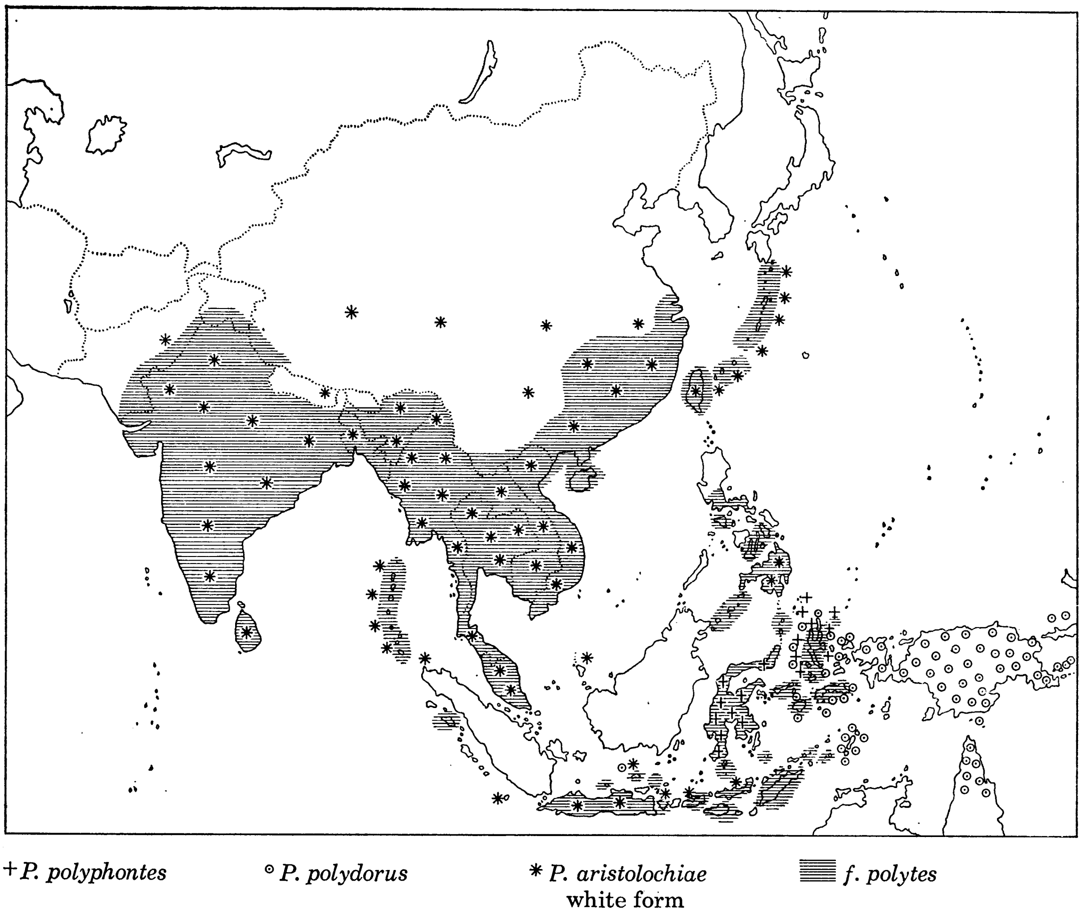


FIGURE 3. The distribution of *P. polytes* f. *polytes* and its models. In addition to the models shown, *Pachlioptera annae* (plate 40*k*) may act as a model on Mindoro and Mindanao, and the closely related *Pachlioptera mariae* (plate 40 *l*) on Mindanao and Cebu. In central Luzon forms intermediate between f. *theseus* and f. *polytes* are found, together with similar intermediates between the white and the black forms of the model *P. aristolochiae*. In Lombok f. *polytes* has been found, although the common mimic is f. *theseus*.

(*d*) f. **theseus** (plate 40*f*)

The hindwing of this form, which always has long tails, is almost identical to that of f. *romulus*. It is, however, slightly more variable with respect to the size of the characteristic red areas, this being partly related to the subspecies concerned. Furthermore, particularly in specimens from Borneo, there is occasionally a small white spot in the region of the distal end of the cell. The forewings are very similar to those of f. *polytes* and lack the white irregular bars characteristic of f. *romulus*. Its geographical distribution is wide but patchy, closely following the distribution of its model, the form of *P. aristolochiae* without a white patch on the hindwing (plate 40*c*). There is an additional model for f. *theseus* in Palawan (*Pachlioptera atropos* (Staudinger)) (plate 40*i*). The geographical distribution of f. *theseus* and its models is given in figure 4.

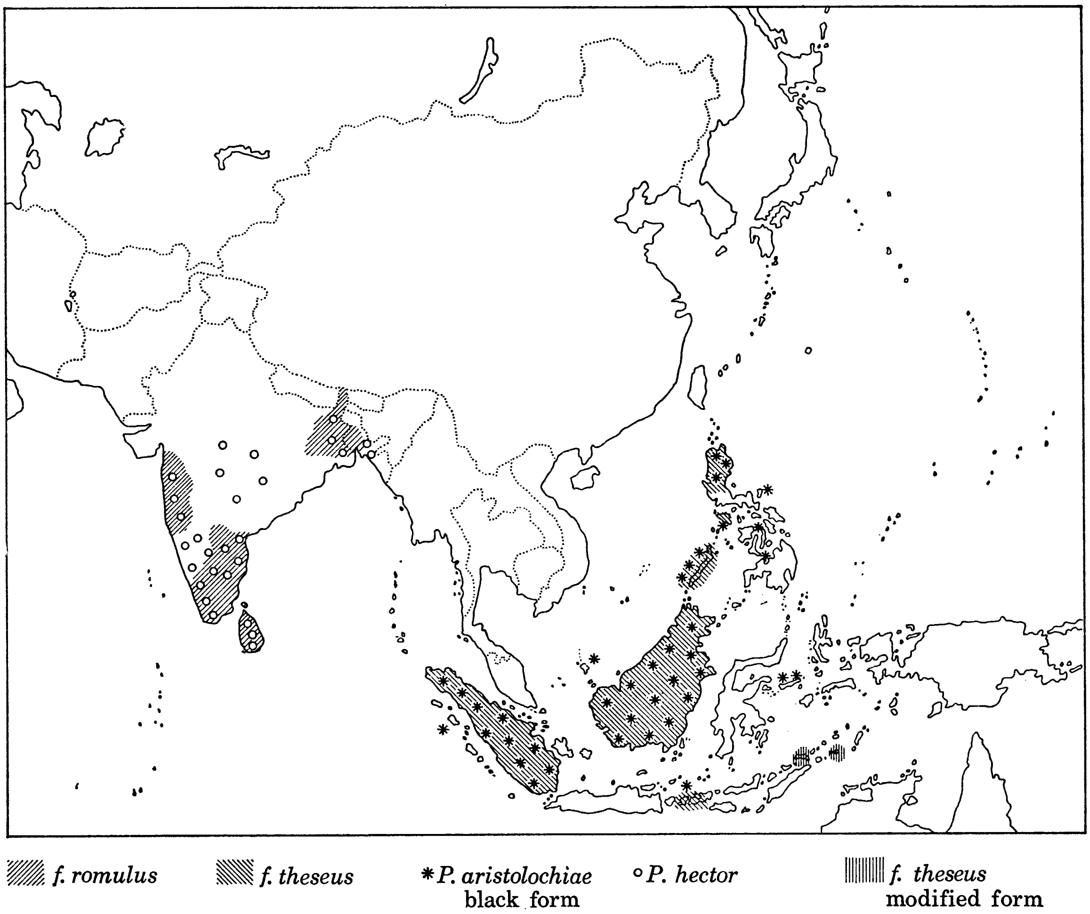


Figure 4. The distribution of *P. polytes* f. *romulus* and f. *theseus* and their models. *P. atropos* also acts as a model for f. *theseus* in Palawan. The modified form of f. *theseus* on the islands of Baber and Wetter looks much like the heterozygotes in race crosses involving this form (page 444).

IV. The genetics of the female forms *CYRUS*, *POLYTES* and *ROMULUS*

(*a*) *Fryer's experiments*

The classical breeding experiments on *P. polytes* were carried out by Fryer (1913). He showed that the mimetic forms f. *polytes* and f. *romulus* were sex-controlled to the female but that the males were capable of transmitting the mimetic factors to their female offspring. Furthermore, he showed that the non-mimetic form f. *cyrus* is recessive to the mimics f. *polytes* and f. *romulus*. He also suggested that a single gene converted *cyrus* to *polytes* and that a second unlinked gene dominant in effect converted *polytes* into *romulus*, this factor having no effect on *cyrus*. Thus the possible genotypes of the three forms are those given in table 2.

Fryer put forward this hypothesis as the most likely, as indeed it was from his data, but pointed out that the critical brood resulting from crossing an insect which possessed the gene for *polytes* but not *romulus* with a *cyrus* and producing a *romulus* had not been obtained. A similar genetic mechanism controlling mimicry had been suggested previously for *P. memnon* by Baur (1911) and Fryer points out that his hypothesis exactly parallels this.

TABLE 2. FRYER'S HYPOTHESIS EXPLAINING THE GENETICS OF THE FORMS OF *P. POLYTES* FOUND IN CEYLON

phenotype	possible genotypes
male	*RRPP RRPp RRpp RrPP RrPp Rrpp rrPP rrPp rrpp*
cyrus	*RRpp Rrpp rrpp*
polytes	*rrPP rrPp*
romulus	*RRPP RRPp RrPP RrPp*

(*b*) *New data on Fryer's hypothesis*

(i) *Sex linkage*

Fryer's hypothesis assumed that sex-linkage is not involved and he himself believed that the male is the heterogametic sex, whereas it is the female. His data, however, show that f. *polytes* is not X-linked (his brood 46), and also that *romulus* cannot be either (his brood 63) since a *romulus* female mated to a male known not to carry *romulus* produced *romulus* among its offspring. Y-linkage is also excluded by Fryer's data.

Our results fully confirm these findings and in addition we have evidence that *theseus* is not X-linked since a female *theseus* mated to a male homozygous for *cyrus* produced *theseus*. Brood 8674 (table 7, p. 444), in which a *polytes* female from Ceylon, where *theseus* does not occur, was mated to a male from Palawan and produced *theseus*, shows that it is not Y-linked.

(ii) *Epistasis*

Fryer's hypothesis of autosomal inheritance and epistasis has been accepted since it was first put forward, but because there were alternatives we set up crosses to try to produce the critical results that Fryer did not obtain (table 3).

TABLE 3. BROODS TESTING FRYER'S HYPOTHESIS OF EPISTASIS BETWEEN THE LOCI *R* AND *P* (CEYLON RACE)

			phenotype of offspring	
brood no.	mother	father	males	females
8158	*romulus* Ceylon	Ceylon	113	83 (40 *romulus*, 43 *polytes*)
8178	*cyrus* Ceylon	Ceylon	26	19 *cyrus*
8234	*cyrus* Ceylon	Ceylon	41	52 (29 *cyrus*, 23 *polytes*)
8250	*romulus* 8158	8178	38	42 (22 *cyrus*, 20 *romulus*)
8251	*romulus* Ceylon	Ceylon	15	16 (12 *cyrus*, 4 *romulus*)
8252	*romulus* Ceylon	Ceylon	29	27 (16 *cyrus*, 11 *romulus*)
8268	*cyrus* 8250	8234	4	7 (5 *cyrus*, 2 *polytes*)
8270	*cyrus* 8252	8234	6	7 (4 *cyrus*, 3 *polytes*)
8272	*cyrus* 8252	8234	20	16 (9 *cyrus*, 7 *polytes*)
8273	*cyrus* 8251	8234	1	4 (1 *cyrus*, 3 *polytes*)
8281	*cyrus* 8250	8234	2	2 (1 *cyrus*, 1 *polytes*)
8282	*romulus* 8158	Ceylon	11	6 (5 *romulus*, 1 *polytes*)
K19	*cyrus* 8234	8282	54	30 (19 *cyrus*, 11 *romulus*)
K20	*polytes* 8234	8282	27	28 (6 *cyrus*, 22 *polytes*)
K30	*cyrus* K19	K20	6	11 (4 *cyrus*, 7 *polytes*)
K31	*cyrus* K19	K20	22	27 (14 *cyrus*, 13 *polytes*)
K35	*cyrus* K19	K20	20	13 (7 *cyrus*, 6 *polytes*)

We took *cyrus* females from large broods segregating for *romulus* and *cyrus* only, so that on Fryer's hypothesis the families were really segregating for *polytes*, and the possible genotypes of the *cyrus* females could only have been *RRpp* or *Rrpp*. These *cyrus* females were crossed (broods 8268, 8270, 8272, 8273, 8281, K 30, K 31, K 35) with males from large broods segregating for *polytes* and *cyrus* only. Thus the males could only have been of the following genotypes: *rrPP*, *rrPp* or *rrpp*. Any broods in which insects appeared which were not *cyrus* must have resulted from males whose genotype was either *rrPP* or *rrPp*, and therefore *romulus* would be expected among the non-*cyrus* progeny. The cross that would produce the fewest *romulus* would be *Rrpp* × *rrPp*. In this, half the non-*cyrus* progeny are expected to be *polytes* and half *romulus*. However, of the 42 non-*cyrus* offspring none was *romulus*, the probability of obtaining this result by chance being $\frac{1}{2}^{42}$. Thus on the evidence of these broods we must reject Fryer's interpretation.

Additional data have been obtained by using broods derived from crossing races. Four such broods were informative since they produced *romulus*. In the first, 7187 (table 4) the female was *romulus* and was derived from a *cyrus* from Hong Kong (where *romulus* does not occur) mated to a male from Ceylon. Thus on Fryer's hypothesis its genotype was *RrPp*. It was mated to a male obtained in a similar way, but from a brood in which all eight female offspring were *cyrus*. Consequently, the genotype of the male would either be *Rrpp* or *rrpp*. If it were the former, it would be expected on Fryer's hypothesis to give a lower proportion of *polytes* among its non-*romulus* offspring than if it were the latter.

TABLE 4. BROODS TESTING FRYER'S HYPOTHESIS OF EPISTASIS BETWEEN THE LOCI R AND P (RACE HYBRIDS)

			phenotype of offspring	
brood no.	mother	father	males	females
6988	*cyrus* Hong Kong	Ceylon	4	8 *cyrus*
7002	*cyrus* Hong Kong	Ceylon	12	10 (4 *cyrus*, 6 *romulus*)
7187	*romulus* 7002	6988	33	35 (19 *cyrus*, 16 *romulus*)
M 67	*cyrus* Ceylon	Ceylon	1	2 *cyrus*
M 70	from wild larvae from Java		2	2 (1 *cyrus*, 1 *polytes*)
M 71	*cyrus* M 67	M 67 (same as M 73)	10	14 (6 *cyrus*, 8 *romulus*)
M 73	*cyrus* M 70	M 67 (same as M 71)	8	2 (1 *cyrus*, 1 *romulus*)
M 75	*cyrus* M 67	M 70	5	6 *cyrus*
M 90	*cyrus* M 75	M 73	7	6 (2 *cyrus*, 4 *romulus*)
M 91	*cyrus* M 75	M 73	8	6 (4 *cyrus*, 2 *romulus*)
M 108	wild pupae from Japan		4	4 (2 *cyrus*, 2 *polytes*)
M 120	*cyrus* M 108	M 108	11	7 *cyrus*
M 122	*romulus* M 90	M 108	3	3 (2 *romulus*, 1 *polytes*)
M 188	*romulus* M 122	M 120	11	17 (9 *cyrus*, 8 *romulus*)

In the second brood, M 188, the female was a *romulus* hybrid which according to Fryer must have been *RrPp* or *RrPP* since her father came from a place where *romulus* is not found. The male parent of brood M 188 was also from an area where *romulus* is not found and its seven female sibs were all *cyrus*. Its most likely genotype, therefore, is *rrpp*.

In the third and fourth broods, M 90 and M 91, the female was a *cyrus* hybrid and therefore of genotype *Rrpp* or *rrpp*. The male (M 73) was also a hybrid produced by crossing a *cyrus* (M 70) (from an area where *romulus* is not found) with a Ceylon male (M 67), the male also having produced a brood segregating for *romulus* and *cyrus* only (M 71). The male parents of broods M90 and M91, since they produced *romulus*, must have been *RrPp* or *rrPp*. They could not be *PP* since they had a *cyrus* mother.

These broods would all be expected to segregate for *polytes* as well as *cyrus*. By assuming that the parents were of those possible genotypes which would give the fewest *polytes* amongst the non-*romulus* offspring one can estimate the minimum expected number of *polytes* and *cyrus* in these broods.

Combining the four broods, eight *polytes* and 26 *cyrus* would be expected. In fact, no *polytes* appeared amongst the progeny, giving $\chi_1^2 = 9.19$ ($P < 0.01$). Thus the hybrid broods also refute Fryer's hypothesis.

(*c*) *The dominance relationships of f.* cyrus, *f.* polytes *and f.* romulus

Fryer indicated that *polytes* is dominant to *cyrus* and that *romulus* is dominant to *polytes*. All our breeding results are in entire agreement with this conclusion. In addition, we have evidence that *romulus* is dominant to *cyrus*.

That *polytes* is dominant to *cyrus* is demonstrated by brood 7160 amongst others (table 5). Here a *cyrus* female with nine *cyrus* sisters mated to a male with *polytes* in its ancestry produced ten *polytes* females only. Had *cyrus* been the dominant one would have expected either three *cyrus* to one *polytes* or a 1:1 ratio. The brood clearly departs significantly from either of these. That *romulus* is dominant to *cyrus* is indicated by the large brood 10920 (table 5) where a female *cyrus* produced no *cyrus* offspring, suggesting that it is recessive to *romulus* or *theseus* (see below) or both. Furthermore, the dominance of *romulus* is shown in brood 7002 in which a pure Hong Kong *cyrus* (where *romulus* is not found) mated to a wild male from Ceylon produced a brood segregating for *cyrus* and *romulus*. *Romulus* can also be shown to be dominant to *polytes* in brood 6968. Here a *romulus* female from Ceylon was mated to a pure Hong Kong male 6867 who had 14 *cyrus* sisters but no *polytes* ones and thus was almost certainly a homozygous *cyrus*. This mating produced both *romulus* and *polytes*, showing that *romulus* is not only dominant to *cyrus* but also to *polytes*. That dominance is complete is shown by the fact that there are only the three distinct forms found in Ceylon with no intermediates.

TABLE 5. THE DOMINANCE RELATIONSHIPS OF F. *CYRUS*, F. *POLYTES* AND F. *ROMULUS*

			phenotype of offspring	
brood no.	mother	father	males	females
6867	*cyrus* Hong Kong	Hong Kong	18	14 *cyrus*
6950	*romulus* Ceylon	Ceylon	41	35 (12 *cyrus*, 15 *romulus*, 8 *polytes*)
6968	*romulus* 6950	6867	6	4 (1 *romulus*, 3 *polytes*)
6998	*cyrus* Ceylon	6950	9	10 *cyrus*
7002	*cyrus* Hong Kong	Ceylon	12	10 (4 *cyrus*, 6 *romulus*)
7160	*cyrus* 6998	6968	9	10 *polytes*
9269	*romulus* Ceylon	Cebu	12	14 (10 *romulus*-like, 4 *polytes*-like)
10846	*romulus* Ceylon	Borneo	27	14 (1 *cyrus*, 5 *romulus*, 8 *theseus*)
10920	*cyrus* (stock hybrid†)	10846	31	26 (15 *romulus*, 11 *theseus*)

† Stock hybrids come from free-flying populations described on p. 442.

(*d*) *Dominance in race hybrids*

Although *romulus* is dominant to *polytes* and *cyrus* in its own race, this relationship can apparently break down in some hybrid matings. Thus in brood 9269 (table 5) a *romulus* from

Ceylon was mated to a wild male from Cebu in the Philippines, where both *cyrus* and *polytes* are known to occur. The offspring segregated into two distinct groups, as judged by the forewing, those carrying the gene for *polytes* and those the one for *romulus*. As regards the hindwings, those of the *polytes*-like insects were moderately variable, particularly with respect to the area of white, which was greatly reduced in two. The hindwing pattern of the *romulus*-like forms showed even more variation in pattern. The amount of red was very inconstant in extent, some specimens having far less than that typical of *romulus*. In addition, there was present in at least five butterflies an orange-white area where the white scales of *polytes* are normally present. Thus the typical *romulus* pattern in the hindwing has broken down, perhaps as the result of dominance modification. Unfortunately we do not know in each butterfly whether the allele from the father is *polytes* or *cyrus*. However, the close resemblance between the hindwing pattern of the 9269 insects and those of known *theseus*/*cyrus* heterozygotes (see plate 41 *d* and *f*) suggests that they may be *romulus*/*cyrus* rather than *romulus*/*polytes*. The forewing white diagonal bars in brood 9269 were diffuse in outline and similar to other *romulus* hybrids (see p. 445).

V. THE ALLELOMORPHISM OF F. *CYRUS*, F. *POLYTES* AND F. *ROMULUS* (table 6)

Fryer assumed that the loci determining *polytes* and *romulus* were unlinked, a conclusion that is not very surprising at such an early date in the history of genetics. Moreover, at least two of his broods, numbers 47 and 74, appeared to exclude the possibility of tight linkage. Our data, on the other hand, show quite conclusively that *polytes* and *romulus* are either controlled by allelomorphs at one locus or by a supergene.

Because all males look alike regardless of their genotype, it was necessary to establish stocks known to be homozygous for *cyrus*. Latterly these were kept as free-flying populations in two greenhouses (Clarke & Sheppard 1971 *b*) and in the course of more than seven generations produced hundreds of females all of which were *cyrus*. Before these populations were established the probable genotypes of the males were determined by the phenotypes of their sisters.

Brood 8158 resulted from a wild *romulus* female. It produced 40 *romulus* and 43 *polytes* offspring. Since *romulus* is dominant to *polytes* we must assume that all these *romulus* were at least heterozygous for *polytes* if the two loci are unlinked. Three of the *romulus* females, broods 8196, 8213 and 8250, were mated to males all of whose sisters were *cyrus*. Among the 26 non-*romulus* offspring none was *polytes*, showing that the *romulus* females were not heterozygous for this form. Thus the two loci are closely linked or the forms are controlled by multiple allelomorphs.

One additional brood (8282) which was reported to us but from which we have not seen the insects, produced a *polytes* female which if not due to contamination would indicate close linkage rather than allelomorphism. It must be remembered that this brood was bred wholly in Ceylon, where wild eggs or larvae could easily be brought in on the foodplant. Fryer's broods 47 and 74 (see above) could also be explained by linkage rather than by contamination. Further evidence to support the hypothesis of very close linkage or allelomorphism is given in table 6 in which a *romulus* female mated to a male with a *polytes* mother produced 20 *romulus* to 12 *polytes* to eight *cyrus* (brood 10667) which appears to be a 2:1:1 ratio. This would be expected since the *romulus* mother resulted from a mating between a *romulus* and a male homozygous for *cyrus* (10627). The *romulus* progeny of 10667 were mated to homozygous *cyrus* males and produced broods either segregating for *romulus* and *cyrus* or for *romulus* and *polytes*. None segregated for all three phenotypes, which would be expected if the loci were unlinked.

Table 6. Allelomorphism of f. *cyrus*, f. *polytes* and f. *romulus*

			phenotype of offspring	
brood no.	mother	father	males	females
8097	*cyrus* Ceylon	Hong Kong	13	13 *cyrus*
8140	*cyrus* Ceylon	Ceylon	32	31 *cyrus*
8158	*romulus* Ceylon	Ceylon	113	83 (40 *romulus*, 43 *polytes*)
8178	*cyrus* Ceylon	Ceylon	26	19 *cyrus*
8196	*romulus* 8158	8097	16	9 (3 *cyrus*, 6 *romulus*)
8213	*romulus* 8158	8178	2	3 (1 *cyrus*, 2 *romulus*)
8250	*romulus* 8158	8178	38	42 (22 *cyrus*, 20 *romulus*)
8282	*romulus* 8158	8140	11	6 (5 *romulus*, 1 *polytes*)
10617	*polytes* Ceylon	Ceylon	9	20 (10 *polytes*, 10 *cyrus*)
10627	*romulus* Ceylon	stock hybrid†	1	2 (1 *cyrus*, 1 *romulus*)
10667	*romulus* 10627	10617	62	40 (8 *cyrus*, 20 *romulus*, 12 *polytes*)
10696	*romulus* 10667	stock hybrid	22	24 (9 *cyrus*, 15 *romulus*)
10703	*romulus* 10667	stock hybrid	19	8 (4 *cyrus*, 4 *romulus*)
10709	*romulus* 10667	stock hybrid	37	15 (9 *romulus*, 6 *polytes*)
10711	*romulus* 10667	stock hybrid	29	23 (10 *romulus*, 13 *polytes*)
10713	*romulus* 10667	stock hybrid	19	7 (4 *cyrus*, 3 *romulus*)
10714	*romulus* 10667	stock hybrid	32	24 (13 *romulus*, 11 *polytes*)
10716	*romulus* 10667	stock hybrid	33	29 (13 *cyrus*, 16 *romulus*)
10718	*romulus* 10667	stock hybrid	29	24 (13 *cyrus*, 11 *romulus*)
10719	*romulus* 10667	stock hybrid	7	5 (3 *cyrus*, 2 *romulus*)
10720	*romulus* 10667	stock hybrid	50	25 (10 *cyrus*, 15 *romulus*)
10721	*romulus* 10667	stock hybrid	50	17 (8 *cyrus*, 9 *romulus*)
10723	*romulus* 10667	stock hybrid	23	15 (6 *cyrus*, 9 *romulus*)

† Stock hybrids come from free-flying populations described on p. 442.

VI. Evidence that the elements of the pattern may be separated by crossing over

We know of three specimens of an extremely rare female form of *P. polytes*. The hindwings had the pattern of f. *polytes* and the forewings that of f. *romulus*. Two of the specimens are in the British Museum (Natural History); the third we obtained as a living specimen from Ceylon but although we mated it no offspring resulted. In view of the dominance relationships of *romulus* and *polytes* these insects would appear to result either from a reversal of dominance of hindwing pattern but not forewing pattern, or from crossing over within the gene or supergene controlling the mimetic patterns. Crossing over seems the more likely in view of our results with *P. memnon* (Clarke *et al.* 1968; Clarke & Sheppard 1971*a*) and *P. dardanus* (see Clarke & Sheppard 1960*a*).

VII. The genetic relationships of f. *theseus* to f. *cyrus*, f. *polytes* and f. *romulus*

The dominance relationships of f. theseus *to f.* cyrus, *f.* polytes *and f.* romulus (table 7)

(*a*) *To f.* **cyrus**

Brood 7011 was a mating of a *theseus* from north Borneo to a male from Hong Kong, where *theseus* does not occur. It segregated for *theseus* and *cyrus*, showing that *theseus* is not recessive. Also a typical *theseus* mated in the wild produced both *theseus* and *cyrus*, showing that in this specimen *theseus* was fully dominant to *cyrus*. However, the hybrid offspring, and particularly the subsequent backcross offspring, of *theseus* to a race where the form does not occur tend to show a breakdown of dominance. The resulting insects have the appearance of f. *polytes* but with a reduced area of white on the hindwing.

TABLE 7. THE DOMINANCE RELATIONSHIPS OF F. *THESEUS* TO F. *CYRUS*, F. *POLYTES* AND F. *ROMULUS*

			phenotype of offspring	
brood no.	mother	father	males	females
7011	*theseus* Borneo	Hong Kong	5	8 (5 *cyrus*, 3 *theseus*-like)
7280	*theseus*-like Palawan	Palawan	5	5 (2 *cyrus*, 3 *theseus*-like)
8674	*polytes* Ceylon	Palawan	20	19 *theseus*-like
8822	*theseus*-like 8674	Ceylon	13	14 *romulus*-like
10846	*romulus* 10720 (Table 6)	Borneo (same as 10851)	27	15 (1 *cyrus*, 6 *romulus*, 8 *theseus*-like)
10851	*polytes* Java	Borneo (same as 10846)	9	14 (7 *polytes*, 7 *theseus*)
10917	*theseus*-like 10851	stock hybrid	7	2 (1 *polytes*, 1 *theseus*)
10923	*polytes* 10851	stock hybrid	15	13 (10 *cyrus*, 3 *theseus*-like)
10933	*theseus* Luzon	Negros	15	11 *theseus*-like

Although the majority of *theseus* from Borneo have no white on the hindwing some have a very small white spot, suggesting that they are heterozygotes. A similar phenotype from Palawan has been shown to be a heterozygote (brood 7280). However, the majority of the *theseus* from Palawan are fully dominant, as are those from Sumatra, where *cyrus* is found, but the intermediate phenotype is almost unknown. Thus in a pure race *theseus* is dominant in most instances but semi-dominant in a few individuals. In contrast to this, on outcrossing dominance breaks down in the majority of individuals.

(*b*) *To f.* ***polytes***

We, in conjunction with Dr Ae, have also studied the dominance relationships of *theseus* from northern Luzon. A female of this form was mated by Dr Ae (brood 10933) to a male from the island of Negros in the Central Philippines where *polytes* and *cyrus* are found, but not *theseus* (figures 2–4). It produced only 11 *theseus*-like hybrids (see below) and no other form (table 7) suggesting that the female parent was a homozygote. Both the male and female progeny were mated to *cyrus* or homozygous *cyrus* males from our colony of this genotype (see above). The results from all the broods are homogeneous and a total of 41 *cyrus* and 35 non-*cyrus* were produced, showing that the male Negros parent of brood 10933 was homozygous *cyrus*. Had it been heterozygous for *polytes* one would have expected an excess of non-*cyrus* offspring.

The F_1 offspring (brood 10933) are extremely uniform in appearance (plate 41*d*) and are almost exactly intermediate between *theseus* (plate 40*f*) and Philippine *polytes* (plate 40*j*), looking like the latter but with the white area reduced in size. The result of back-crossing males and females of this brood to our *cyrus* stock was to produce a range of forms varying between insects identical to *theseus* through intermediates (plate 41*f*) to those (plate 41*g*) indistinguishable from f. *polytes* from Java. That the insects looked like Java f. *polytes* rather than like those from the Philippines is probably the result of our *cyrus* stock being largely derived from Java material.

The evidence from the F_1 and the back crosses suggests that *theseus* has an intermediate heterozygote in race hybrids. However, an F_1 was mated with a sib and produced five F_2

females, all of which closely resembled the F_1. None was typical *theseus* but at least one (plate 41 *e*) had a hindwing window as big as normal f. *polytes* from the Philippines. This evidence suggests that the intermediate appearance of the heterozygote may not be due to a breakdown in dominance but result from f. *theseus* and f. *polytes* being controlled by the same allelomorph and only differing as a result of the presence of different modifiers.

There is additional evidence on the relationship of *polytes* and *theseus* where neither comes from the Philippines. In brood 10851 a *polytes* from Java was mated to a male from Borneo and produced *polytes* and *theseus* only. Since the male was known to be heterozygous for *theseus* (from brood 10846) and no *cyrus* were produced in 10851, it would appear that the *polytes* female was a homozygote and *theseus* is dominant to *polytes*. This view is supported by brood 10917 in which one of the *theseus* was mated to a male homozygous for *cyrus* and produced *theseus* and *polytes*. On the other hand, brood 10923 suggests that *polytes* is the dominant since a female of this form mated to a *cyrus* produced *cyrus* and insects intermediate between *polytes* and *theseus*. However, in all these and related broods the amount of white on the hindwing was so variable that many insects could not be assigned with certainty to one form or the other (e.g. the butterfly shown in plate 41 *h*). Thus, as with the Philippines material, the explanation may be that the two forms differ only by modifiers.

(*c*) *To f.* **romulus**

Romulus appears to be dominant or almost dominant to *theseus*. A female *romulus* heterozygous for *cyrus* and not carrying *theseus* (being a Ceylon–Java hybrid) was mated to a wild male from Borneo (brood 10846). One of the *romulus* offspring was mated to a male of our homozgous *cyrus* stock and segregated for *romulus* and *theseus* only (brood 10895, table 8) showing that *romulus* is the dominant. The *romulus* were very similar to the typical form, except that the white diagonal bars on the forewings were rather more diffuse in outline. As in previous broods, the hindwing pattern of *theseus* was variable, in that some had white scales. In other respects it was identical with that of the *romulus* sibs.

Additional evidence for the dominance of *romulus* comes from the hybrid brood 8822 in which a hybrid *theseus*-like insect, offspring of 8674, when mated to a pure Ceylon male produced 14 female offspring all of them resembling *romulus*. Despite the fact that only half the *romulus* could have been heterozygous for *theseus*, we could not distinguish between the insects. As in the previous brood the diagonal forewing bars were variable in outline.

VIII. THE ALLELOMORPHISM OF F. *ROMULUS* AND F. *THESEUS* (table 8)

Theseus and *romulus* are allelomorphic or controlled by very closely linked loci. In brood 10846 a *romulus* heterozygous for *cyrus* was mated to a wild male from Borneo and produced one *cyrus*, five *romulus*- and eight *theseus*-like insects. Since *romulus* is dominant to *theseus*, the only backcross broods which are informative are those in which a *romulus* female mated to a *cyrus* homozygote have produced *theseus*, or where a *cyrus* female mated to a 10846 male has produced *romulus* and *theseus*. We only have two such broods, 10895 and 10920, which between them produced 25 *romulus*, 17 *theseus* and no *cyrus*, giving strong evidence that *romulus* and *theseus* are allelomorphic or at least very closely linked.

IX. THE ALLELOMORPHISM OF F. *THESEUS* AND F. *POLYTES* (table 8)

Since *theseus* and *romulus* are allelomorphic, as are *polytes* and *romulus*, then *theseus* and *polytes* must be. In fact, we have suggested (see above) that the two forms may only differ in the linked and unlinked modifiers present and not in the major gene. The matter can only finally be settled by back-crossing the F_1 *theseus*/*polytes* hybrid with *cyrus* and examining the brood for segregation; for only then can the variation of pattern in the hybrids be reduced sufficiently. We have one such brood (7245), but this is too small from which to draw any firm conclusion. Even here at least four races are involved. The female *cyrus* parent had been produced by hybridizing insects from Ceylon and Hong Kong, and the male parent (7080) from the F_1 between a Thai male and a *theseus* female from Borneo. The brood produced seven insects, none of which was *cyrus*, thus supporting the hypothesis of allelomorphism. Some of the offspring were clearly *polytes*-like and some *theseus*-like (though with some white on the hindwings), but on the evidence we could not be sure whether the brood was segregating for two distinct forms or not.

TABLE 8. ALLELOMORPHISM OF F. *THESEUS* TO F. *ROMULUS* AND F. *POLYTES*

			phenotype of offspring	
brood no.	mother	father	males	females
6978	*cyrus* Ceylon	Hong Kong	0	1 *cyrus*
7080	*theseus* Borneo	Thailand	18	9 (6 *polytes*-like, 3 *theseus*-like)
7245	*cyrus* 6978	7080	5	7 (4 *polytes*-like, 3 *theseus*-like)
10627	*romulus* Ceylon	stock hybrid	1	2 (1 *cyrus*, 1 *romulus*)
10667	*romulus* 10627	Ceylon	62	40 (8 *cyrus*, 20 *romulus*, 12 *polytes*)
10720	*romulus* 10667	stock hybrid	50	25 (10 *cyrus*, 15 *romulus*)
10846	*romulus* 10720	Borneo	27	14 (1 *cyrus*, 5 *romulus*-like, 8 *theseus*-like)
10895	*romulus*-like 10846	stock hybrid	25	16 (10 *romulus*, 6 *theseus*)
10920	*cyrus* stock hybrid†	10846	31	26 (15 *romulus*, 11 *theseus*)

X. THE GENETICS OF TAIL LENGTH IN MALES AND FEMALES OF *P. POLYTES*

Because of the variability in the size of the butterflies it is necessary to adjust their tail length when making comparisons between them. Ideally this should be done by estimating the regression of tail length on wing size and using this to adjust tail length for a constant wing size. Since the data are not adequate to do this we adjusted each tail length by multiplying it

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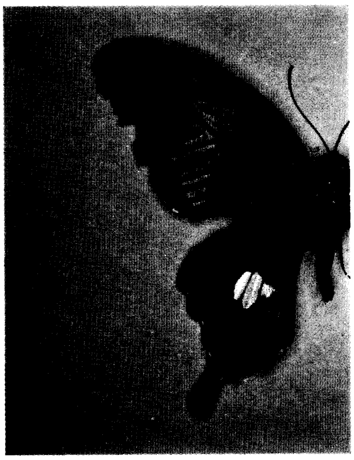
DESCRIPTION OF PLATE 41

(*a*) *Papilio polytes* f. *cyrus*
(*b*) *P. polytes* male
(*c*) *P. polytes* f. *cyrus*, tailless, from Philippines
(*d*) F_1 female 10933, see p. 444 and table 7
(*e*) F_2 female from sib-mating of 10933, see p. 445
(*f*) Female of intermediate *theseus-polytes* phenotype, from back-cross to *cyrus* of 10933, see p. 444
(*g*) f. *polytes*-like female from back-cross to *cyrus* of 10933 (see p. 444)
(*h*) Female of intermediate *theseus-polytes* phenotype, brood 10923, see p. 445 and table 7
(*i*) *P. ambrax* female
(*j*) *P. ambrax* male
(*k*) Male hybrid *polytes* × *ambrax*, see p. 451 and table 11
(*l*) Female hybrid *polytes* × *ambrax*. The tail is broken.

a

b

c



d

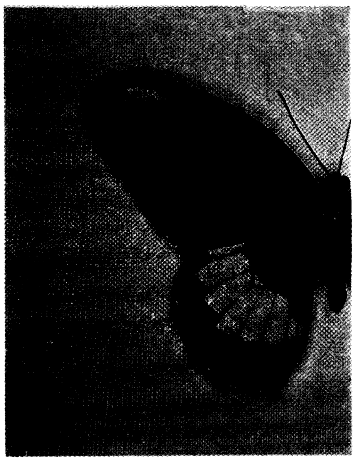
e

f

g

h

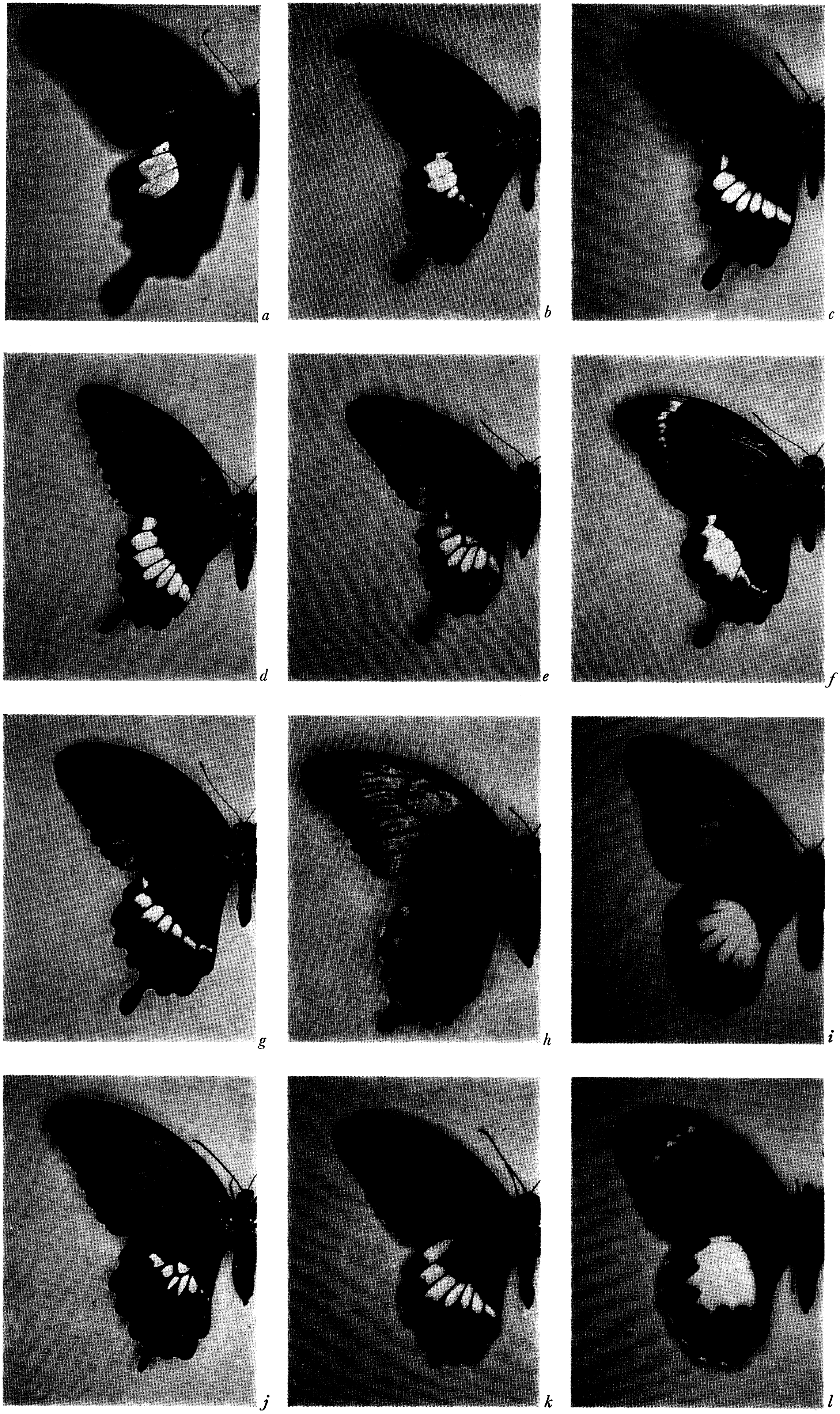
i



j

k

l


a
b
c
d
e
f
g
h
i
j
k
l

by the constant 30.01 (the mean wing length) and dividing by the actual value (excluding the tail) (see Clarke & Sheppard 1960*b*, 1962*a*).

An examination of the tail length of the males and three female forms in race *polytes* shows that the males have a mean tail length of about 7.6 mm and the *cyrus* females of about 8.6 mm (table 1). The slightly longer tails of the male-like females compared with the males seem to be characteristic of most races. The *polytes* and *romulus* females have longer tails, being 9.4 and 9.1 mm respectively. In race *borealis* the butterflies do not have significantly different tail lengths from their counterparts in race *polytes*. In striking contrast to this situation the males of race *alphenor* from the Philippines have tail lengths of only 1.7 mm and in the *cyrus* females they are hardly longer – 2.1 mm (plate 41*c*). The two mimetic forms in the Philippines (*polytes* and *theseus*) have tails that are as long (9.5 and 8.8 mm respectively) as those of the mimetic individuals of races *polytes* and *borealis*. Thus the phenotype of the pattern appears to have only a slight effect on tail length in the west but a very considerable one in the east. The control cannot be vested in the genotype as such since all the males in the Philippines have short tails, regardless of whether they are carrying a gene controlling a mimetic female pattern or not.

In order to investigate the genetic control of the situation we have crossed race *alphenor* (Philippines) with races *borealis* and *polytes* (and hybrids between them) and have investigated tail length in the F_1 and subsequent broods. In all the crosses the mimetic females had long tails regardless of the geographical origin of the gene responsible for the mimicry. Considering the males and the f. *cyrus* females we see that the tail length of the F_1 is intermediate between that of the parental races (table 10). In the back-cross to *alphenor* (mating type 13 (3 × 1), see table 10) the average tail length of the males and females is still further reduced. In the one brood that we have of this type there is a suggestion of Mendelian segregation into short-tailed and tailless types, but there appeared to be a deficiency of tailed individuals (two out of 12 in brood 7902, table 9).

In the second back-cross (brood 7988) between a mimetic female and an *alphenor* the mean tail length of the four males was 3.32 mm – that is to say still slightly longer than in pure *alphenor*. In the other second back-cross (brood 8000), using one of the apparently tailed females of the back-cross, the tails were somewhat longer and again there seemed to be a suggestion of segregation (two looking tailless to seven tailed, table 9).

In brood 7998 a sib mating of the first back-cross between two individuals judged to be tailless (2.4 and 2.3 mm respectively) the mean tail length of the offspring was close to that of

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DESCRIPTION OF PLATE 42

(*a*) *Papilio helenus*
(*b*) Male hybrid *polytes* × *helenus* (brood 7872, table 11, and see p. 449)
(*c*) *P. hipponous*
(*d*) Male hybrid *hipponous* × *polytes* (see table 11, and p. 450)
(*e*) Female *polytes*-like hybrid, *hipponous* × *polytes* (brood 8235, table 11 and p. 450)
(*f*) *P. fuscus*
(*g*) Male hybrid, *polytes* × *fuscus* (table 11 and p. 451)
(*h*) Female *romulus*-like hybrid, *fuscus* × *polytes* (brood 9403, table 11 and p. 451)
(*i*) *P. aegeus*, non-mimetic female
(*j*) Female hybrid, *polytes* × *aegeus*
(*k*) Male hybrid, *polytes* × *aegeus*
(*l*) Male *P. aegeus*.

the parents, but four individuals, one male and three females, had longer tails than the others. This cross would suggest that increased tail length is recessive, but the other broods that it is not. It seems, therefore, that several genes must be affecting tail length, but some of them may be more effective than others, giving a suggestion of segregation in certain broods. The genes concerned must be regarded as modifiers of a specific pattern phenotype since they only exert their effect in males and f. *cyrus* females and not in the mimetic forms. It is less satisfactory to regard the major genes producing the mimicry as merely having a pleiotropic effect on tail length which is sex controlled to the female, since we know from race *nicanor* that the *polytes* pattern can be associated with a tailless female. Furthermore, some of our species hybrids (see pages 449 to 453) which included the gene controlling f. *polytes*, have much reduced tail length.

TABLE 9. ADJUSTED TAIL LENGTH IN BROODS WHICH SUGGEST MENDELIAN SEGREGATION FOR THIS CHARACTER

tail length/mm

			offspring		
				females	
brood no.	mother	father	males	f. *cyrus*	f. *theseus*
7902	10.00	1.23	1.88	2.27	9.10
	(*theseus*)	Palawan	2.14	2.36	9.27
	F_1 Hong Kong ×	(race *alphenor*)	2.27	2.71	9.54
	Palawan		3.51	2.71	10.52
			3.61	2.75	
			5.70	8.14	
7988	9.54	1.86	1.86	—	—
	(*theseus* 7902)	Palawan	3.25	—	—
			3.72	—	—
			4.46	—	—
7998	2.36	2.27	0.97	1.64	—
	(*cyrus* 7902)	(7902)	1.52	1.74	—
			1.56	4.08	—
			2.38	4.32	—
			3.13	4.68	—
			3.98	—	—
8000	8.14	1.86	1.65	3.86	—
	(*cyrus* 7902)	Palawan	2.31	4.67	
			4.02	8.21	
			6.88	—	—
			6.98		
			7.57	—	—

That several specific modifiers are concerned with the control of tail length in males and f. *cyrus* females is confirmed by breeding results using race *theseus*. Here the males have a mean tail length of 4.4 mm and the *cyrus* females of 4.7 mm (table 1), values intermediate between races *alphenor* and *polytes*. The F_1 with the races from continental Asia produces males with a mean tail length of 5.6 mm and females of 8.4 mm. The first back-cross to these mainland races produced males and females with tail lengths very close to those of the mainland races (7.2 and 8.8 mm respectively). Although the mean tail length varied considerably from brood to brood there was no good evidence of segregation into two classes within broods. Thus here again it seems as if more than one modifier is concerned with the control of tail length. Thus in the study of this character we find the various epistatic relationships between the mimetic and non-mimetic patterns being controlled multifactorially.

Table 10. Mean tail length according to mating type and phenotype

	phenotype														
	males			f. *cyrus* ♀♀			f. *polytes* ♀♀			f. *romulus* ♀♀			f. *theseus* ♀♀		
	mean	s.d.	no.	mean	s.d.	no.	mean	s.d.	no.	mean	s.d.	no.	mean	s.d.	no.
1 = race *alphenor* Philippines	1.7	0.4	115	2.1	0.4	63	9.6	1.7	24	—	—	—	8.6	1.3	21
2 = races *polytes* and *borealis* and hybrids between them	7.7	0.6	86	8.8	0.6	45	9.9	0.8	22	9.7	0.6	8	—	—	
3 = 2 × 1	5.6	1.2	201	7.8	1.5	27	9.7	0.8	58	8.5	1.0	9	10.0	0.7	47
4 = race *theseus*	5.2	1.2	46	7.3	1.3	7	—	—	—	—	—	—	8.7	0.8	19
5 = 3 × 3	—	—	—	—	—	—	9.2	—	1	—	—	—	—	—	—
6 = 4 × 2	5.6	0.9	20	8.4	0.7	5	9.4	0.6	6	—	—	—	10.1	0.4	3
7 = (none)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8 = 2 × 3	6.6	1.3	45	8.9	0.5	12	9.2	1.6	11	8.8	0.8	17	—	—	—
9 = (none)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10 = 2 × 8	6.8	0.1	2	—	—	—	—	—	—	—	—	—	—	—	—
11 = (none)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12 = 6 × 6	5.0	2.6	2	5.5	—	1	9.5	0.5	2	—	—	—	9.3	0.6	3
13 = 3 × 1	3.2	1.4	6	3.5	2.3	6	—	—	—	—	—	—	9.6	0.6	4
14 = 13 × 1	4.3	2.2	10	5.6	2.3	3	—	—	—	—	—	—	—	—	—
15 = 13 × 13	2.3	1.1	6	3.3	1.3	6	—	—	—	—	—	—	8.3	—	1
16 = 14 × 2	7.1	1.1	9	8.5	0.8	11	—	—	—	9.3	1.4	2	—	—	—
17 = 18 × 18	5.3	—	1	—	—	—	—	—	—	—	—	—	8.3	—	1
18 = 6 × 2	7.2	0.8	35	8.8	0.6	16	9.8	0.4	11	9.8	—	1	9.7	1.0	11
19 = 2 × 18	7.6	1.2	16	8.2	1.6	4	9.6	—	1	—	—	—	9.4	0.9	9
20 = 19 × 19	11.4	5.2	5	—	—	—	8.5	—	1	—	—	—	9.0	0.6	3
21 = 1 × 19	6.9	0.6	2	—	—	—	9.0	—	1	—	—	—	8.4	—	1

XI. HYBRIDS BETWEEN *P. POLYTES* AND OTHER SPECIES

By hand-pairing it has been possible to obtain hybrids between *P. polytes* and several other closely related species (see also Ae 1966). In one case a spontaneous mating occurred between *P. memnon* and *P. polytes* when the butterflies were flying freely in a greenhouse.

The details of the fertile crosses are shown in table 11. With the exception of *P. ambrax* Boisduval, all the hybrids are with sympatric species.

1. *Hybrids with* P. helenus *L.*

P. helenus (plate 42 *a*) is a tailed, non-mimetic insect, the males and females being similar. The fore and hindwings are black, and the latter have a large whitish patch extending to the costal margin. The hybrids, which were all males and tailed, have black forewings with very small white spots on the outer margin (plate 42 *b*). The whitish area on the hindwing is similar to that in *P. polytes* (plate 41 *b*) except that it is reduced towards the inner margin and broader towards the costal border. There are also reduced red lunules at the anal angle of the hindwing. Thus in almost every respect the hybrids are intermediate in appearance between the two parental forms. On the underside they are indistinguishable from the male *P. polytes*. The hybrids are therefore similar to those produced by Ae (1966) using a different race of *P. polytes*.

TABLE 11. HYBRIDS BETWEEN *P. POLYTES* AND OTHER SPECIES

			offspring	
brood no.	mother	father	males	females
7872	*cyrus* Palawan	*P. helenus* Hong Kong	5	0
8020	*ambrax* New Guinea	*P. polytes* Hong Kong × Palawan	3	0
8235	*P. hipponous* Palawan	*polytes* Ceylon (had 29 *cyrus* and 23 *polytes* sisters)	5	4 (2 *polytes*-like, 1 *cyrus*-like, 1 unscorable)
8319	*P. hipponous* Palawan	*polytes* Ceylon	21	8 *cyrus*-like
9076	*romulus* Ceylon	*P. ambrax* New Guinea	27	4 (1 probably *polytes*-like, 3 unscorable – none grew properly)
9079	*romulus* Ceylon	*P. ambrax* New Guinea	4	0
9107	*P. ambrax* New Guinea	*polytes* (ex wild *romulus* Ceylon. 1 *polytes* and 1 *romulus* sisters)	7	4 *polytes*-like
9124	f. *polytes* Hong Kong	*P. fuscus* New Guinea	7	0
9128	f. *polytes* Hong Kong	*P. ambrax* New Guinea	1	0
9131	*cyrus* Hong Kong	*P. aegeus* New Guinea	4	2 *polytes*-like
9170	*romulus* Ceylon	*P. memnon* Java	6	0
9322	*romulus* Ceylon (with *cyrus* sisters)	*P. ambrax* New Guinea	24	1 ? *romulus-ambrax* or *cyrus-ambrax*
9332	*cyrus* Ceylon	*P. fuscus* New Guinea	6	0
9335	*cyrus* Ceylon	*P. fuscus* New Guinea	1 deformed	
9403	*P. fuscus* New Guinea	*polytes* Ceylon (this male when mated to *cyrus* produced *romulus* and *cyrus*	4	7 (3 *cyrus*-like, 4 *romulus*-like)
11943	*romulus* Ceylon	*P. canopus* subsp. *hypsicles*	5	0

2. *Hybrids with* P. hipponous *Felder*

P. hipponous (plate 42*c*) is a tailed, monomorphic insect closely resembling *P. polytes* f. *cyrus* (plate 41*a*), though it has more yellow in the light hindwing band and this band tends to be continued on to the forewing.

We obtained both male and female tailed hybrids. The males (plate 42*d*) are indistinguishable from *P. polytes* except that on the underside the submarginal lunules are paler. Among the females some resemble f. *cyrus* and some f. *polytes*, the ones resembling f. *cyrus* being extremely similar to the males. The f. *polytes*-like (plate 42*e*) differ from normal *polytes* (plate 40*d*) in that the extension of the hindwing band on to the forewing typical of *P. hipponous* is present, though less marked. The white area on the hindwing typical of f. *polytes* is extended to the inner margin and to the costal border, giving an appearance intermediate between that of f. *cyrus* and f. *polytes*. The red submarginal lunules are absent or reduced to traces except at the anal angle. On the underside the features by which it differs from f. *polytes* on the upper surface are repeated, except for the submarginal lunules which are rather more strongly represented, though very pale.

3. *Hybrids with* P. ambrax *Boisduval*

P. ambrax is a sexually dimorphic, tailless insect. In the male (plate 41*j*) the forewings are black with a scattering of white scales on the costal border just proximal to the apex. There is a wide pale green-blue area on the hindwing extending from the costal to the inner margin and taking in the distal third of the cell. It is bordered distally by a black marginal band, which becomes wider towards the anal angle. There are a number of white flecks on the outer border of the forewing, between the veins. The underside of the hindwing is black with a red anal mark.

The forewing of the female (plate 41*i*) is like that of f. *polytes*, but has, in addition, a white area near the inner margin. The hindwing resembles that of f. *polytes* from the *nicanor* race. The female of *P. ambrax* is a mimic of *P. polydorus* (plate 40*h*), hence its close resemblance to f. *polytes*.

The male hybrids (plate 41*k*) resemble *polytes* males more than *ambrax* ones in that although they have the apical pale area on the forewings the hindwing is extremely similar to *P. polytes* in appearance. The tails are intermediate in length between the parents and resemble those of race *theseus*. The female hybrids in brood 9107 (plate 41*l*) have forewings extremely similar to f. *polytes* from some areas. The hindwing also closely resembles this form, although the white patch is smaller than that in most races, but similar to some specimens from Java. The tails are short. Since we are not certain of the genotype of the father, we are unable to say whether the females are heterozygous for the gene controlling f. *cyrus* or that controlling f. *polytes*. We do not think they are heterozygous for f. *romulus* since in brood 9322 a female was produced which is almost certainly heterozygous for this form. Its wings did not expand properly but it could be seen to have a large white patch on the forewing in the area where the two diagonal lines of *romulus* are normally to be found and a hindwing with a small orange central area closely resembling the *romulus* hybrids described on page 442.

4. *Hybrids with* P. fuscus *Goeze*

P. fuscus (plate 42*f*) is a monomorphic, non-mimetic, tailed insect. It resembles *P. helenus* except that there is a pale blue interrupted arc which extends from the costal border to the anal angle of the forewing. The pale area on the hindwing is more irregular and extends as a thin line to the anal angle.

Only male hybrids (plate 42*g*) were produced when the female was *P. polytes*. The forewings resemble those of *P. polytes* and the tailed hindwings have a whitish area similar to that in this species except that the outline of the individual spots between the veins is indistinct as in *fuscus*. Furthermore, their outer margins tend to be concave as in that species and not convex as in *P. polytes*. On the underside the orange lunules typical of *polytes* are almost absent.

In brood 9403, where *fuscus* was the female parent, two female forms appeared among the offspring. Since the male had been shown to be heterozygous for f. *romulus* and f. *cyrus* by test mating, the two kinds of offspring resulted from the segregation of these two allelomorphs. The *cyrus*-like females closely resembled the male hybrids. The forewing of the *romulus*-like females (plate 42*h*) had a large whitish area apparently produced by the diagonal white bars characteristic of *romulus* (plate 40*e*) coalescing (see also brood 9322 above). The hindwings were remarkably different from those of both parent species. They were tailed, and had the orange-red submarginal lunules typical of *romulus*. However, all the other red spots of this form were absent, giving a dull black wing with a faint scattering of blue scales and a vestige of the pale band which is so prominent on the hindwing of *P. fuscus*.

5. *Hybrids with* P. aegeus *Donovan*

P. aegeus is a large tailless insect, sexually dimorphic. In much of its range the female is monomorphic but in some areas it is polymorphic and mimetic, imitating species of the genera *Taenaris* and *Hyantis* (Vane-Wright 1971). The forewing of the male (plate 42*l*) is dark, somewhat resembling *P. ambrax* except that the scattering of white scales on the forewing is replaced by a pale band from the costal to the outer margin just proximal to the apex. The hindwing strongly resembles that of *P. ambrax* except that there is a noticeable red anal spot on the underside (and frequently on the upperside as well) and the pale area tends to be less extensive. The underside of the hindwing has a row of submarginal red lunules present together with the red anal spot. Proximal to the lunules there is a row of blue crescents bordered on the inside by pale scales. The non-mimetic female (plate 42*i*) has a dark forewing with a pale grey band distal to the basal area almost extending to the outer margin. On the hindwing there is a white patch reaching into the cell and a dark submarginal band with red lunules and some blue scaling. The whole appearance is somewhat like f. *polytes* but not similar enough for it to be considered a mimic of *P. polydorus*.

The male hybrids (plate 42*k*) are extremely similar to the *helenus* hybrids except for a trace of pale scaling on the forewing, where the subapical band is found in *P. aegeus*, and an extension of the pale area of the hindwing to the inner margin. The tails are mere vestiges.

The forewing of the female hybrid (plate 42*j*) resembles that of the female *aegeus* except for the pale band, which is darker. The white area on the hindwing is much smaller than in the *aegeus* female and even than that in most f. *polytes* females. It also tends to be somewhat more elongated towards the costal and anal borders. The red lunules on the hindwings are rather less conspicuous than in either *P. aegeus* or f. *polytes*, but they are of the red colour of *aegeus*. There are also vestiges of the blue scaling typical of *aegeus*. The underside is very similar. Thus this form looks extremely like a rather dark f. *polytes*. The tails are short.

6. *Hybrids with* P. memnon *L.*

The males of *P. memnon* are monomorphic and non-mimetic, and tailless in all areas except in Palawan and the Celebes, where they are tailed. The fore and hindwings are black with blue scaling which varies in intensity and position from race to race. The females are often polymorphic and mimetic and sometimes resemble the males rather closely (see Clarke *et al.* 1968).

The hybrids, all of which are males, are almost tailless and strikingly resemble *P. memnon*, the chief difference being that they are much smaller and have rather less blue scaling on the upper side than is typical of their male parental species. The underside of the hindwing is dark, like male *P. memnon*, except that there are traces of the orange lunules of *P. polytes* and a few white scales in the centre of the wing which appear to correspond in position to the widest part of the pale band characteristic of *P. polytes* males.

7. *Hybrids with* P. canopus *Westw. subsp.* hypsicles *Hewitson*

Papilio canopus is found in the Lesser Sunda Islands, the Tenimber Islands, North Australia and the New Hebrides. In both sexes, there is a strong resemblance to the males and f. *cyrus* females of *P. polytes*, except that the white or yellowish submarginal row of spots on the hindwing is continued in *P. canopus* as far as the apex of the forewing. *P. canopus* is not sexually dimorphic, nor polymorphic, though there is regional variation in the width and whiteness of the forewing band. The geographical distribution of tail length is the opposite of that in *P. polytes*, since in the western part of its range (Sumbawa, Timor and Alor) *P. canopus* is tailless, whereas in the Tenimber Islands, North Australia and the New Hebrides it is tailed. *P. canopus* is non-mimetic except on the island of Sumba, where f. *sumbanus* is said to be a good mimic of *Euploea lewa* (Seitz 1908).

We received larvae of subsp. *hypsicles* from the New Hebrides and bred from them one male insect. A mating (brood 11943, table 11) with a female *romulus* from Ceylon proved fertile and five F_1 males resulted, but no females. In the hybrids the white submarginal forewing border of *canopus* had disappeared, and the butterflies markedly resembled Ceylon *polytes* males both in pattern and tail length.

In many of the species crosses we have obtained no or few females, and in no instance have we obtained a second generation. Thus we are not able to say much about the inheritance of the patterns by which the species differ other than to note that both the pattern and the tail length of the hybrids tend to be intermediate between the parents when they differ, suggesting a lack of dominance.

The female hybrids carrying a gene controlling a mimetic form derived from *P. polytes* show a considerable breakdown in the perfection of the mimetic pattern when the other species concerned is monomorphic and non-mimetic (*P. fuscus* × *P. polytes* and *P. hipponous* × *P. polytes*). In the one instance (*polytes* × *aegeus*), where the other species was non-mimetic but had a pattern somewhat resembling f. *polytes* the mimicry was much improved in the hybrid despite the fact that no gene producing mimicry had been introduced from *P. polytes*. Thus the latter species must possess modifiers which improve mimicry in the presence of *aegeus* genes which give some slight resemblance to the model *P. aristolochiae*. Whether the pattern in *P. aegeus* is controlled by the same gene as that producing f. *polytes* or whether it is quite independently controlled we cannot say.

In only one of the hybrids (female *ambrax* × *polytes* male) are we unable to determine whether or not a gene controlling mimicry was introduced from the male *P. polytes* parent. The resulting female hybrids were good mimics of *P. polydorus* and of course the female parent has a pattern very similar to many forms of f. *polytes*. We do not yet know, but it seems likely that the same gene is involved in producing the pattern in both species since they are very closely related.

None of the male hybrids exhibited any trace of the female mimetic patterns; thus unlike the breakdown in the mimetic resemblance on hybridization there was no breakdown in the sex limitation of the mimetic pattern to the female. A similar result had previously been obtained in *P. dardanus* (Sheppard 1961). The results suggest that a gene complex determining sex-controlled inheritance of these patterns is common to all the species studied, even the monomorphic ones, and that the condition probably evolved before the species themselves existed.

XII. Discussion

To understand the effects of natural selection on microevolution it is necessary not only to know in detail the selective forces acting on the characters under investigation, but also the genetic architecture that has evolved as the result of that selection. One of the few situations where the selective forces are fairly well understood is Batesian mimicry. We therefore thought it of interest to make a comparative study of the genetic control of mimicry in a wide variety of insects. The present investigation concerns the fifth *Papilio* butterfly which we have studied in preparation for comparing the genetic situation with other families of butterflies and perhaps other orders of insects. The butterflies previously investigated are the monomorphic mimic *Papilio polyxenes* (Clarke & Sheppard 1953, 1956) and the polymorphic species *Papilio glaucus* (Clarke & Sheppard 1959*a*, 1962*b*), *P. dardanus* (Clarke & Sheppard 1959*b*, 1960*d*, *e*, 1962*c*) and *P. memnon* (Clarke *et al.* 1968; Clarke & Sheppard 1971*a*).

Both in the monomorphic and polymorphic species the mimetic patterns appear to have originally arisen as the result of a single mutation whose effect was gradually altered towards more perfect mimicry by the accumulation of modifiers. Thus *P. polyxenes* produces less perfect mimicry in species hybrids, as does *P. glaucus* in central Florida where the model is rare and the mimicry therefore less effective (Brower & Brower 1962).

More complex mimicry, involving many models and mimics, appears to generate linkage between the major genes concerned, thus producing a supergene (Clarke & Sheppard 1960*c*, 1971*a*). Either close linkage or suitable epistatic interactions between loci are advantageous because they reduce the proportion of inappropriate patterns due to segregation. It is interesting to note that Conn (1971) detected both epistatic interactions and linkage in the Dipteran *Merodon equestris* (Fab.) which mimics various species of bumblebee. Despite the fact that the linkage was not very close he found a linkage disequilibrium in a natural population.

As in our previous investigations, the mimicry in *P. polytes* tends to become less perfect when the major gene controlling a mimetic pattern is hybridized with a race where it is absent. Thus there is evidence that each race carries modifiers which perfect the mimicry. The breakdown is less marked in *P. polytes* than in *P. memnon* or in *P. dardanus*, perhaps because the mimicry itself is much less complex and at least one of the major genes is extremely widely distributed. Nevertheless, f. *romulus*, which is confined to the Indian subcontinent, does show some deterioration in the mimetic resemblance to its model *P. hector* when hybridized with Java material, the characteristic forewing diagonal stripes becoming more diffuse in outline. In hybrids with the more distant race *alphenor* from the Philippines the resemblance breaks down further, the mimicry on the hindwing also becoming less good. In the species hybrids with *P. ambrax* and *P. fuscus* the mimicry was quite poor (see above).

There are only two other mimetic patterns in *P. polytes*, f. *polytes* mimicking the three models *P. aristolochiae* (with white on the hindwing), *P. polyphontes* and *P. polydorus*, and f. *theseus* mimicking *P. aristolochiae* (with no white on the hindwing) and *P. atropos*.

F. *polytes* shows variations in pattern which follow those of its local models. The genetic studies have shown that this variation, where investigated, is genetically controlled by modifiers and not by different allelomorphs at a major locus.

Owing to the very widespread distribution of f. *polytes* it has been impossible adequately to test the perfection of the mimicry in a gene complex where f. *polytes* is normally absent. However, in a species cross with *P. aegeus* we have shown that *P. polytes* possesses modifiers which can strikingly improve a non-mimetic pattern, somewhat similar to f. *polytes*, so that it becomes a much better mimic. In contrast, when f. *polytes* is hybridized with a species which is non-mimetic and monomorphic (*P. hipponous*) the mimicry becomes much less perfect, showing that the other species does not possess modifiers improving the mimicry.

The form *theseus* is somewhat less variable in pattern as are its models. The occurrence of this form is closely correlated with the presence of its models and in consequence the distribution of the mimics is geographically very discontinuous (figure 4, p. 438). This raises the interesting question of whether the various forms of f. *theseus* have arisen independently as the result of separate mutations, or whether they have arisen by the modification of f. *polytes* in the absence of its own models (the models of f. *theseus* and f. *polytes* are allopatric).

The genetic evidence both in the Philippines and in Borneo suggests that f. *theseus* has been produced by modification of the effect of the gene which elsewhere controls f. *polytes*. Thus, on outcrossing, the *theseus* pattern tends to become similar to and sometimes indistinguishable from f. *polytes*. The genetic control of f. *polytes* and f. *theseus*, therefore, closely parallels the situation found in *P. dardanus*, where f. *hippocoon* and f. *hippocoonides* carry the same major gene but differ multifactorially (Clarke & Sheppard 1960*b*).

Since we have been unable to complete our genetic investigation of *theseus*, particularly with respect to Sumatra and Lombok, it is possible that the situation is rather more complex than that in the *dardanus* example mentioned above, and it may ultimately be found to parallel the genetic control of f. *cenea* and f. *ochracea* in *P. dardanus* (Clarke & Sheppard 1962*c*). Here there are two isoalleles which produce the *cenea* pattern in the South African gene complex. One allelomorph is found in Southern Africa, the other in two mountain top colonies in Northern Kenya. In these mountain populations there are modifiers which alter the effect of the local allelomorph to produce a pattern resembling the sympatric model. These modifiers have no effect on the allelomorph absent from these localities but present in the rest of Africa. Thus the modifiers utilized in the perfection of the mimicry only affect the isoallele in whose presence they were selected and not allelomorphs producing the same pattern elsewhere.

Besides the interesting similarity between the genetic control of f. *polytes* and f. *theseus* in *P. polytes* and that of f. *hippocoon* and f. *hippocoonides* or f. *ochracea* and f. *cenea* in *P. dardanus*, there are almost exact parallels in the control of tail length, and here both species differ from the situation in *P. memnon*. In *P. dardanus* the models always lack the tails characteristic of Papilios. Consequently over most of the range of the species where mimics are common the populations are homozygous for a gene causing absence of tails in the females but not affecting the tail length of the non-mimetic males. In Ethiopia, however, where the mimics are rare, the alternative allelomorph, allowing the presence of tails in the female, is fixed. In this situation there has been the evolution of a gene complex which reduces the tail length in the mimics (relative to the non-mimetic females) thus improving their resemblance to the tailless models (Clarke & Sheppard 1962*a*).

In *P. polytes* a very similar situation is to be found in some areas except that the models are usually tailed and the non-mimetic males and females may be tailed or tailless depending on the locality (table 1, p. 435). Thus the mimics and the non-mimetic forms are tailed in continental Asia, but to the south east the length of the tails of the males and the non-mimetic females is reduced (but not that of the mimics). In the Philippines the tails of the non-mimetic forms are virtually absent but the mimics still retain their full tail length. South of the Philippines, in the Moluccas, the model is tailless and here both the mimetic and non-mimetic forms also have tails which are greatly reduced or absent. Thus the tail length of the mimics shows a high degree of correlation with their appropriate models ($r_{12} = 0.89$), whereas there is no such correlation between the tail length of the model and the local non-mimetic form (f. *cyrus*, $r_8 = 0.13$, males, $r_{10} = 0.16$). There seems no doubt that a situation parallel to that found in Ethiopian *P. dardanus* exists in the eastern range of *P. polytes* except for the fact that here the situation is reversed because the models are tailed rather than tailless.

The genetic investigations show that the difference in tail length between mimetic and non-mimetic forms is due to the presence of specific modifiers, which only produce their effect in the male and non-mimetic female. Thus in race *theseus* the situation exactly parallels *P. dardanus* in that modifiers have been selected which increase the difference between mimetic and non-mimetic forms and thus help to maintain the mimetic resemblance. In the Philippines the situation has evolved even further since in the non-mimetic forms the tails have disappeared.

We do not know how the absence of tails in the mimics on the Moluccas is controlled genetically, but judging by the high variance of tail length among the mimics in the South Moluccas it is probably multifactorial, and thus differs from *dardanus*, where the absence of tails in the mimics is due to a major gene.

The investigation raises the interesting problem as to why the males and non-mimetic females become progressively more tailless from west to south-east. We have no direct evidence that the cline is due to the operation of selection but the fact that only specific modifiers are involved suggests that natural selection is probably responsible. It is certainly maintaining the resemblance between model and mimic with respect to tail length.

As with *P. dardanus* and *P. memnon*, the polymorphic forms are controlled by what appears to be a multiple allelomorphic series rather than by independently segregating loci as had been previously supposed. There is also some evidence that the locus concerned is complex. There are three aberrant forms known which may well have been produced by crossing over within the chromosomal region concerned, since they have the forewing pattern of f. *romulus* but the hindwing pattern of f. *polytes*.

P. polytes has strikingly supported our previous findings concerning the evolution of the genetic architecture of a species resulting from the selection for Batesian mimicry, an architecture that contrasts markedly with the situation found in the genetic analysis of Müllerian mimicry, where selection is for monomorphism rather than polymorphism (Bovey 1941, 1966; Dryja 1959; Emsley 1964; Bullini, Sbordoni & Ragazzini 1969; Sheppard 1963; Turner & Crane 1962; Turner 1971, see also Clarke & Sheppard 1971*a*).

In our investigations we have found that supergenes are involved more often than epistasis in reducing the frequency of inappropriate patterns. That both situations often can be found within one species is strongly suggested by the recent genetic investigation of Conn (1971). Epistatic interactions are also known in another Dipteran mimic of bumble bees, *Volucella bombylans* (L.) (Gabritchevsky 1924; Keeler 1926) and multiple allelomorphs (or a supergene) in a lygaeid bug (*Oxycarenus multiformis* Samy) (Samy 1971).

Because of the consistency within the Papilios with respect to the presence of modifiers and of a basic complex locus or supergene controlling the mimicry, rather than the presence of independent loci and suitable epistatic interactions, it has now become important to extend the study to other groups of Lepidoptera to see if the evolution of supergenes, rather than epistatic relationships, is general or only characteristic of this genus.

We dedicate this paper to Professor E. B. Ford, F.R.S., who has done so much to stimulate research into the evolution of mimicry.

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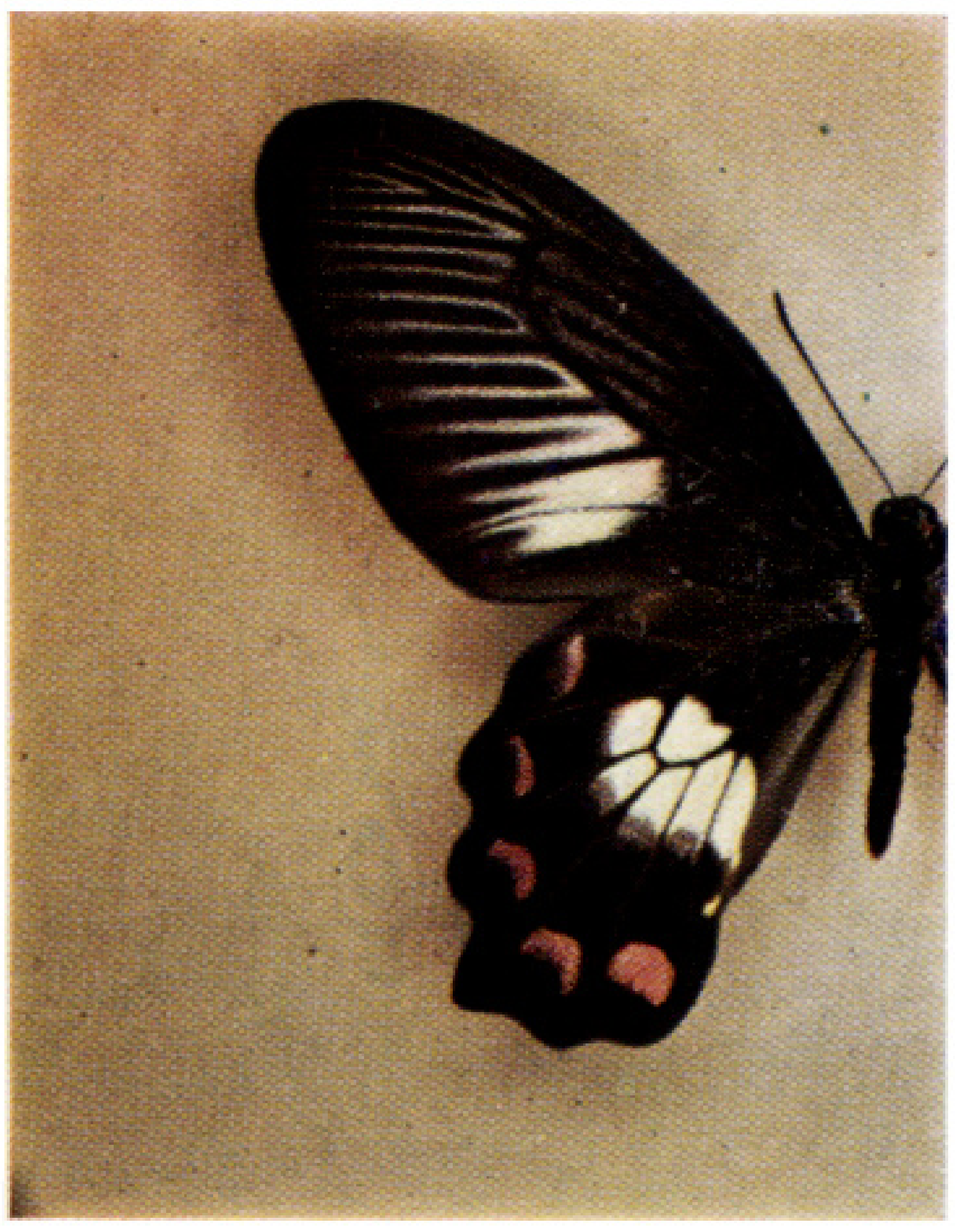


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