THE GENETICS OF PAPILIO DARDANUS, BROWN. II. RACES DARDANUS, POLYTROPHUS, MESERES, AND TIBULLUS

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IN Part I (CLARKE and SHEPPARD 1959) we described the genetics of *P. dardanus* race *cenea* from South Africa. The present paper concerns four other races of the butterfly—*dardanus*, *polytrophus*, *meseres* and *tibullus*. The map (Figure 1) shows the distribution of these and their geographical relationships

FIGURE 1.—Distribution and geographical relationship of *P. dardanus* races.

with *P. dardanus cenea*. In addition the areas inhabited by the Madagascan race *meriones* and the Abyssinian race *antinorii* are indicated, and these forms will be the subject of a separate paper (Part III).

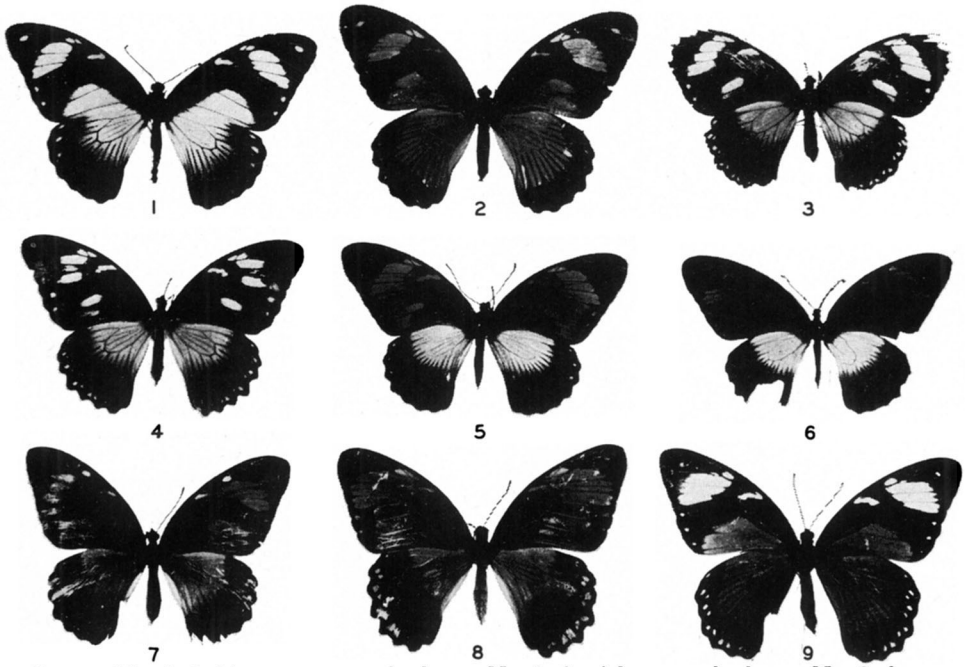
RACE DARDANUS

This has the most extensive range of any of the races of *P. dardanus*. It is found down the West Coast of Africa from Sierra Leone to Angola, and spreads eastwards towards Uganda and Tanganyika Territory to Lake Victoria. In these areas it merges into the transitional race *meseres*. In the western part of its range the female is almost invariably the mimetic form *hippocoon*, and this closely resembles the form *hippocoonides* already described under race *cenea* from South Africa (Part I).

In race *dardanus* we have bred *hippocoon* both from the eastern and western parts of its range and have also investigated f. *trophonissa*, f. *niobe* and f. *planemoides*. The mimetic form *cenea* has not so far appeared in our material but we have carried out a race cross using this form from South Africa (see below).

F. hippocoon

This form (Plate, No. 1) which mimics *Amauris niavius niavius* is very similar to *hippocoonides*, and, wherever we have tested it in relation to other forms,



PLATE—No. 1. f. *hippocoon*, race *dardanus*. No. 2. f. *niobe*, race *dardanus*. No. 3. f. *cenea* showing breakdown of mimicry. No. 4. f. *cenea*, showing no breakdown of mimicry. No. 5. f. *planemoides*, race *dardanus*. No. 6. f. *proto-planemoides*. No. 7. f. *poultoni*, race *polytrophus*. No. 8. f. *dorippoides*. No. 9. f. *trophonissa*, race *dardanus*.

we have found that it behaves similarly to *hippocoonides*. As in Part I, therefore, we have assumed that *hippocoon* and *hippocoonides* and the hybrids between the two are equally satisfactory for testing either for dominance relationships or allelomorphism.

Hybrids between f. hippocoon *and f.* cenea *from South Africa:* It is of interest that when f. *hippocoon* from the West Coast of Africa (where *cenea* does not occur) is crossed with f. *cenea* from South Africa, the mimetic pattern of f. *cenea* is broken down (Plate, No. 3). On the other hand, when f. *hippocoon* from the eastern range of *dardanus* (where f. *cenea* does occur but at a low frequency) is crossed with f. *cenea* from South Africa, the breakdown of the mimetic pattern is very much less (No. 4). This suggests that on the west coast the population does not possess the modifying genes perfecting the mimicry of f. *cenea*, whereas these are present further east. In contrast the mimetic pattern of f. *trophonius* is not appreciably altered when crossed with f. *hippocoon* from race *dardanus*. This we believe to be because f. *trophonissa* is found throughout the range of the race (CLARKE and SHEPPARD 1960 for elaboration of this point).

F. niobe

This is a bright orange insect with an orange body (Plate, No. 2). It has the pattern of *trophonissa*, but with the subapical spot of the forewing orange instead of white. It is therefore much like f. *salaami* from South Africa (see Part I) but the hind wings are more rayed as in *hippocoon*.

Autosomal inheritance of f. niobe: It is clear that the gene controlling this form is, like the others investigated, autosomal. Thus, in brood 3228 a *niobe* female, mated to a male which cannot have carried *niobe*, produced seven *niobe* daughters, showing that the gene cannot be on the X chromosome. That it cannot be sex-linked on the Y chromosome is demonstrated in brood 3029, where a female *hippocoon* which could not have carried *niobe*, when mated to a male which had eleven *niobe* sisters, produced 23 males, ten *hippocoon* females and eight *niobe* females (see Table 1).

TABLE 1

Autosomal inheritance of f. niobe (*race* dardanus)

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring		
			Males	*hippocoon* females	*niobe* females
3029	*hippocoon*	heterozygous *niobe*/*hippocoon* $H^{Ni}h$*	23	10	8
3228	*niobe* 3029 $H^{Ni}h$	*hh*† (cannot be carrying *niobe*)	9	3	7

* $H^{Ni}h$ = *niobe*/*hippocoon*.
† The designation of the genotype of the male known to be homozygous for *hippocoonides*, *hippocoon* or the hybrid between the two.
N.B. The full list of the genetic symbols used to indicate the various genotypes in all races of *P. dardanus* will be given at the end of Part III.

Dominance relationships of f. niobe: In brood 3017 a female *niobe* 2779 mated to a male known to be homozygous for *hippocoon(ides)* produced six males, two *hippocoon(ides)* and four *niobe* females. (A *hippocoon* or *hippocoonides* of hybrid origin is written as *hippocoon(ides)* in this paper if race *dardanus* or *antinorii* is involved.) Again in brood 3029 a *hippocoon* female 2862 (in which no *niobe* had appeared) mated to a male 2802 (which had *niobe* among its sibs), produced 23 males, ten *hippocoon(ides)* and eight *niobe* females. Broods 3017 and 3029 therefore prove that f. *niobe* is dominant to f. *hippocoon(ides)* and pure *hippocoon*.

When crossed with f. *cenea* (from South Africa) *niobe* either forms a recognizable heterozygote with *cenea* or else is fully dominant to it. In brood 2779 a *niobe* female 2666 (not carrying *cenea*) mated to a male 2640 heterozygous for *cenea* and *hippocoonides* (and not carrying *niobe*) produced 11 males, two *cenea*, three *hippocoon(ides)*, two *niobe* and two females with *cenea* patterning and *niobe* coloring (H^cH^{Ni}, the heterozygotes called red-brown *cenea*). In contrast, in brood 2802 a *cenea* female which could not have been carrying *niobe* was mated to a male heterozygous for *niobe* and *hippocoon*. Their offspring were 27 males, six *cenea*, six *hippocoon(ides)* and 11 *niobe* females. No recognizable heterozygotes were produced in this brood. F. *cenea* thus behaves with f. *niobe* much as it does with f. *leighi* (see Part I).

Niobe can also be formed as the heterozygote between f. *trophonius* and f. *planemoides*. In brood 3059 a *trophonius* female heterozygous for *hippocoon(ides)* (and not carrying *niobe*) was mated to a male heterozygous for f. *planemoides* and f. *hippocoon* (the male had five *hippocoon* and five *planemoides* sisters and ten brothers, none of which when mated produced *niobe*). The offspring of brood 3059 were one male, one *hippocoon(ides)*, one *trophonius* and five "synthetic" *niobe* females. We have shown, however, on several occasions that f. *niobe* does not usually arise in this way, and that it is more often inherited as a unit. Thus in brood 3029 a male carrying *niobe* was mated to a *hippocoon* female and produced 23 males, ten *hippocoon(ides)* and eight *niobe* females. Again in brood 3017 a *niobe* female mated to a male homozygous for *hippocoon(ides)* produced six males, two *hippocoon(ides)* and four *niobe* females. Broods 2967 and 3228 give similar information. In none of these instances has *niobe* given rise to *planemoides* or *trophonius* (see Table 2). It is not known how often *niobe* is formed in the wild by a combination of *trophonius* and *planemoides*, but this could well happen since the forms are sympatric in the eastern part of the range of race *dardanus*.

More work on *niobe* is necessary before we have formal proof that it is controlled by a gene at the same locus as the other forms, though this is suggested by our data.

F. trophonissa

This orange insect with a white subapical spot (Plate, No. 9) resembles the mimic f. *trophonius* from South Africa (Part I) except that the upper side of the hindwing has more marked longitudinal rays. In brood 2862 (Table 3) a *tro-*

TABLE 2

Dominance relationships of f. niobe, (*race* dardanus)

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring: Males	Recognizable heterozygote *niobe/cenea* females	Recognizable heterozygote *cenea* females	Recognizable heterozygote *hippocoon* females	*niobe* females	*trophonius* females	*trophonius/planemoides*, synthetic *niobe* females
2779	*niobe* $H^{Ni}h$	*polytrophus* $H^{c}h$	11	2	2	3	2	0	0
2802	*cenea* $H^{c}h$	$H^{Ni}h$	27	6	0	6	11	0	0
2967	*niobe* 2802 $H^{Ni}h$	*hh*	6	0	0	6	5	0	0
3017	*niobe* 2779 $H^{Ni}h$	*hh*	6	0	0	2	4	0	0
3029	*hippocoon* *hh*	$H^{Ni}h$ 2802	23	0	0	10	8	0	0
3059	*trophonius* $H^{T}h$	$H^{Pl}h$ 2863 see Table 5	1	0	0	1	0	1	5
3228	*niobe* 3029 $H^{Ni}h$	*hh*	9	0	0	3	7	0	0

hh=*hippocoonides*, *hippocoon* or the hybrid. Such an insect of hybrid origin is written *hippocoon(ides)* or *h'(ides)*.
$H^{c}h$=*cenea/hippocoon*.
$H^{Ni}h$=*niobe/hippocoon*.
$H^{T}h$=*trophonius/hippocoon*.
$H^{Pl}h$=*planemoides/hippocoon*.

phonissa female mated to a wild male produced 17 *trophonissa* and 18 *hippocoon* females. If *hippocoon* were dominant to *trophonissa*, all the offspring of 2862 would carry the latter form. In fact this is almost certainly not the case because in broods 3015 and 3040 (Table 3) no butterflies resembling the recognizable *trophonius/planemoides* heterozygote (i.e., synthetic *niobe*) or *trophonissa* appeared. Therefore, *trophonissa*, like *trophonius*, is almost certainly dominant to *hippocoon*. If this is so, brood 3002 (Table 3), where the father is not carrying *trophonissa* shows that *trophonissa* is neither sex-linked on the X nor on the Y chromosome (because *hippocoon(ides)* was produced), but is, like the genes controlling the other forms, autosomal. It seems highly probable that *trophonissa* is a modified *trophonius* and controlled by the same major gene. Thus in race crosses between the South African *trophonius* and *hippocoon*, the hybrids resemble *trophonissa* having the rayed hindwing characteristic of this form and of *hippocoon*.

TABLE 3

Dominance relationships and autosomal inheritance of f. trophonissa (*race* dardanus)

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring			
			Males	*hippocoon* or *h'(ides)* females	*trophonissa* females	*planemoides* females
2862	wild *trophonissa*	wild male race *dardanus*	13	18	17	0
3002	*$H^{T}h$ trophonissa* 2862	*leighi/ hippocoon(ides)* also carrying part of gene complex of *antinorii*, Brood 2876 (see Part III)	20	8	6	4 (2 of these were *proto-planemoides*)
3015	*$H^{Pl}h$ planemoides* 2863 see Table 5	*hh* 2862	15	9	0	4
3040	*$H^{Pl}h$ planemoides* 2863 see Table 5	*hh* 2862	14	13	0	11

$H^{Pl}h$ = planemoides/hippocoon.
$H^{T}h$ = trophonissa/hippocoon.
hh = hippocoon.

F. planemoides

This form has an irregular orange band on the forewing and white hindwings with a wide black border (Plate, No. 5). It is a mimic of *Bematistes poggei.*

Autosomal inheritance of f. planemoides: Broods 3015 and 3040 show that the gene controlling *planemoides* is not sex-linked on the X chromosome, and brood 3005 shows that it is not sex-linked on the Y. The gene therefore is autosomal (Table 4).

Dominance relationships of f. planemoides: In brood 2863, (Table 5) a wild *planemoides* female from Entebbe produced 11 males, five *hippocoon* and five *planemoides* females. A female *planemoides* of brood 2863 mated to a male from brood 2862 (which segregated *trophonissa* and *hippocoon*, Table 3) gave 15 males, nine *hippocoon* and four *planemoides* females (brood 3015, Table 5). Mating 3040 (Table 4) shows a similar situation, and these two broods show that *planemoides* is dominant to *hippocoon.*

Race crosses using f. planemoides: When a female f. *planemoides* from race *dardanus* was crossed with a male known to be homozygous for *hippocoonides* from race *polytrophus* (where the mimicry is imperfect, often due to the presence of male-like yellow scales), the mimetic pattern of *planemoides* was broken down. This occurred in brood 3049 (Table 5) where a *planemoides* female 2863 was mated to a male homozygous for *hippocoonides* with some *polytrophus* but no

TABLE 4

Autosomal inheritance of f. planemoides (*race* dardanus)

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring		
			Males	*hippocoon* females	*planemoides* females
3005	*hippocoonides* unknown brood	$H^{Pl}h$ 2863 wild	8	2	4
3015	*planemoides* 2863 see Table 5	*hh*	15	9	4
3040	*planemoides* 2863 see Table 5	*hh*	14	13	11

$H^{Pl}h$ = *planemoides/hippocoon.*
hh = *hippocoon.*

dardanus in its ancestry. The offspring of mating 3049 were eight males, two *hippocoon(ides)* and three *proto-planemoides* females. In these the normal orange band on the forewing was interrupted by a horizontal black bar (Plate, No. 6). (The prefix *proto-* signifies that the form concerned is an imperfect mimic).

As with form *niobe*, "synthetic" *planemoides* was formed in one of the crosses. In brood 3002 (Table 5) a female *trophonissa* 2862 was mated to a male 2816 (see Part III) heterozygous for *leighi/hippocoonides (niavioides)* and which, therefore, carried part of the gene complex for the Abyssinian race *antinorii*. Neither of the butterflies had *planemoides* in their known ancestry. The brood produced eight *hippocoon(ides)*, six *trophonissa*, two normal-looking *planemoides* and two *proto-planemoides* females. In contrast when *leighi* from race *cenea* (not carrying part of the *antinorii* gene complex) is crossed with race *dardanus*, the *leighi* pattern (which is nonmimetic) does not appreciably alter, and *planemoides* is not produced (see brood 1462, Table 5). Although the complete relationship of the two forms is not yet fully worked out, it appears that with a certain combination of modifiers *leighi* can be converted to *planemoides*, and in this connection FORD (1936) has pointed out that the patterns of *planemoides* and *leighi* are rather similar. It is of interest that in brood 3002 the expected *salaami* which is the recognizable heterozygote between *leighi* and *trophonius* (see Part I) did not appear. The reason for this is not known, but it is certain that *proto-planemoides* cannot have been of this genetic constitution since if it were it would have segregated in brood 3176 (Table 5). Whether *planemoides* is an allelomorph of the other forms has not yet been established, but it seems probable that it will prove to be so.

In summary, therefore, the following are the findings in race *dardanus:*

(1) F. *trophonissa* is almost certainly dominant to f. *hippocoon.*

(2) F. *niobe* is dominant to f. *hippocoon.*

TABLE 5

Dominance relationships of f. planemoides (*race* dardanus)

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring					
			Males	*planemoides* females	*proto-planemoides* females	*hippocoon* or *h'(ides)* females	*leighi* females	*trophonissa* females
1462	*leighi* race *cenea* H^Lh	race *dardanus* *hh*	11	0	0	5	*5	0
2863	*planemoides* wild	race *dardanus* wild	11	5	0	5	0	0
3002	*trophonissa* 2862 H^Th	H^Lh carrying part of gene complex of *antinorii* Brood 2816 (Part III)	20	2	2	8	0	6
3015	*planemoides* 2863	race *dardanus* *hh*	15	4	0	9	0	0
3049	*planemoides* 2863	*hh*	8	0	3	2	0	0
3176	*proto-planemoides* 3002	*hh*	4	0	3 (1 a gynandromorph)	1	0	0

* No breakdown of *leighi pattern*, c.f. brood 3002.
H^Lh = *leighi/hippocoonides.*
H^Th = *trophonissa/hippocoon.*
hh = *hippocoon.*

(3) F. *niobe* is sometimes dominant to f. *cenea* from South Africa and sometimes forms a recognizable heterozygote with it.

(4) Although f. *niobe* is usually inherited as a unit it can be synthesized by combining f. *trophonissa* with f. *planemoides*, and the frequency of the two forms makes it likely that this, in fact, may sometimes happen in the wild.

(5) F. *planemoides* is dominant to f. *hippocoon.*

(6) F. *planemoides* and f. *proto-planemoides* have been synthesized in the laboratory in a race cross. The parents were a male carrying South African *leighi* and also part of the gene complex of *antinorii* and a female *trophonissa* from race *dardanus.*

(7) The nonmimetic pattern of f. *leighi* from South Africa does not alter appreciably when this form is crossed with race *dardanus* from the west coast, where *leighi* does not occur.

(8) F. *cenea* from race *dardanus* has not so far been tested with f. *hippocoon* but in a race cross using f. *cenea* from South Africa, *cenea* was dominant to *hippocoon.* There was variable breakdown in the *cenea* mimetic pattern according to the area from which *hippocoon* was obtained.

(9) It is not yet known whether the various forms of *dardanus* are allelomorphic, but it is likely that they will prove to be so.

RACE POLYTROPHUS

This race inhabits the mountain range in the center of Tanganyika Territory and Kenya Colony on the east side of Lake Victoria. It thus occupies a position between the transitional race *meseres* and race *tibullus* (Figure 1).

It is characteristic of race *polytrophus* that some of the female forms are imperfect mimics, and these usually possess some yellow male-like pigment which can be identified by its fluorescence under ultraviolet light. The incompletely developed forms corresponding to the different mimics have the prefix *proto-* added to each.

We have not as yet investigated race *polytrophus* extensively, but we have obtained a certain amount of information regarding some of the forms. Furthermore, we have produced butterflies of the "*proto-*" form in various hybrids between the yellow nonmimetic forms (both from Abyssinia and from Madagascar) and butterflies from race *cenea* and race *dardanus*. These are discussed in Part III. The following are the forms of race *polytrophus* which we have bred:

F. proto-cenea.

This form includes all specimens of *cenea* which possess fluorescent yellow pigment. FORD, quoting VAN SOMEREN's data on the frequency of the *polytrophus* forms at Nairobi, shows that out of 150 females, 47 were normal *cenea* and 18 *proto-cenea*. The relative frequency of these is of importance when analysing the broods bred by VAN SOMEREN and also reported in FORD's monograph (1936). Thus in 19 families where the female parent was *cenea*, there were produced 91 *cenea* and 36 *proto-cenea* butterflies (28 percent of the latter form). On the other hand, where *proto-cenea* was the parent, the totals in 12 families were 31 *cenea* and 49 *proto-cenea* (61 percent of the latter form). These figures strongly suggest that *proto-cenea* is either dominant or epistatic to *cenea*. Our own data support this view because, as is shown in Table 6a, in two broods where a *proto-cenea* female was mated to a male which could not have carried *cenea* this form was produced.

VAN SOMEREN's data (given later) also suggest that *proto-cenea* (in this instance from race *tibullus*) is dominant to *hippocoonides*, and our data demonstrate this for race *polytrophus*. Thus in brood 2629 (Table 6b) a *hippocoon(ides)* female with no race *polytrophus* in its ancestry, when mated to a *polytrophus* male with seven *proto-cenea* and two *cenea* sisters, produced one *proto-cenea*, three *cenea* and five *hippocoon(ides)* females in its offspring. This brood also proves that the gene controlling *proto-cenea* is not on the Y chromosome since if it were, *proto-cenea* could not have appeared. Moreover, several broods prove that the form is not sex-linked on the X chromosome—for example, brood 2624, where the male could not have been carrying *proto-cenea*, and yet this form appeared in the offspring (Table 6b).

TABLE 6

Relationship between proto-cenea *and* cenea

a. Race crosses showing dominance of *proto-cenea* to *cenea*. In each family the father is from a race where *proto-cenea* does not usually occur.

Brood no.	Origin and form of mother	Origin of father	Offspring: Males	*proto-cenea* females	*cenea* females	*natalica* females	*hippo-coon(ides)* females	*troph-onius* females
2626	*proto-cenea* race *polytrophus*	*race cenea* (known not to be carrying f. *cenea*)	6	3	1	4	0	3
2801	*proto-cenea* 2629 (see b below)	race *dardanus* (known not to be carrying f. *cenea*)	42	4	13 α	0	16	0

b. Families showing (1) dominance of f. *proto-cenea* to f. *hippocoon(ides)*, (2) autosomal inheritance of f. *proto-cenea* and (3) probability that *proto-cenea* and *cenea* are not allelomorphs.

Brood no.	Form and origin of mother	Origin of father	Offspring: Males	*proto-cenea* females	*cenea* females	*hippo-coon(ides)* females
2624	*proto-cenea* race *polytrophus*	race *cenea* (known not to be carrying f. *cenea*)	12	3	0 α	5
2629	*hippocoon(ides)* (no race *poly-trophus* in ancestry)	race *poly-trophus* male β	14	1 γ	3	5
2913	*hh* race unknown	race *polytrophus* 2748 (Table 8)	15	12	0	7

α Plus one *cenea* missing and therefore not scorable for *proto-cenea*.
β This male had two *cenea*, seven *proto-cenea* and one *poultoni* sisters.
γ This female fluoresced only slightly but was the mother of 2801 which produced *proto-cenea* in her offspring when mated to a race *dardanus* male which could not have been carrying the fluorescent form (see Table 6 a).

Allelomorphism: The intensity of fluorescence in the *proto-cenea* examined by us appeared to depend on how little ("white" *cenea*) or how much ("brown" *cenea*) nonfluorescent buff pigment was present. The former fluoresced brilliantly, the latter little or not at all. This masking of the fluorescence by the brown pigment makes the scoring of fluorescence rather unreliable, and this is particularly important when dealing with the question of allelomorphism.

The data quoted by FORD (1936) suggest that *proto-cenea* and *cenea* are not allelomorphs since on several occasions *hippocoonides* females mated to wild males have produced all three forms i.e., *proto-cenea*, *cenea*, and *hippocoonides*, whereas if they were alleles, only two of them could have appeared. Neverthe-

less, in the wild there is always the possibility that the female has been mated to several males of different genotypes. In the present work this cannot happen, but our data on allelomorphism is scanty. However, in brood 2629 (Table 6b) all three forms appeared, and in brood 2732 (Table 7) a *hippocoon(ides)* mother produced *proto-cenea*, *cenea* and *poultoni*. Although these broods suggest that *proto-cenea* and *cenea* are not allelomorphs, yet because of the scoring difficulty it may be that the results are due to modifiers affecting the amount of buff pigment and that *cenea* and *proto-cenea* are in fact allelomorphic.

F. poultoni

This is an orange butterfly not unlike *niobe*, but less rayed on the hindwing and with a grey or fawn body with black dots (Plate, No. 7). We have obtained two forms, one pale and the other bright orange, and the exact relationship between these is not yet established. However, in the vast majority of cases, the *poultoni* offspring are of the color carried or expressed by the parent, though the occasional exception occurs due possibly to the presence of modifiers (see brood 2732 and 3096, Tables 7 and 8).

Autosomal inheritance of f. poultoni: Broods 2732 and 2750 show that the gene or genes controlling both bright and pale *poultoni* are not sex-linked on the Y chromosome, and broods 2892 and 3075 show that neither is carried on the X. It is therefore clear that the genes responsible for both forms of *poultoni* are carried on an autosome (Table 7).

Dominance relationships: (a) f. pale poultoni: In brood 2750 (Table 7) a female *hippocoon(ides)* which could not have carried *poultoni*, mated to a male who

TABLE 7

Autosomal inheritance of bright and pale poultoni

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring: Males	pale *poultoni* females	bright *poultoni* females	*cenea* females	recognizable heterozygote *poultoni*/*cenea* females	*hippocoon(ides)* females	yellow *hippocoon(ides)* females	*dorippoides* females
2732	*hippocoon(ides)* *hh*	wild (from *poultoni* mother)	36	1	17	*16	0	0	0	0
2750	*hippocoon(ides)* *hh*	wild (from *poultoni* mother)	37	5	0	0	0	9	0	0
2892	pale *poultoni* 2750	(not carrying *poultoni*) H^ch	23	3	0	†8	6	4	0	0
3075	bright *poultoni*	H^yh	11	0	4	0	0	4	3	6

hh = *hippocoon(ides)*.
H^ch = *cenea/hippocoon(ides)*.
H^yh = yellow/*hippocoonides*. H^y is the allelomorph controlling the male-like pattern (see Part III).
* Of these 16 *cenea* females one showed strong, one slight and ten a trace of fluorescence. Four showed no fluorescence. All were "brown" *cenea*.
† Six of these *cenea* fluoresced and two were missing.

had a *poultoni* mother, (but whether of the bright or pale form is unknown) produced nine *hippocoon(ides)* and five pale *poultoni* females. This shows that pale *poultoni* is dominant to *hippocoon(ides)*. Broods 3300 and 3365 confirm this (Table 8).

(b) f. bright poultoni: Brood 2732 (Table 7) was a mating between a female *hippocoon(ides)* (which could not have carried *poultoni* or *cenea*), to a male whose mother was a wild *poultoni* of unknown color. The offspring of brood 2732 were 16 *cenea*, 17 bright *poultoni* and one pale *poultoni* female. This shows that the father must have been heterozygous *cenea/poultoni* (see below, allelomorphism). As no *hippocoon(ides)* appeared in brood 2732 it is clear that bright *poultoni* also is dominant to *hippocoonides*.

When crossed with *cenea* both bright and pale *poultoni* usually form a recognizable heterozygote with *cenea* pattern and *poultoni* coloring (H^cH^{bp} or H^cH^{pp}, called orange and buff *cenea* respectively)—as also occurs occasionally when both *niobe* and *leighi* are crossed with *cenea*. These *cenea/poultoni* heterozygotes have appeared in broods 2747, 2748 and 2892, (Table 8), and on three occasions when they have been mated to males homozygous for *hippocoon(ides)* their offspring have segregated for *poultoni* and *cenea* only, (broods 3054, 3055 and 3096, Table 9).

The only evidence which we have regarding *poultoni* and *trophonius* suggests that they, too, form a recognizable heterozygote. Thus, in brood 2927 (Table 9) a hybrid female heterozygous for *trophonius* and the yellow nonmimetic form *antinorii* (from brood 2741, see Part III) when mated to an unknown male, produced one male and one female of *trophonius* pattern and color, but with the white subapical spot replaced by pale orange. Brood 3080 (Table 9) was a mating between this female and a male homozygous for *hippocoon(ides)*, and from it only *trophonius* (13) and pale *poultoni* (15) females were obtained—no other form appearing. Clearly, therefore, the unknown male carried pale *poultoni*, and the mother of brood 3080 was a heterozygote *trophonius*/pale *poultoni*.

The dominance relationships of bright and pale *poultoni* to f. *leighi*, f. *natalica*, f. *planemoides* and f. *niobe* are not yet known.

Allelomorphism (Table 9): In brood 3054 a female pale *poultoni/cenea* heterozygote 2892 (which can only have received *poultoni* from her mother and *cenea* from her father) mated to a male homozygous for *hippocoon(ides)* produced four *cenea* females and one bright *poultoni* female. Brood 3055 was a similar mating (a female 2892 pale *poultoni/cenea* with an *hh* male) and this produced eight *cenea* and three pale *poultoni* females. Brood 3096 again was between a female pale *poultoni/cenea* heterozygote 2892 and a male homozygous for *hippocoon(ides)*. This produced one male and one female bright *poultoni*. Broods 3054, 3055 and 3096, therefore, show that *poultoni* and *cenea* are allelomorphs since no *hippocoon(ides)* females appeared.

Brood 3080 shows that pale *poultoni* and *trophonius* are allelomorphs. In this mating a female 2927, heterozygous for *trophonius* and pale *poultoni* (each form being inherited from a different parent), when mated to a male homozy-

TABLE 8

Dominance relationship of bright and pale poultoni *to* hippocoonides *and* cenea

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring: Males	bright *poultoni* females	pale *poultoni* females	*hippocoonides* females	recognizable heterozygote *cenea*/*poultoni* females	*cenea* females
2747	race *polytrophus* f. *cenea* H^ch	race *polytrophus* from wild *poultoni* mother	4	0	1	0	3	3 α
2748	race *polytrophus* f. *proto-cenea* H^ch	race *polytrophus* from wild *poultoni* mother	9	0	0	0	5	9 β
2892	race *polytrophus* pale *poultoni* 2750 $H^{pp}h$ (see Table 7)	race *polytrophus* H^ch	23	0	3	4	6	8 γ
3096	recognizable heterozygote *cenea*/bright *poultoni* δ 2892	*hh*	1	1	0	0	0	0
3300	pale *poultoni* 3055 $H^{pp}h$ (see Table 9)	*hh*	2	0	2	2	0	0
3365	pale *poultoni* 3080 $H^{pp}h$ (see Table 9)	*hh*	7	0	8	3	0	0

H^ch = heterozygous *cenea/hippocoonides*.
hh = *hippocoonides*.
$H^{pp}h$ = pale *poultoni/hippocoonides*.
α Two *proto-cenea* and one butterfly missing.
β Five *proto-cenea*, three *cenea* plus one *cenea* missing and not scored for *proto-cenea*.
γ Six *proto-cenea* and two butterflies missing.
δ From a pale *poultoni* mother.

gous for *hippocoon(ides)* produced 13 *trophonius* and 15 pale *poultoni* females. As *poultoni* has been proved to be an allelomorph of f. *trophonius* and f. *cenea*, it follows that it is also an allele of f. *leighi* and f. *natalica*. It is also an allelomorph of the yellow nonmimetic forms of races *antinorii* and *meriones* (see Part III).

F. dorippoides

There is a form, *proto-salaami*, occurring both in race *polytrophus* and occasionally in race *meseres*, which is similar to the South African *salaami* except that the black bar between the subapical orange spot and the lower part of the forewing is less distinct. *Proto-salaami* intergrades on the one hand to f. *poultoni* where the black bar is complete and on the other to *dorippoides* where it is

TABLE 9

Allelomorphism of poultoni, trophonius *and* cenea

Brood no.	Form of mother and genotype where known	Origin of father and genotype where known	Offspring: Males	bright *poultoni* females	pale *poultoni* females	*trophonius* females	recognizable heterozygote *trophonius*/pale *poultoni* females	*cenea* females
2927	*trophonius/antinorii* F_1 hybrid*	*$H^{pp}h$*	1	0	0	0	1	0
3054	recognizable heterozygote *cenea/poultoni* 2892 (see Tables 7 and 8)	*hh*	15	1	0	0	0	4
3055	recognizable heterozygote *cenea/poultoni* 2892 (see Tables 7 and 8)	*hh*	10	0	3	0	0	8
3080	recognizable heterozygote *trophonius*/pale *poultoni* 2927 (see above)	*hh*	23	0	15	13	0	0
3096	recognizable heterozygote *cenea/poultoni* 2892 (see Tables 7 and 8)	*hh*	1	1	0	0	0	0

* From brood 2741, see Part III.
hh = *hippocoonides*.
$H^{pp}h$ = Pale *poultoni/hippocoonides*.

absent, and here the forewing, except for the black border, is entirely orange, (Plate, No. 8). *Dorippoides* received its name because it resembles the model *Danais chrysippus dorippus*, but FORD (1936) doubts whether it is in fact a mimic.

F. *dorippoides* appeared in three of our race crosses though in none of them had it occurred in the known ancestry of either parent. In each instance, however, the butterflies inherited the gene controlling either bright or pale *poultoni* from one parent and some part of the *antinorii* gene complex from the other, and this combination can certainly produce *dorippoides*. The shade of orange of the *dorippoides* corresponds to that of the bright or pale *poultoni* parent. The matter is dealt with in more detail in Part III. Our synthesis of *dorippoides* agrees with the hypothesis which we have also put forward below to explain VAN SOMEREN's data for the same form, referred to under *proto-salaami*.

F. proto-trophonius (lamborni)

This is a *trophonius*-like insect but with the subapical spot and part of the orange area of the forewing pale yellow (FORD 1936. Plate 2). It has not appeared in our wild stock but we have on one occasion produced a butterfly resembling it by crossing f. *trophonius* from South Africa with the nonmimetic race *meriones* from Madagascar, (discussed in Part III). Though this might suggest that *proto-trophonius* is a modified *trophonius*, yet it seems highly probable that the two forms are in fact controlled by different genes because (1) on backcrossing a *trophonius* from a South African × *polytrophus* hybrid to *polytrophus* for four generations we did not produce *proto-trophonius*, the orange insect remaining similar to the original *trophonius*, despite the fact that *proto-trophonius* is 17 times commoner than *trophonius* in race *polytrophus* (FORD 1936). (2) f. *trophonius* × f. *planemoides* give f. *niobe*, whereas *proto-trophonius* × f. *planemoides* probably give *proto-salaami*, a less extreme form of f. *dorippoides* (see VAN SOMEREN's data).

In summary, therefore, the following are the findings in race *polytrophus:*

(1) *Proto-cenea.* This is dominant to *hippocoon(ides)* and either dominant or epistatic to *cenea.* The data suggest that *proto-cenea* and *cenea* are *not* allelomorphs, but difficulties in scoring the two forms make this conclusion very tentative.

(2) Both bright and pale *poultoni* are dominant to *hippocoon(ides).*

(3) Both bright and pale *poultoni* usually form a recognizable heterozygote with *cenea*, the insects having the *cenea* pattern and the *poultoni* coloring.

(4) The evidence (from one insect only) suggests that *poultoni* and *trophonius* also form a recognizable heterozygote.

(5) F. *poultoni*, f. *cenea* and f. *trophonius* are all allelomorphs, and therefore the gene for *poultoni* is at the same locus as all the other South African forms. (It is also an allelomorph of the yellow nonmimetic forms of races *antinorii* and *meriones*, see Part III).

(6) We have synthesized f. *dorippoides* from parents in whose known ancestry the form has not appeared.

(7) A form resembling f. *proto-trophonius (lamborni)* has been produced by crossing f. *trophonius* with f. *meriones* from Madagascar, but it has been shown that this form in *polytrophus* is probably controlled by a different gene from that of f. *trophonius.*

RACE MESERES AND RACE TIBULLUS (VAN SOMEREN'S DATA)

Race *meseres* (also known as the transitional race) is found in Uganda and Tanganyika Territory east of Lake Victoria. Further east it merges with race *polytrophus* and to the west with *dardanus.* It comprises seven forms of female (FORD 1936). Rarely the mimetic pattern is imperfect and when this occurs the prefix *proto-* has been added as in *polytrophus.* Race *tibullus* is found for an uncertain distance north of the Mombasa district and extends southwards to Delagoa Bay. The female forms are similar to those in race *cenea*, (see Part I)

but in the northern part of its range where it merges into race *polytrophus* imperfect mimics are occasionally found.

We have no personal experience of either *meseres* or *tibullus*, and we are indebted to DR. VAN SOMEREN who has allowed us to quote his breeding experiments with these two races.

It will be seen from his family S1 in our Table 10 that a female *hippocoonides* from race *tibullus* mated to a wild *tibullus* male produced nine *proto-cenea* and eight *hippocoonides* females. Four of these females (one *proto-cenea* and three *hippocoonides*) were used in race crosses with *meseres* males. It will be seen that the results strongly suggest, but do not prove, that *proto-cenea* is dominant to *hippocoonides* as the chance of the *meseres* male parent in S3 being heterozygous for *proto-cenea* is small, the frequency of the form being very low in this race. Because brood S1 contained no female forms other than *proto-cenea* and *hippocoonides* (nor did the F_2, F_3, or F_4 generations from this family—number

TABLE 10

VAN SOMEREN'S data

Brood no.	Brood no. and form of female	Origin of male	Offspring						
			Males	*hippo-coonides* females	*plane-moides* females	*leighi* females	*proto-trophonius* females	*proto-salaami* females	*proto-cenea* females
S1	h *tibullus*	w *tibullus*	14	8	0	0	0	0	9
S2	h (S1) *tibullus*	w *meseres*	6	2	0	1	0	0	0
S3	p-c (S1) *tibullus*	w *meseres*	8	1	0	3	0	0	5
S4	h (S1) *tibullus*	w *meseres*	20	4	6	0	0	0	0
S5	h (S1) *meseres*	w *meseres*	20	11	3	0	0	0	0
S6	h *meseres*	w *meseres*	21	12	0	0	0	0	0
S7	p-p *meseres*	w *meseres*	6	0	0	0	0	3	0
S8	h (S6) *meseres*	(S7) *meseres*	29	0	9	0	10	0	0
S9	p (S8) *meseres*	(S8) *meseres*	17	6	8	0	0	8	0
S10	p-t (S8) *meseres*	(S8) *meseres*	6	0	3	0	5	0	0
S11	p-t (S10) *meseres*	(S10) *meseres*	10	1	12	0	2	0	0
S12	h (S9) *meseres*	(S9) *meseres*	3	0	3	0	0	0	0

* Brood S1 is pure race *tibullus* and four subsequent broods from it (not shown in table) have produced nothing but *proto-cenea* and *hippocoonides* (numbers not given). The males of all the other broods are of race *meseres* as are the females of broods S6 to S12.

h=*hippocoonides*. p=*planemoides*. l=*leighi*. p-t=*proto-trophonius*. p-c=*proto-cenea*. p-p=*proto-planemoides*. p-s=*proto-salaami*. w=wild.

not given by VAN SOMEREN and not shown in Table 10), it is highly probable that the brood was not carrying the genes for *planemoides* or *leighi*. His data (broods S2, S3, S4 and S5), therefore, agree with ours in showing *leighi* dominant to *hippocoonides* and in addition to this they show that f. *planemoides*, as it is not sex-linked, is also dominant to *hippocoonides* in these race crosses. In Table 10 it will be found also that within the race *meseres*, a female *proto-planemoides*, an insect which looks intermediate between f. *planemoides* and f. *leighi* (Plate, No. 6), mated to a male of unknown constitution produced three *proto-salaami* females and six males (brood S7). One of these S7 males mated to a *hippocoonides* produced only *proto-trophonius (lamborni)* and *planemoides* (brood S8). Thus, as *proto-trophonius* is not sex-linked (FORD 1936), it is also dominant to *hippocoonides*, a view fully in agreement with the other broods in the same table. If the genes controlling *planemoides* and *proto-trophonius* are not allelomorphs (though they probably are, see below), then *proto-trophonius* must be dominant; if it were not it would have appeared among the offspring of brood S9. In other words, the parents of S9 must have both been heterozygous for *planemoides* and neither can have carried *proto-trophonius* since none appeared in S9. On the assumption that the two are controlled by independent loci we cannot assume that in this brood *proto-salaami* is a combination of *planemoides* and *proto-trophonius* since no *proto-salaami* appeared in S8.

VAN SOMEREN's data give useful information about the inheritance of *proto-salaami*. An F_2 generation (brood S9) produced *proto-salaami*, a form which although present in the female sibs of one male grandparent was not present among the sibs of the parents. This suggests at first sight that *proto-salaami* is dominant to *hippocoonides*, as is strongly indicated in FORD's paper, but cannot express itself in the presence of *planemoides* or *proto-trophonius*. However, brood S9 is inconsistent with this view which would necessitate a ratio of 12:3:1 or a 12:2:2 *planemoides* to *proto-salaami* to *hippocoonides*. Moreover, the families in FORD's monograph strongly suggest that *proto-salaami* is also dominant to *proto-trophonius*, which is not in accord with the newer data. A less unlikely hypothesis is that in VAN SOMEREN's families *proto-salaami* is a recessive, and that brood S9 is an example of a 9:4:3 ratio. The other broods do not contradict this hypothesis, if we assume that the male parent of S8 was heterozygous for the gene producing *proto-salaami*, and that brood S10 resulted from two parents neither of which was carrying the gene. Whatever view we take, it is clear that *proto-salaami* is genetically controlled in two distinct ways. Firstly, from FORD's paper (1936) and our own results with f. *poultoni* (a form of *proto-salaami*) it can be seen that *proto-salaami* can be inherited as a single unit dominant in effect; secondly, from VAN SOMEREN's results it is clear that *proto-salaami* is either a recessive or, more likely, the heterozygote between allelomorphs controlling *planemoides* and *proto-trophonius*. It has often been pointed out that the pattern of *planemoides* is easily derived from that of *leighi*, and in view of the results with f. *salaami* from South Africa it seems more probable that *planemoides* and *proto-trophonius* are allelomorphs at the same locus as those

controlling all the South African forms, and that *proto-salaami* is the recognizable heterozygote between *planemoides* and *proto-trophonius*. Brood S8 is fully consistent with this view if the male parent (and his three female sibs, brood S7) were a heterozygote. On this hypothesis there is, however, a deficiency of *proto-trophonius* in brood S9 and of *proto-salaami* in brood S10 and S11. Nevertheless, because there seems to be some deficiency of *hippocoonides* in broods S10 and S11 combined and particularly of *proto-trophonius* in brood S11 (even if we assume that the forms are controlled by independent loci), it may be that there was abnormal segregation due to viability effects. This is a likely proposition as VAN SOMEREN reported that the butterflies in brood S11 were particularly undersized, and it is here that there is the notable excess of *planemoides* and deficiency of *proto-trophonius*.

In summary, therefore, VAN SOMEREN's findings are: (1) f. *proto-cenea* is almost certainly dominant to f. *hippocoonides*. (2) f. *proto-planemoides* and f. *proto-trophonius* are dominant to *hippocoonides*. (3) f. *proto-salaami* must be inherited in at least two ways, sometimes as a unit dominant to *hippocoonides* or sometimes not as a dominant but in all probability as the heterozygote between *planemoides* and *proto-trophonius*.

SUMMARY

A genetic investigation into races *dardanus*, *polytrophus*, *meseres* and *tibullus* of *Papilio dardanus*, together with some hybridization experiments between them, has been carried out.

(1) In race *dardanus* it was found that f. *trophonius*, f. *niobe* and f. *planemoides* were all dominant to f. *hippocoon*, and that *trophonius* and *planemoides* gave a recognizable heterozygote resembling *niobe*. The *cenea/niobe* heterozygote was variable and not always distinguishable from *niobe*.

In race *polytrophus*, f. *proto-cenea* was found to be dominant to f. *hippocoonides* as were the two forms bright and pale *poultoni*. The last two, however, produced intermediate forms with *cenea* and are *allelomorphic* with this and all the other South African forms. Furthermore, in race *meseres*, a *poultoni*-like form (*proto-salaami*), is sometimes inherited not as a single dominant but probably as the heterozygote between *planemoides* and *proto-trophonius*.

(2) Race crosses show that when the gene complexes are disturbed by hybridization the effects of the genes become far less constant. For example, the mimetic pattern of *cenea* breaks down when the form is hybridized with the West African material where the mimicry does not occur.

(3) Dominance is commoner and more complete between forms that are sympatric as compared with those that are allopatric. This suggests that dominance has been evolved.

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