THE GENETICS OF PAPILIO DARDANUS, BROWN. I. RACE CENEA FROM SOUTH AFRICA

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THE evolution of mimicry, although it may depend on the occurrence of extensive genetic changes some of which took place a long time ago, may nevertheless often be analyzable in considerable detail. However, despite the fact that much work has been done on the theoretical side (FISHER 1930) little progress has been made by means of direct experiments. An investigation utilizing the techniques of genetics, ecology and ethology would not only solve many of the problems of the evolution of mimicry itself but might throw considerable light on the factors governing evolution in general.

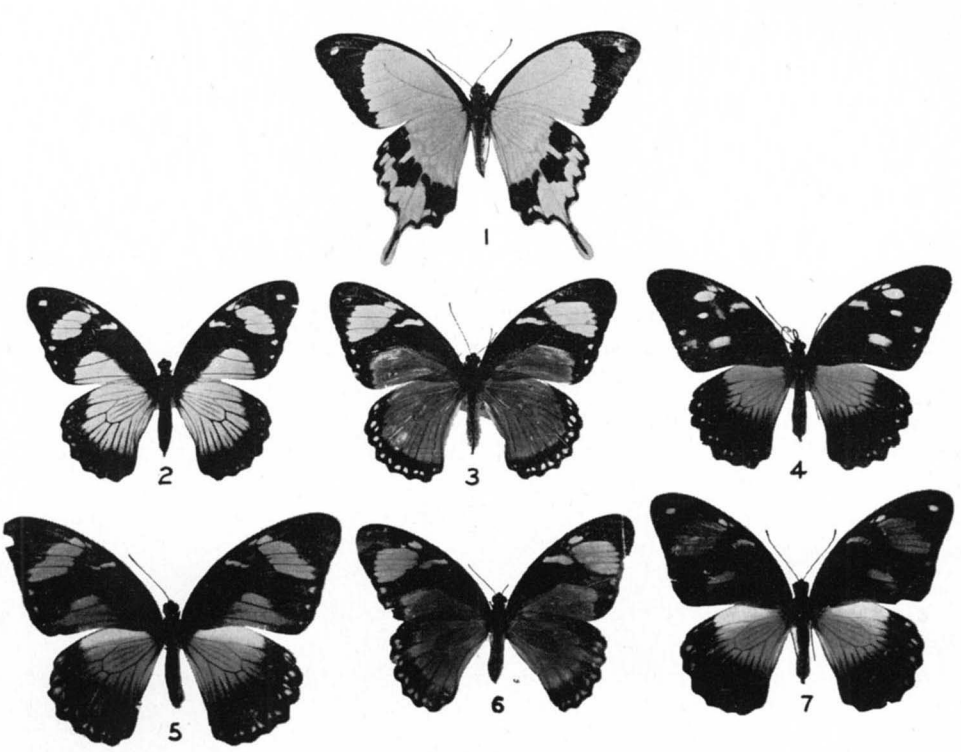
To investigate the genetic changes which have occurred during the evolution of mimicry it is necessary to make interrace and even interspecific crosses (FORD 1953). In order to obtain the maximum amount of information it is desirable to choose a species which has many mimetic and nonmimetic forms and in which some or all the mimetic forms are missing in some races. It is also necessary to know the geographical distribution of the races in detail together with the relative abundance of mimics and models in the various areas. The African swallowtail *Papilio dardanus* Brown, with its striking polymorphism in the female, fulfils these requisites better than most butterflies, and has been used in the present investigation.

This paper is the first of three dealing with the formal genetics of the various races of the insect. Only relevant broods are given in the tables but copies of the complete data, comprising over three thousand matings, are available on request.

Papilio dardanus, *race* cenea: This race inhabits South Africa, northwards to Delagoa Bay. The males are monomorphic, yellow, tailed and nonmimetic as they are wherever the species is found (Figure 1). The female forms that have been studied by us are the nonmimetic f. *leighi*, f. *natalica* and f. *salaami* and the mimics f. *hippocoonides*, f. *cenea*, f. *trophonius* (Figures 2–7) and a modification of f. *trophonius* in which the large apical spot on the forewings is buff and not the normal white (for a description of the forms, their models and their distribution see FORD 1936 and CLARKE and SHEPPARD 1959a). It should be noted that the name *cenea* is used to designate both the South African race and also one of the common mimetic female forms occurring within this and other races.

MATERIALS AND METHODS

Several well-known South African naturalists, MESSRS. GOWAN C. CLARK, C. G. C. DICKSON, D. A. SWANEPOEL and R. W. WELLS, have kindly sent us eggs, larvae and pupae of *P. dardanus cenea* from Natal.



FIGURES 1–7.—Forms of *P. dardanus* race *cenea*. FIGURE 1.—Male (light areas are pale yellow). FIGURE 2.—Female f. *hippocoonides* (light areas are white). FIGURE 3.—Female f. *trophonius* (light subapical spot is white, medium dark areas are bright orange). FIGURE 4.—Female f. *cenea* (light areas on forewing are white, base of hind wings buff). FIGURE 5.—Female f. *natalica* (light areas are all buff). FIGURE 6.—Female f. *salaami* (subapical spot light orange, medium dark areas are bright orange). FIGURE 7.—Female f. *leighi* (spots on forewing light orange, base of hind wing pale buff).

The method of breeding the butterflies in England is described by us in detail elsewhere (CLARKE and SHEPPARD 1959a,b) and since the earlier paper there have been two main alterations in the technique. Firstly, we have found that the caterpillars thrive much better on *Choisya ternata* (the Mexican orange flower) than on Citrus, and secondly, that the best way to have the material sent from Africa is in the form of living butterflies folded flat in cellophane envelopes.

RESULTS

Some observations on f. hippocoonides

This form which mimics the Danaid *Amauris niavius dominicanus* is very similar in pattern to f. *hippocoon* which occurs in other races of *dardanus* and which mimics *A. niavius niavius*, a different subspecies of the model for *hippocoonides*. In crosses between *hippocoon* and *hippocoonides* (in which the genotype of the male is known in this respect) we have found that there is no clear-cut

segregation in the F_2 (or equivalent) and backcross matings. This indicates that the two forms result from the modification of a single major gene (CLARKE and SHEPPARD 1960). Consequently, in this paper we have not distinguished between *hippocoonides*, *hippocoon* or hybrids between the two and all have usually been referred to as *hippocoonides*. The three types of insect serve equally the important purpose of providing broods homozygous for the white female form.

Inheritance of the forms of race cenea

As previously ascertained, (CLARKE and SHEPPARD 1959a), *cenea* is dominant to *hippocoonides* as is *leighi*, and neither is sex-linked. Further evidence of these dominance relationships is given by broods 1457, 1462, 1690, 1707, 2156, and 2185, where the male parent was homozygous for *hippocoonides*, *hippocoon* or the hybrid (Table 1).

It was previously known that *leighi* was probably dominant to *cenea* (CLARKE and SHEPPARD 1959a) and brood 1415 helps to strengthen this view since a *cenea* female mated to a male both of whose parents could have been heterozygous for *leighi* gave rise to seven *leighi* females, whereas if *cenea* were dominant at least a 1:1 ratio would be expected, the departure from this ratio being significant ($P>0.02$). This is confirmed by brood 2235, where a *cenea* female mated to a male heterozygous *leighi/trophonius* gave only *leighi* and *trophonius* offspring. Further evidence is provided by broods 1273 and 1386. In brood 1273, a female *leighi* which had not had f. *trophonius* in its known ancestry produced a female *trophonius* in its offspring indicating that the wild male to which it was mated was carrying *trophonius*. This female *trophonius* was mated to a male which had

TABLE 1

Dominance relationships of f. hippocoonides, *f.* leighi *and f.* cenea

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Males	*cenea* females	*hippocoonides* females	*trophonius* females	*leighi* females
1273	*leighi** *trophonius*	wild male not carrying	0	0	0	1	0
1386	1273 *cenea*†	*cenea* male offspring of	4	4	0	7	0
1415	wild	*leighi* mother	6	0	0	0	7
1457	*cenea*	*hh*‡	10	1	2	0	0
1462	*leighi*	*hh*	11	0	5	0	5
1690	*cenea*	*hh*	24	10	7	0	0
1707	*cenea*	*hh*	7	9	0	0	0
2156	*leighi*	*hh*	11	0	5	0	6
2185	*leighi* *cenea*	*hh* male from *salaami*	3	0	1	0	3
2235	wild	family§	19	0	0	8	16

* Not known to have *trophonius* in its ancestry.
† f. *leighi* is so rare that a wild *cenea* is highly unlikely to be carrying the gene responsible for this form: moreover there is much subsequent evidence that *leighi* is nearly always dominant to *cenea*.
‡ The designation of the genotype of the male known to be homozygous for *hippocoonides*, *hippocoon* or the hybrid.
§ See Table 4.

no *cenea* in its known ancestry (brood 1386). The offspring of brood 1386 segregated *cenea* and *trophonius*. If, as seems probable from other evidence, *leighi*, *trophonius* and *cenea* are allelomorphs (see below) then the female *trophonius* 1273 must have been *trophonius/cenea* and therefore as she could not have inherited *cenea* from her father, for she received *trophonius* from him, she must have inherited it from her *leighi* mother, thus proving the dominance of *leighi* over *cenea* (see Table 1).

That the dominance relationship between *leighi* and *cenea* can occasionally be upset is shown by a consideration of broods 1372, 1466, 1634 and 1740, all of which are very closely related to one another. Brood 1372 had one *leighi* and three *cenea* females; one of the latter was highly abnormal in that although it had the *cenea* patterning (except that the spots near the apex of the forewing were larger and more circular than normal) the coloring was orange like that of *leighi*. This particular butterfly was mated (brood 1466) to a male with *cenea* but no *leighi* in its known ancestry. The offspring were four *cenea* females and one *leighi* female, but again one of the "*cenea*" had the orange spots like its mother. This butterfly was mated (brood 1634) to a brother, and again two "*cenea*" with orange spots were produced. One of these, when mated (brood 1740) to a male homozygous for *hippocoonides* (*hippocoon*) (and therefore not carrying *cenea* or *leighi*) produced a very abnormal looking *leighi*, the butterfly in some respect looking like f. *natalica*. The fact that the *cenea* which were heterozygous for *leighi* were decidedly abnormal, coupled with the fact that at least one of the *leighi* produced was itself highly abnormal, indicates that in these broods we have a modifier or modifiers which have broken down the normal dominance relationship and in fact nearly reversed them. Many other *leighi/cenea* heterozygotes must have existed (broods 1020, 1157, 1176, 1192, 1365 and 2235) but no other orange-spotted *cenea* have appeared showing that the pattern of these insects was abnormal and probably due to the presence of a single gene modifier (see Table 2).

That *trophonius* is not recessive to all other forms was shown in our previous paper (CLARKE and SHEPPARD 1959a). Subsequently broods 1680, 1705, 1792 and 1807, in which the male parent was known not to be carrying *trophonius* have shown that it is not sex-linked and that it is dominant to *hippocoonides* (and *hippocoon*). Moreover brood 1824, (among others) confirms this finding, for here a good 3:1 ratio of *trophonius* to *hippocoonides* was obtained. Furthermore, *trophonius* is dominant to *cenea* as is shown by broods 1591 and 1705 where a *trophonius* mated to a male not carrying *cenea* produced both *trophonius* and *cenea* (see Table 3). Brood 1386 (see Table 1) is also confirmatory.

The relationship between *trophonius* and *leighi* is an interesting one. The pattern of *salaami* is the same as that of *trophonius* except that the white apical patch on the forewing is replaced by the orange color found in this area in *leighi* (Figure 7). Moreover, *salaami* is very rare in South Africa. It has however appeared in our broods but only when both *leighi* and *trophonius* are also present (broods 1426, 1458, 1547, 1848, 1854, and 2072), with the exception of brood

TABLE 2

Variations in leighi-cenea *dominance*

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Males	*cenea* females	*leighi* females	**Recognizable *leighi/cenea* heterozygotes**	*hippo-coonides* females	*tro-phonius* females
1020	*leighi** H^Lh	H^ch	5	1	4	0	2	0
1157	*leighi* H^Lh or H^LH^c	H^ch or hh	12	1	4	0	0	0
1176	*leighi*	H^ch or hh	17	4	6	0	5	0
1192	*leighi* H^Lh	male known to be carrying *cenea*	7	4	1	0	2	0
1365	*leighi* known not to be carrying *cenea*	H^ch (presumed)	10	4	1	0	3	0
1372	***cenea***	H^Lh	**0**	**2**	**1**	**1**	**0**	**0**
1466	***leighi/cenea* heterozygote H^cH^L 1372**	H^ch **(presumed)**	**8**	**3**	**1**	**1**	**0**	**0**
1634	***leighi/cenea* heterozygote H^cH^L 1466**	**1466 H^cH^L or H^Lh or H^ch**	**0**	**0**	**0**	**2**	**0**	**0**
1740	***leighi/cenea* heterozygote H^cH^L 1634**	hh	**3**	**0**	**1 abnormal**	**0**	**0**	**0**
2235	*cenea* wild	male from *salaami* family†	19	0	16	0	0	**8**

The families in which the *leighi/cenea* heterozygotes were recognizable are in heavy type.
* See text for explanation of genetic symbols.
† See text.

1719, where a female *leighi* is known to have been mated to a male carrying *trophonius*, and 2012, 2038 and 2118 where the broods were very small. In fact the data are consistent with the hypothesis that *salaami* is formed by a combination of *trophonius* and *leighi*. Broods 1426, 1458, 1719, 1848, 1854, 2005, 2012, 2038, 2072 and 2286 are particularly relevant for here a 1:1:1:1 ratio is expected on the hypothesis that *salaami* is the heterozygote of *trophonius* and *leighi* and the combined numbers for these broods fit well with this assumption (see Table 5). It might be argued that *salaami* is recessive to all other forms but the fact that it never appears in large broods except when both *trophonius* and *leighi* are present, and that *salaami* always produces *trophonius* and/or *leighi* among its

TABLE 3

Dominance relationship of f. trophonius *to f.* hippocoonides *and f.* cenea

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Males	*cenea* females	*hippocoonides* females	*trophonius* females
1591	*trophonius** H^TH^c 1458	*hh*	13	6	0	4
1680	*trophonius*	*hh*	5	0	2	2
1705	*trophonius* H^TH^c	*hh*	12	6	0	6
1792	*trophonius* H^Th	*hh*	33	0	17	9
1807	*trophonius*	*hh*	6	0	0	2
1824	*trophonius* H^Th	H^Th	47	0	6	36

* See also Table 4.

offspring (broods 1547, 2099, 2108, 2209 and 2223) makes this interpretation almost certainly wrong (see Table 4).

Natalica was shown by FORD (1936) to be dominant to *hippocoonides*. Brood 1758 confirms this finding. Brood 2120 of a *cenea* female to a male homozygous for *hippocoonides* produced *natalica* thus demonstrating the dominance of *cenea* to *natalica*. Brood 1960 shows that *natalica* is recessive to *leighi* as indicated by the 2:1:1 ratio of *leighi* to *natalica* to *hippocoonides*. Brood 2208, one of these *leighi* mated to a male homozygous for *hippocoonides*, produced *leighi* and *natalica* thereby proving the dominance of *leighi*.

Natalica seems to interact with *trophonius* in much the same way as *leighi* does, for in broods 1743, 1987 and 2379, where both *natalica* and *trophonius* are segregating, a form of *trophonius* appears with the white of the apical patch on the forewing replaced by buff (see Figures 1–7). Such forms have been found in the wild (WELLS, personal communication) but are apparently unnamed. Such a form has never appeared except in these three broods segregating for *trophonius* and *natalica*, and the ratios in the broods are consistent with a 1:1:1:1 ratio suggesting that these abnormal *trophonius* are in fact heterozygous for *natalica* and *trophonius*. Moreover, one of these abnormal *trophonius* mated to a male not carrying *trophonius* or *natalica* (brood 1967) produced both, showing that the female parent was heterozygous for both. A second such female (1930) produced one offspring which was *trophonius*. No brood in which *trophonius* and *natalica* are segregating has failed to produce these atypical *trophonius*, (see Table 6).

Thus it appears that:

1. *hippocoonides* is recessive to all the other forms.
2. *cenea* is recessive to *trophonius* and usually to *leighi*, although the heterozygote may sometimes be recognizable.

TABLE 4

Composition of f. salaami

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Males	*cenea* females	*hippocoonides* females	*trophonius* females	*leighi* females	*salaami* females
1426	*leighi* (no *trophonius* in ancestry)	wild	9	0	0	1	4	6
1458	*trophonius* 1386*	male carrying *leighi*	22	2	0	3	6	2
1547	*salaami* 1426	1426	5	0	0	3	2	1
1673	*hippocoonides* *hh*†	H^TH^L	11	0	0	4	8	0
1719	*leighi* (no *trophonius* in ancestry)	1547	3	0	0	0	1	1
1848	*leighi* 1719	male carrying *trophonius*	11	0	1	1	3	2
1854	*leighi* H^Lh	male carrying *trophonius*	47	0	14	12	7	14
2005	*leighi* H^Lh	male carrying *trophonius*	14	0	7	5	7	2
2012	*trophonius* H^Th	male carrying *leighi*	7	0	2	0	0	3
2038	*leighi* H^Lh	1824†	1	0	1	0	0	2
2072	*leighi* 1854	1824†	7	0	2	2	2	2
2099	*salaami* 1854	*hh*	3	0	0	5	6	0
2108	*salaami* 1854	H^ch or H^cH^c	27	0	0	23	9	0
2118	*leighi* 1854	1824†	1	0	0	0	0	1
2209	*salaami* 2005	*hh*	4	0	0	1	2	0
2223	*salaami* 2012	*hh*	9	0	0	4	5	0
2286	*leighi* 1960‡	male carrying *trophonius*	20	0	0	4	7	7

* See also Table 1.
† See text on allelomorphism.
‡ See also Table 6.

TABLE 5

Totals of salaami *broods showing expected 1:1:1:1 ratio on the hypothesis that f.* salaami *is the heterozygote between f.* leighi *and f.* trophonius

Brood	*leighi*	*trophonius*	*salaami*	*cenea*	*hippocoonides*
1426	4	1	6	0	0
1458	6	3	2	2	0
1719	1	0	1	0	0
1848	3	1	2	0	1
1854	7	12	14	0	14
2005	7	5	2	0	7
2012	0	0	3	0	2
2038	0	0	2	0	1
2072	2	2	2	0	2
2286	7	4	7		
Total	37	28	41	29	

TABLE 6

Dominance relationships of f. natalica

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Males	*cenea* females	*hippo-coonides* females	*tro-phonius* females	*natalica* females	*leighi* females	Atypical *trophonius*‡ females
1743	*natalica* $H^{na}h$	H^Th	8	0	4	3	4	0	2
1758	*natalica* $H^{na}H^{na}$	*hh*	6	0	0	0	12	0	0
1930	*natalica/trophonius* 1743 $H^{na}H^T$	H^ch or *hh**	0	0	0	1	0	0	0
1960	*natalica* $H^{na}h$	H^Lh	35	0	14	0	6	30	0
1967	*natalica* $H^{na}H^T$ 1743	H^ch or *hh*	3	0	0	2	1	0	0
1987	*trophonius* H^Th 1743	1758	25	0	6	8	7	0	3
2120	*cenea* H^cH^{na}	*hh*	12	4	0	0	7	0	0
2208	*leighi* H^LH^{na} 1960	*hh*	58	0	0	0	28	31	0
2379	*trophonius*† 2223	2208	10	0	3	6	4	0	2

* Not carrying either *trophonius* or *natalica*.
† See Table 4.
‡ See text.

3. *natalica* is dominant to *hippocoonides* and recessive to *cenea* and *leighi* but produces an intermediate form with *trophonius*.
4. *leighi* is dominant to *hippocoonides*, *natalica* and nearly always to *cenea*, but it forms an intermediate (*salaami*) with *trophonius*.
5. *trophonius* is dominant to *hippocoonides* and *cenea*, but forms an intermediate with *natalica* and *leighi*.

Allelomorphism

The data taken as a whole suggest that *hippocoonides*, *cenea*, *leighi*, *trophonius* and *natalica* are all allelomorphs of one another. Thus in no instance has any female mated to a male known to be homozygous for *hippocoonides* (which is recessive to all other forms) or a male mated to a *hippocoonides* female produced more than two forms among its offspring, whereas more than two forms have appeared in many other broods. Such are 1020, 1176, 1192, 1743, 1848, 1854, 1987, 2005, 2072, details of which are shown on the tables. There are also many others which can be seen in the completed data, e.g. 1328, 1514, 1747, 1819, 1826, 1831, 1928, 1945, 2047, 2188. Secondly, if we discount *salaami* and *trophonius* with a buff apical patch (which are probably heterozygotes) more than three forms are never found within one brood. Finally including *salaami* and buff tipped *trophonius* we never find more than four forms in any one brood. That is to say we sometimes find *cenea*, *trophonius*, *leighi* and *salaami* or *hippocoonides*, *trophonius*, *leighi* and *salaami*, but never both *hippocoonides* and *cenea* with *trophonius*, *leighi* and *salaami* (Tables 2 and 4). This last combination could appear within one brood if the genes are not allelomorphs, but cannot occur if they are. However, the hypothesis that the forms are controlled by allelomorphs rests on a firmer foundation than this. Brood 1705 (Table 3) which was from a *trophonius* mother known to be heterozygous for *cenea* and mated to a male which was homozygous for *hippocoonides* gave six female *cenea* and six female *trophonius*. On the hypothesis that *cenea* and *trophonius* are not allelomorphs all the six *trophonius* females should be heterozygous for *cenea* as no *hippocoonides* appeared among the six non-*trophonius* offspring. Therefore (again on the hypothesis) all the *trophonius* should also be heterozygous for *cenea*. If, however, *trophonius* and *cenea* are controlled by allelomorphs (calling that producing *hippocoonides h*, that for *cenea* H^c and that for *trophonius* H^T), the female parent would have been H^cH^T and the male parent *hh*. Consequently, the offspring would be H^ch (*cenea*) and H^Th (*trophonius*). Thus, unlike the results if the forms are controlled by independent loci, none of the *trophonius* should be carrying the gene producing *cenea*. Brood 1824, (Table 3) in which a male of this brood (carrying *trophonius*) was mated to a female heterozygous for *trophonius*, produced 36 female *trophonius* and six female *hippocoonides* thus demonstrating ($P<0.05$) that the female from 1705 was not carrying *cenea*. These broods therefore strongly support the view that *hippocoonides*, *cenea* and *trophonius* are allelomorphs.

Brood 1854, (Table 4) segregated in a 1:1:1:1 ratio indicating that the *salaami* were heterozygous for both *leighi* and *trophonius* (see above). Two of these

salaami mated to *hippocoonides* males (broods 2099, 2108, see Table 4) produced only *trophonius* and *leighi*, making it almost certain that *leighi* and *trophonius* are allelomorphs. (Brood 1673, Table 4 is also consistent with this, the male probably being a heterozygote). Were this not so we would expect some *cenea* or *hippocoonides* to appear among their progeny. The demonstration that one of these *leighi* is not carrying *trophonius* and that the *trophonius* is not carrying *leighi* would complete the proof.

Brood 1960 (Table 6) segregated in a 2:1:1 ratio for *leighi*, *natalica* and *hippocoonides*. This demonstrates that the *natalica* must be heterozygous for *hippocoonides* and the *leighi* will either be heterozygous for *natalica* or *hippocoonides* or both, if these are not controlled by multiple allelomorphs. One of these *leighi* (brood 2208, Table 6) mated to a male homozygous for *hippocoonides* produced 31 *leighi* and 28 *natalica* and no other form. Consequently the *leighi* cannot have been heterozygous for both *natalica* and *hippocoonides* and therefore these forms must be controlled by three multiple allelomorphs. Thus we see that the evidence is strongly in favor of *hippocoonides*, *natalica*, *cenea*, *leighi* and *trophonius* being controlled by allelomorphs which we can call h, H^{na}, H^{c}, H^{L} and H^{T} respectively.

DISCUSSION

There is a representative of f. *salaami* in race *dardanus dardanus* from Southwest and Central Africa. This is form *niobe*, which mimics *Bematistes tellus* Auriv. However, *niobe* cannot always be a heterozygote between *trophonius* and *leighi* (or an allied form called *planemoides*) for it is often at too high a frequency for this to be possible. Moreover, the data quoted by FORD show that *niobe* must usually be inherited as a single unit. The most likely explanation to account for the genetics of *niobe* is that the genes that we have been calling allelomorphs are really very closely linked and that a crossover between an allelomorph controlling either *leighi* or *planemoides* and one controlling *trophonius* can give, in coupling, a combination which produces *niobe*. When there is an appropriate model, as there is for *niobe*, the coupling combination is selected for, but when there is no such model, as in South Africa, there is no such selection. Moreover, in South Africa, *planemoides* is absent and so only a crossover in a heterozygote between *leighi* and *trophonius* could give the coupling phase. Such heterozygotes will be extremely rare, probably not more frequent than one in a thousand individuals, perhaps less. Furthermore, even if a crossover occurs the product is unlikely to persist for there is no model to confer an advantage on it.

The view that the apparent allelomorphism is really due to the presence of two or more very closely linked loci controlling color and pattern is consistent with what is known about other polymorphisms. The close linkage would be expected to evolve even if not initially present if certain combinations of color and pattern controlled by separate loci are advantageous, whereas other combinations are disadvantageous (FISHER 1930; SHEPPARD 1953, 1955; KIMURA 1956).

SUMMARY

1. The genetics of all the South African (race *cenea*) polymorphic female forms of *Papilio dardanus* have been investigated. They are *hippocoonides*, *cenea* and *trophonius* which are mimetic, and *natalica*, *leighi* and *salaami* which are nonmimetic.

2. The forms all show sex-controlled inheritance appearing only in the female, which, in contrast to the monomorphic, nonmimetic males, are tailless. The genes controlling the forms behave as a multiple allelomorphic series.

3. *Salaami* is the heterozygote between *leighi* and *trophonius*.

Cenea is recessive to the latter form and dominant to *hippocoonides* and *natalica*. It is also usually recessive to *leighi* but a modifier has been found which causes the dominance to be almost completely reversed so that the heterozygote in such broods is similar to *cenea* but just distinguishable from it. *Natalica* is dominant to *hippocoonides* and recessive to *leighi* and *cenea*, and forms an intermediate heterozygote (which has no varietal name) with *trophonius*.

4. It is suggested that although the forms behave like a multiple allelomorphic series they are more probably controlled by closely linked loci and that the Central African *niobe* is controlled by the genes for *trophonius* and *leighi* or *planemoides* in coupling. In South Africa, on the other hand, where *planemoides* is absent the genes for *trophonius* and *leighi* are usually in repulsion and in the heterozygote they give *salaami*.

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