THE EVOLUTION OF MIMICRY IN THE BUTTERFLY *PAPILIO DARDANUS*

C. A. CLARKE and P. M. SHEPPARD
Departments of Medicine and Zoology, University of Liverpool

Received 23.v.59

1. INTRODUCTION

WHEN Bates put forward the mimicry hypothesis which bears his name, Darwin (1872), although accepting it, had some difficulty in explaining the evolution of the mimetic resemblance of several distinct species to one distasteful model by a series of small changes, a requirement of his general theory of evolution. He said " it is necessary to suppose in some cases that ancient members belonging to several distinct groups, before they had diverged to their present extent, accidentally resembled a member of another and protected group in a sufficient degree to afford some slight protection; this having given the basis for the subsequent acquisition of the most perfect resemblance ". Punnett (1915) realised that the difficulty is even more acute when one is dealing with a polymorphic species whose forms mimic very distantly related models. Knowing that, in those butterflies which had been investigated genetically, the forms differed by single allelomorphs he concluded that the mimicry did not evolve gradually and did not confer any advantage or disadvantage to the individual. He argued that an allelomorph arises at a single step by mutation and that therefore the mimicry also arises by chance at a single step. Goldschmidt (1945) although not denying that mimicry confers some advantage to its possessors also maintained that the resemblance arises fully perfected by a single mutation of a gene distinct from that producing the colour pattern in the model, but producing a similar effect in the mimic. Fisher and Ford (see Fisher, 1930; Carpenter and Ford, 1933; Ford, 1953) on the other hand have put forward a view intermediate between the extreme ones of Darwin on the one hand and Goldschmidt on the other. They maintain that a resemblance between the mimic and model as good as that often found in nature cannot reasonably be expected to arise by chance. They therefore suggest that a mutant becomes established which gives a sufficient resemblance to be advantageous and that this is gradually improved by the selection of modifiers which alter the effects produced by the mutant.

Ford (1953) has raised serious theoretical objections to Goldschmidt's (1945) hypothesis and he pointed out how the validity of each hypothesis can be tested. He notes that a particular mimic usually varies in appearance in parallel with the local race of its model and that on his own hypothesis one would expect these allopatric

mimetic forms of one model to differ multifactorially. However, if mimicry arises by mutation and is not thereafter modified, as is postulated by Goldschmidt, one would expect such local variation in the mimic to be controlled by multiple allelomorphs as Goldschmidt himself predicts. In 1954 we decided to investigate this problem genetically.

2. MATERIAL AND METHODS

The work has been carried out in two stages. Firstly, it was necessary to understand the mode of inheritance of various sympatric varieties and secondly, to make suitable race crosses to test the two hypotheses. Ford (1953) suggested that the best material for such a study might be the butterfly *Hypolimnas dubius* since both sexes

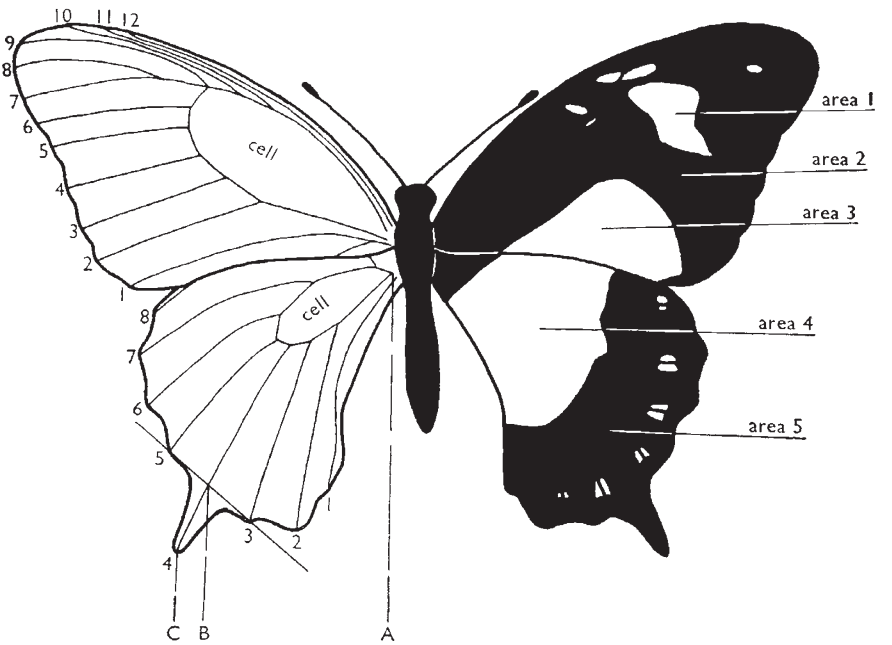


FIG. 1

are polymorphic and mimetic and the genetic status of the forms is relatively well known. However, we decided to use the African butterfly *Papilio dardanus* Brown. Although it suffers from the disadvantages that it is only polymorphic and mimetic in the female and has an almost bewildering variety of forms, whose genetics were unknown at the time, it had the overwhelming advantages that (*a*) it can be hand-mated, (*b*) it will lay eggs readily in captivity, (*c*) it has a larva one of whose food plants, *Citrus*, was known to be available in England, (*d*) the butterfly is widely distributed and common over much of Africa and (*e*) it has a large number of relatively distinct races whose distribution has been worked out in detail.

A description of the races and forms can be obtained from the excellent paper by Ford (1936) and the standard works he cites. An account of the forms we have investigated can be obtained from Clarke and Sheppard (1960). The pattern differences between the forms can be described in terms of the numbered areas, and the length of the tails, if present, can be measured by the length BC and that of the wing BA (fig. 1). The method of determining these points and of adjusting

tail length to take into account variations in the size of the wing itself are given by Clarke and Sheppard (1960).

The details of the breeding techniques are given by Clarke and Sheppard (1959*a*) and an account of the genetics of most of the major varieties by Ford (1936) and Clarke and Sheppard (1959*b*, and in preparation). The *hippocoonides*, *cenea*, *natalica*, *trophonius*, *leighi*, pale-*poultoni* and the yellow male-like non-mimetic forms of the female are controlled by a multiple allelomorphic series or by closely linked genes whose effects are sex-controlled. Bright-*poultoni*, *niobe* and *planemoides* are determined unifactorially by genes whose effects are sex-controlled and they are probably members of the same allelomorphic series as all the others. The absence of tails in the females is determined by a single locus not linked to the multiple-allelomorphic series and its effect is also sex-controlled.

3. RESULTS

(i) *Modification of the* hippocoonides *pattern*

The form *hippocoonides* is a black and white insect found in South and East Africa (races *cenea*, *tibullus* and *polytrophus*) which mimics *Amauris niavius dominicanus* (plate 1, no. 1). The mimic has a narrow black border to the hindwing (area 5) with small white spots on it near its distal edge. The proximal edge of this black area (situated $\frac{1}{2}$ to $\frac{3}{4}$ of the way from the margin of the wing to the cell) is fairly distinct in outline and has short black rays extending from it towards the cell, and situated parallel to and midway between the veins of the wing (plate 1, no. 3).

In West and Central Africa (race *dardanus*) there is an allopatric form *hippocoon* which mimics *A. n. niavius* the western race of the model of *hippocoonides*. The mimic like the model differs from the eastern form in the amount of black on the hindwing (area 5). Area 4 is much reduced in size since the black of area 5 extends to the cell or nearly to it. The white spots near the margin of the wing are much reduced in size or absent and the proximal edge of area 5 is far less distinct than in *hippocoonides* since it shades off gradually into the white area owing to a liberal scattering of black scales along the border. The rays are also extended in length and end near the cell (plate 1, no. 4). All these characters are concerned in the mimetic resemblance since all enhance the black appearance of the hindwing, a characteristic of the western model (plate 1, no. 2).

On crossing a *hippocoon* stock with *hippocoonides* from South Africa an F_1 generation is produced which normally is much like the less extreme *hippocoon* forms in appearance. That is to say, although the individuals have a broad black border to the hindwing it is usually slightly narrower than the average for *hippocoon* since it does not usually reach the cell, the black rays are slightly shorter and there is a greater tendency for the white spots near the margin of the hindwing to appear. However, in two F_1 families out of three, using the west coast (Ghana) *hippocoon*, the F_1 were *hippocoonides*-like in appearance (one insect excepted) but not in thirteen families using the Uganda stock of *dardanus*. Thus there is some evidence that the genetic control

of the difference between *hippocoon* and *hippocoonides* is not the same in all individuals.

In the F_2 and first backcross to *hippocoonides* of the *hippocoon*-like F_1 there is no clear cut segregation into *hippocoonides*-, *hippocoon*- or F_1-like individuals. Not only are all grades of intermediates found but the various characters which determine the difference between *hippocoon* and *hippocoonides* segregate and are themselves variable in expression. Thus one can have a narrow black border (area 5) with marked rays (plate 2, no. 8), with no rays (no. 7), a broad border with long rays (no. 6), with short rays, and also independent assortment of the expression of the white spotting near the margin of the wing (nos. 4-8).

We are therefore led to the conclusion that *hippocoon* and *hippocoonides* do not differ by a pair of allelomorphs but by a minimum of three and probably many more than three loci.

In race *antinorii* from Abyssinia there is a black and white form *niavioides* which mimics *Amauris niavius* but is a much poorer mimic than either *hippocoon* or *hippocoonides*. It has the normal pattern of the mimic on the forewing but not only does the hindwing have tails (see below) but the black border (area 5) is far more irregular in outline than in the model or the other two forms and the white spots near the margin of the wing tend to be far larger and less well defined in shape. The F_1 hybrid between *niavioides* and *hippocoonides* has a hindwing border which is more regular in outline and gives a better mimetic pattern. In the F_2 there is considerable variability but no clear cut segregation into *niavioides*-, *hippocoonides*- and F_1-like individuals. In fact, of 31 insects examined none were of the typical *niavioides* form. Thus here again we must conclude that *hippocoonides* and *niavioides* differ by more than one pair of allelomorphs.

(ii) *Modification of the* cenea *pattern*

The form *cenea*, a good mimic of *Amauris echeria* and *A. albimaculata* (plate 1, nos. 8 and 6), is found in South and East Africa as far west as the north shore of Lake Victoria (race *dardanus*). It is not found in West Africa nor are its models. The variety is dominant to *hippocoonides*, and to *hippocoon* taken from the area of Lake Victoria. The *cenea*/*hippocoon* heterozygotes differ slightly from the South African forms (plate 1, no. 8, and plate 2, no. 1) and are like those found in the vicinity of Lake Victoria and in Kenya (race *polytrophus*). The difference involves the white spots in area 1 which are variable in size, often being slightly enlarged, or, in a small minority of wild individuals and of our heterozygotes, being actually joined up to form a white patch of variable size. Thus in race *dardanus*, from an area where *cenea* is uncommon (7 per cent. or less of the population) and from Kenya (race *polytrophus*) where the models are rare, the mimics are more variable and slightly less perfect in their resemblance. In contrast to this, the only two families we have so far obtained in which

the *cenea/hippocoon* heterozygote has been produced using *dardanus* from West Africa (Ghana) the white spots of area 1 of the forewing were absent and replaced by a large white patch similar to that of *hippocoon*. Thus all these insects resembled the most extreme forms of the eastern hybrids. Moreover unlike the latter the black border of the hindwing (area 5) is very much broader, actually reaching the cell (plate 2, no. 2). Our data as far as they go suggest that there is considerable variability in the gene-complex of race *dardanus* with respect to modifiers affecting the expression of *cenea*. In the east there are modifiers giving quite good mimicry but not as perfect as in South Africa where the mimic is common. In the west, however, these modifiers appear to be absent or much rarer and consequently the mimicry is far less perfect.

(iii) *Modification of the* trophonius *pattern*

The form *trophonius* is found throughout South, East and West Africa and it mimics *Danaus chrysippus* (plate 1, nos. 5 and 7). It has the same black pattern as *hippocoonides* but areas 3 and 4 are orange-brown not white. In both the east and the west it has a narrow black border in area 5, thus conforming to the pattern of the model, but in the west the black rays between the veins are elongated and the form is called *trophonissa* by entomologists. It is dominant to *hippocoonides* and *hippocoon* and produces normal mimicry in hybrids between South African *trophonius* and both eastern (Uganda) and western (Ghana) *hippocoon* (plate 2, no. 3).

The only difference between the hybrids and South African *trophonius* is that the rays are sometimes rather longer in the hybrid thus conforming to the *trophonissa* pattern. It seems that in contrast to the situation found with *cenea* the *dardanus* race does not vary much with respect to modifiers affecting the mimicry of *trophonius*, a form found throughout its area of distribution.

(iv) *Modification of the* planemoides *pattern*

The mimic *planemoides* resembles *Bematistes poggei*, the male of *B. macarista* and perhaps the female form *aurivillii* of *Acraea alciope*. It is found commonly in Central Africa where its models are common but elsewhere only as a rarity often with a rather incomplete development of the mimetic pattern (proto-*planemoides*). The form, which is dominant to *hippocoon*, has hindwings which are white and have a broad black border (area 5) similar to that in *hippocoon* but with the white spots, if present, replaced by orange-brown. The forewings are in the main black but there is a broad irregularly shaped bar of orange-brown pigment covering area 1, area 2, and the distal half of area 3.

On crossing *planemoides* from Entebbe with Kenya stock of the race *polytrophus*, *planemoides/hippocoonides* heterozygotes were obtained. These had the general coloration and pattern of *planemoides* except that the

orange-brown area on the hindwings was divided by a broad black bar covering area 2. Thus the mimetic pattern became imperfect when part of the gene-complex of *polytrophus* was introduced into the genetic constitution of the heterozygotes. These imperfect mimics were similar to many taken from wild populations or bred from wild females of the *polytrophus* race. One insect similar to our hybrids is figured in colour by Ford (1936, plate 4, no. 3). The results indicate that in the gene-complex of *polytrophus* from Kenya, where the models are rare or absent, the mimetic pattern of *planemoides* partially breaks down.

(v) *Hybridisation with the Abyssinian and Madagascan races*

Besides the crosses between races of the main African stock, hybrids have also been obtained between some of the mimetic forms of Central and South Africa and the isolated races *meriones* from Madagascar and *antinorii* from Abyssinia. The results have been reported by Clarke and Sheppard (1960) but a summary of them will be given here.

By far the commonest female form in the Abyssinian race is black and yellow and looks much like the male. This form accounts for 80 per cent. and probably more of the female forms and has tails like all the other Abyssinian females. This contrasts with the other races we have considered in which the females are always tailless. The next commonest form in race *antinorii* is *niavioides* which as we have seen is a modified *hippocoonides*. Besides this form there is a much rarer mimic of *D. chrysippus* called *ruspinae*, looking just like a tailed *trophonius*, and a tailed *cenea*, which has only been reported twice, mimicking *A. echeria*. Both *niavioides* and "*cenea*" are completely recessive to the yellow male-like form (the presumed primitive pattern) and *cenea* is dominant to *niavioides*. The gene controlling the *trophonius* pattern is also dominant in its effect to *niavioides* and produces a good mimic of *D. chrysippus*. However, the hybrid F_1 heterozygote between the yellow form and *trophonius* produces a confused result. The colour pattern of the hindwings is like *trophonius*, but although area 3 is orange-brown in colour, area 2 is yellow not black and area 1 shows varying amounts of yellow and orange-brown pigment. Thus the mimicry has completely broken down in this hybrid genotype. Since no insect resembling this heterozygote has ever been seen in the wild, despite the fact that several *ruspinae* have been caught, we must come to one of two conclusions; either (*a*) on replacing the hybrid gene-complex by a pure *antinorii* one, this intermediate pattern would vanish and mimicry would be restored, or (*b*) *trophonius* does not occur in race *antinorii* and *ruspinae* is controlled by a different gene, the *antinorii* gene-complex being adjusted to the latter, but not to *trophonius*.

The race *meriones* is monomorphic, all the females being like the males and tailed. In the F_1 heterozygotes between this race and the forms *cenea* and *hippocoonides* the mimicry breaks down. The pattern

of the *hippocoonides* heterozygote is rather like that of *niavioides* except that the pale areas are yellow, but a paler yellow than in *meriones* itself. On backcrossing into the South African race the black pattern becomes identical with *hippocoonides* but the pale areas remain pale yellow. Insects indistinguishable from this have been produced among the second, third and fourth backcross generations of yellow insects, derived from Abyssinia to Central African stock. It therefore seems beyond dispute that the South and Central African races possess modifiers which materially increase the mimetic resemblance between the yellow/*hippocoonides* heterozygotes and the model *Amauris niavius dominicanus* (for plate see Clarke and Sheppard, 1960).

The *cenea*/yellow heterozygote is quite unlike *cenea* and is very similar to the *hippocoonides*/yellow F_1 except that the yellow is more orange and area 1 shows a tendency to break up into yellow spots surrounded by black.

The *trophonius*/yellow heterozygote has an appearance very different from the similar hybrid with race *antinorii*. However, this depends chiefly on the fact that area 2 is black not yellow. The amount of orange-brown pigment in area 1 is very variable in both these hybrids. On one specimen, area 1 is orange-brown but on another it is of the palest yellow. Moreover in the latter individual the black bar area 2 is reduced and there is pale yellow pigment next to it in area 3. Thus the insect is an almost exact replica of proto-*trophonius* an imperfect mimic found in race *polytrophus*.

(vi) *The inheritance of tails*

In the Madagascan race the tails of the females (mean 14.8 mm.) are as long or longer than those of the males (mean 14·4 mm.). The tailless condition is controlled by a single allelomorph (*T*) which shows no dominance, the heterozygotes of the F_1 generation having an intermediate tail length and considerable variability from individual to individual (mean 4·4 mm.). The tailed insects (*Tt*) of the first backcross to South African stock have rather shorter tails than most of the F_1 heterozygotes suggesting that the South African race has modifiers shortening tail length in the heterozygote.

In the similar *antinorii* F_1 hybrid heterozygotes and the first backcross to race *antinorii* the heterozygotes have a shorter mean tail length than in the previous Madagascan hybrid (mean 1·9 mm.) and about half the individuals appear to be tailless, so that this condition is dominant in many individuals. On examining the pure *antinorii* females we find that the mean tail length of the yellow females (12·5 mm.) is less than that of the males (14·2 mm.; $P<0.001$) and the variance is greater ($P<0.001$) as it is also compared with that of the Madagascan males ($P<0.001$) or females ($P<0.001$). The mean tail length of the mimetic *antinorii* females (9·0 mm.) is even less than in the yellow ones ($P<0.001$) and there is a suggestion that the variance is

greater. These findings also apply to the tailed (*tt*) individuals of the first backcross to *antinorii* (difference of means $P<0{\cdot}001$, of variance $P<0{\cdot}05$) (see Clarke and Sheppard, 1960). Thus the monomorphic *meriones* and polymorphic *antinorii* races differ with respect to modifiers affecting tail length.

4. DISCUSSION

Races *antinorii* and *meriones* are particularly pertinent to any discussion on the ability of disruptive selection (Mather, 1955) gradually to alter a mimic towards a more perfect resemblance. It is certain that the absence of tails increases the resemblance between model and mimic to a quite remarkable degree. Now judging by the greater mean length of the tails of *meriones* females as compared with males and the small variance in them and in the males of all races (see Clarke and Sheppard, 1960), we may conclude with a fair degree of confidence that the tailed condition is advantageous in the yellow non-mimetic pattern. If this be so, in the polymorphic Abyssinian race where the allelomorph *T* for the absence of tails is not found, one would expect disruptive selection and the consequent accumulation of modifiers reducing tail length in the mimics. Moreover, since Thoday (1959) has shown that disruptive selection leads to increased variance within the population, one would also expect the female variance, particularly that of the mimetic forms, to be greater in the *antinorii* than in the monomorphic *meriones* race.

The data from wild caught specimens show that in *antinorii* the females have a shorter mean tail length than the males and that this is particularly marked in the mimetic forms. The first backcross to *antinorii* of the F_1 hybrid with Central African stock is in agreement with respect to the shorter mean tail length of the mimetic females. Moreover, as predicted, the variance is greater in the females, particularly the mimetic ones, than in the males of any race or of the *meriones* females.

Now it might be argued that the allelomorphs for mimetic patterns were themselves affecting tail length thus reducing the mean below that of the yellow females. But the effect of a gene cannot be taken in isolation from the particular gene-complex in which the allelomorph finds itself. What we wish to know is whether or not race *antinorii* possesses modifiers, not present in the absence of mimicry (race *meriones*), which reduce tail length in the female and in particular whether some of these are specific in action to the mimetic forms. The difference in the mean tail length of *meriones* females and the of yellow *antinorii* ones indicates that the two races do differ in modifiers and that the increased variance suggests that there is considerable segregation for them in *antinorii*. The even larger variance in the wild mimetic females of pure *antinorii* and the backcross family is consistent with the view that some of these modifiers are specific to the mimics. Thus in the backcross brood both the longest and shortest tailed homozygous

(*tt*) individual is to be found among the mimetic forms despite the fact that the mean tail length is less than is that of the yellow females. The tailed (*tt*) individuals among the F_2 hybrids are also instructive since in them a greater segregation of modifiers would be expected, if such exist. Moreover, if modifiers specific to mimetic individuals are rarer in the tailless main African races as they might be expected to be (where yellow tailed individuals are absent), there should be an increase of variance and a decrease in the difference in mean tail length between yellow and mimetic females. The data such as they are give no indication of a difference in mean between yellow (9·5 mm.) and mimetic (9·5 mm.) females and do suggest a considerable increase in variance over the backcross (difference in variance between *tt* F_2 and B_1 yellow females $P<0{\cdot}01$).

The genetic evidence on tail length taken as a whole strongly supports the thesis that there is disruptive selection acting which is resulting in the accumulation of modifiers which reduce tail length particularly in the mimics, so that they conform more closely to the models. Evidence for strong disruptive selection in race *antinorii* has already been mentioned by Clarke and Sheppard (1960). They pointed out that the presence of dominance between the yellow form and *hippocoonides* and *cenea* but its absence between yellow and its allopatric forms strongly suggests that disruptive selection has already resulted in the elimination of intermediate heterozygotes which would not possess either the advantageous pattern of the mimics or the male-like female.

Over and above the evidence of the genetics of the tailed condition and of dominance there is no doubt from the results so far obtained (race crosses using *hippocoon*, *hippocoonides*, *cenea*, *trophonius* and *planemoides*) that a gene controlling a mimetic pattern produces a closer resemblance to the model in the gene-complex of a wild population where both mimic and model are found than in one where the model and mimic are absent or than in a hybrid genotype. Furthermore there is some evidence from *cenea* and *niavioides* that when the mimic is relatively uncommon the mimetic resemblance is sometimes less perfect than in a population in which it and the model are common. When the mimic becomes relatively very abundant compared with the model mimicry again begins to break down (race *polytrophus*). This would be expected since, when the mimic is " too common ", birds cannot learn that the pattern indicates inedibility in the model, the advantage of the mimetic pattern vanishes and selection no longer stabilises it.

Since the genes we are considering do not produce perfect mimicry in all the gene-complexes of the species we must conclude that, if Goldschmidt's hypothesis is correct, an allelomorph producing mimicry can only establish itself if by chance it occurs in a very favourable gene-complex. Moreover, we must also conclude that once established, selection is powerful enough to stabilise the gene-complex

so that the good resemblance produced by the gene is maintained. Such an extreme view does not accord with the facts. In *P. dardanus* the mimetic forms are found wherever the models are common so that on Goldschmidt's view a suitable gene-complex must have occurred by chance (at a time when the mutant was available) in all areas where appropriate models are at high frequency notwithstanding that in other areas, anyhow at the present time, such suitable gene-complexes do not occur! Now we know from the work of Brower (1958) that in the laboratory, in circumstances in which birds could examine their prey for two minutes, imperfect resemblances protect to some extent. It is therefore unreasonable to assume that in the wild, when the bird may see the insect for only a few seconds, imperfect mimicry will not confer some advantage. This is in accord with the finding that where the mimic is rare, mimicry is sometimes less perfect. It has already been shown that if we accept Goldschmidt's view we must also assume that selection is powerful enough to stabilise the gene-complex to give good mimicry even if the mimic only accounts for some 10 per cent. of the female population. But such powerful selection would also be strong enough to alter the gene-complex to give a better mimetic resemblance if an imperfect mimic established itself. We may therefore safely reject Goldschmidt's hypothesis and accept that developed by Fisher and Ford.

5. SUMMARY

1. The main polymorphic forms of *P. dardanus* are controlled by a multiple allelomorphic series.

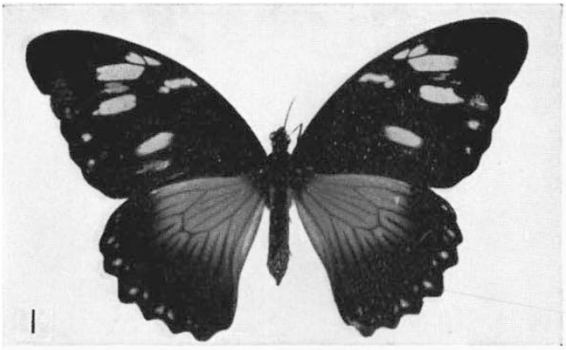
2. The varieties *hippocoon* and *hippocoonides*, which mimic different subspecies of the model *A. niavius*, differ at three and probably many more than three loci.

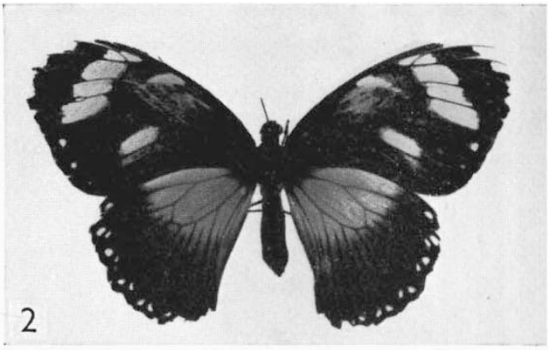
3. Allelomorphs controlling the varieties *hippocoonides*, *cenea*, *trophonius* and *planemoides* produce a much less perfect resemblance to the models when the gene-complex is modified by hybridisation with a race not possessing the particular mimic.

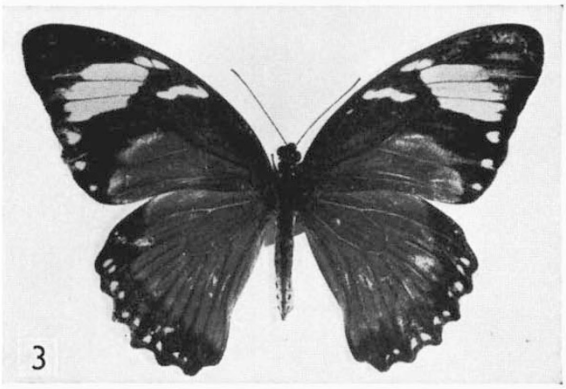
4. The absence of tails on the hindwings of the main African races is due to a single gene, the condition showing incomplete dominance.

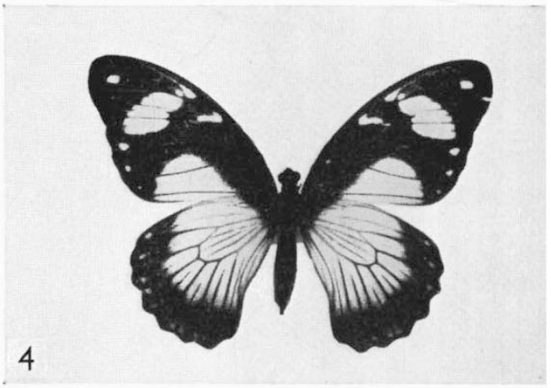
5. In the tailed Abyssinian and Madagascan races the length of the tails is multifactorially controlled. In the monomorphic Madagascan race the variance of tail length is as small in the females as it is in the males of all races. In Abyssinia, the females have a shorter mean tail length than the males and greater variance, these features being particularly marked in the mimetic individuals.

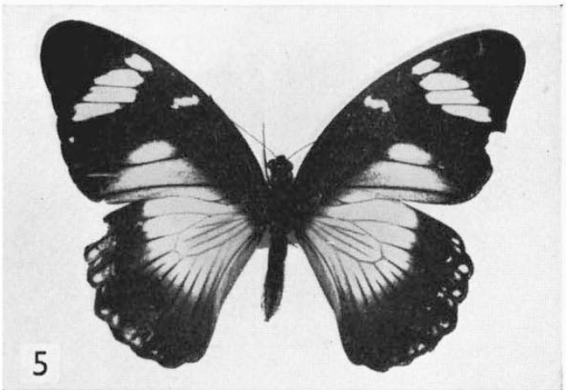
6. The results support the view that the original mimetic resemblance produced by a new mutant is enhanced by the selection of modifiers and when perfected the pattern is stabilised by selection. In Abyssinia there appears to be disruptive selection which is accumulating modifiers reducing female tail length in the mimics. Owing to

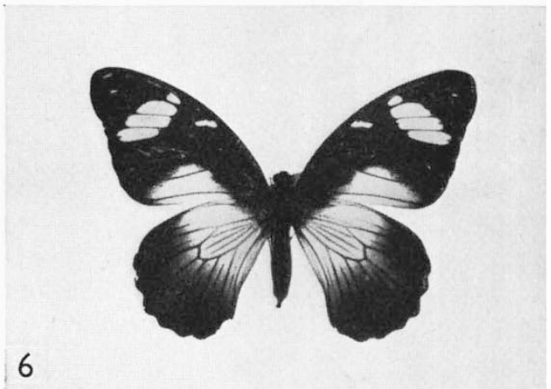


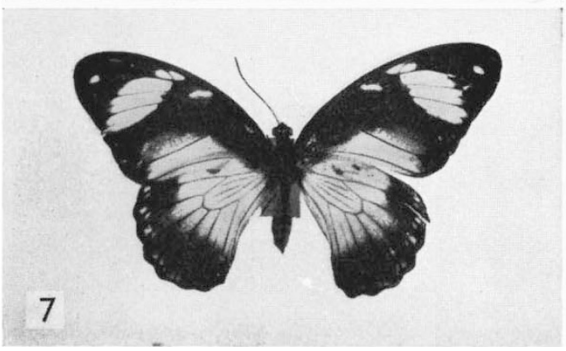












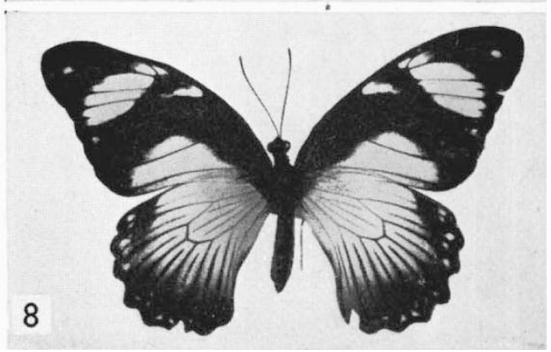
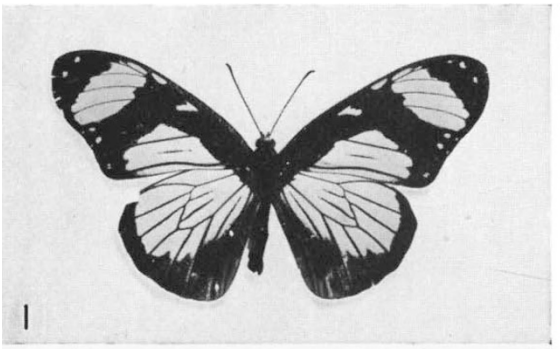
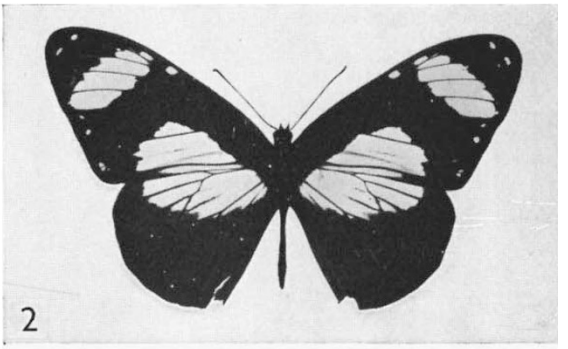
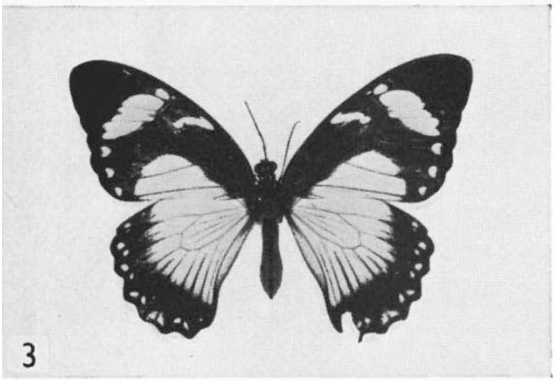


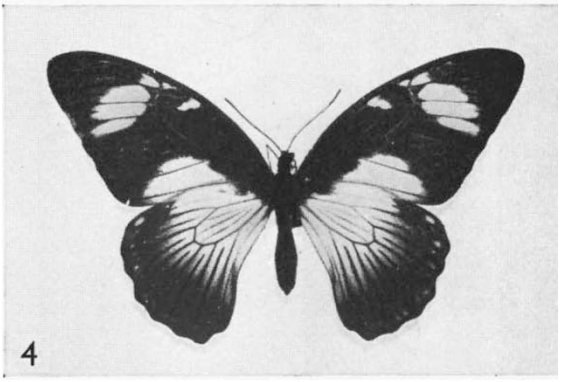
Plate II

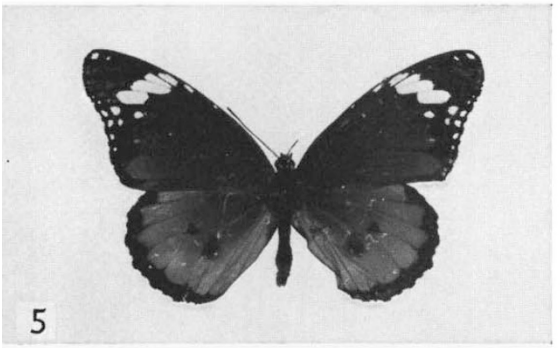
1. Heterozygote from a South African *cenea* × Central African *hippocoon*. It is similar in pattern to the local Central African *cenea*.
2. Heterozygote from a South African *cenea* × West African *hippocoon*. The mimicry in this form is less perfect particularly with respect to the forewing white spots.
3. Heterozygote from a South African *trophonius* × West African *hippocoon*. In this cross the mimicry remains well developed in contrast to 2.
4. to 8. These are examples from an $\mathbf{F_2}$ family from a South African *hippocoonides* stock × a Central African *hippocoon* stock. The insects are chosen to show the extremes of development and the independent assortment of the differences between *hippocoon* and *hippocoonides* (see text).

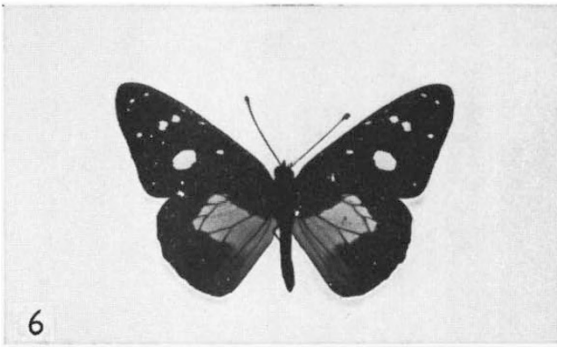


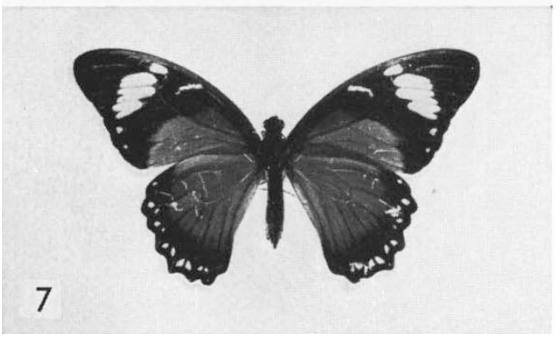












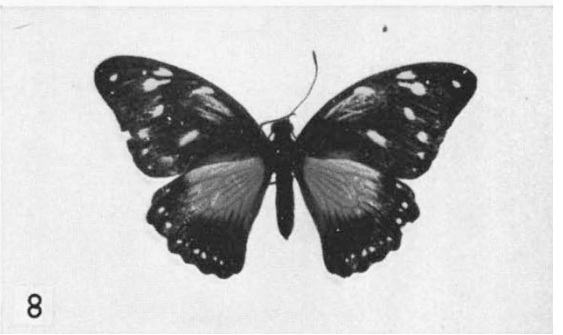


Plate I

1. *Amauris niavius dominicanus* from East and South Africa.
2. *A. n. niavius* from West Africa.
3. *P. dardanus* form *hippocoonides* mimicking 1.
4. Form *hippocoon* mimicking 2.
5. The ubiquitous *Danaus chrysippus*.
6. *Amauris albimaculata* from Central, East and South Africa.
7. Form *trophonius* mimicking 5.
8. Form *cenea* mimicking 6.

the segregation of these modifiers there is greater variance of tail length in the polymorphic Abyssinian than in the monomorphic Madagascan race.

Acknowledgments.—We are very grateful to Dr E. B. Ford, F.R.S., for his constant encouragement throughout the study and for his helpful comments on the manuscript. Our thanks are also due to the Nuffield Foundation without whose support most of this work could not have been undertaken.

6. REFERENCES

BROWER, J. 1958. Experimental studies of mimicry in some North American butterflies. Part 3. *Danaus gilippus berenice* and *Limenitis archippus floridensis*. *Evolution, 12*, 273-285.

CARPENTER, G. D. H., AND FORD, E. B. 1933. *Mimicry*. Methuen, London.

CLARKE, C. A., AND SHEPPARD, P. M. 1959*a*. The breeding of *Papilio dardanus* Brown in England. Technique and some results. *The Entomologist, 92*, 89-95.

CLARKE, C. A., AND SHEPPARD, P. M. 1959*b*. The genetics of some mimetic forms of *Papilio dardanus* Brown, and *Papilio glaucus* Linn. *J. Genet., 56*, 236-259.

CLARKE, C. A., AND SHEPPARD, P. M. 1960. The evolution of dominance under disruptive selection. *Heredity, 14*, 73-87.

DARWIN, C. 1872. *The Origin of Species*, 6th ed. Murray, London.

FISHER, R. A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

FORD, E. B. 1936. The genetics of *Papilio dardanus* Brown (Lep.). *Trans. Roy. Ent. Soc. Lond., 85*, 435-466.

FORD, E. B. 1953. The genetics of polymorphism in the Lepidoptera. *Advance. Genet., 5*, 43-87.

GOLDSCHMIDT, R. B. 1945. Mimetic polymorphism, a controversial chapter of Darwinism. *Quart. Rev. Biol., 20*, 147-164, 205-230.

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

PUNNETT, R. C. 1915. *Mimicry in Butterflies*. Cambridge Univ. Press, London.

THODAY, J. M. 1959. Effects of disruptive selection. *Proc. 15th Int. Cong. Zool.*, pp. 127-130.