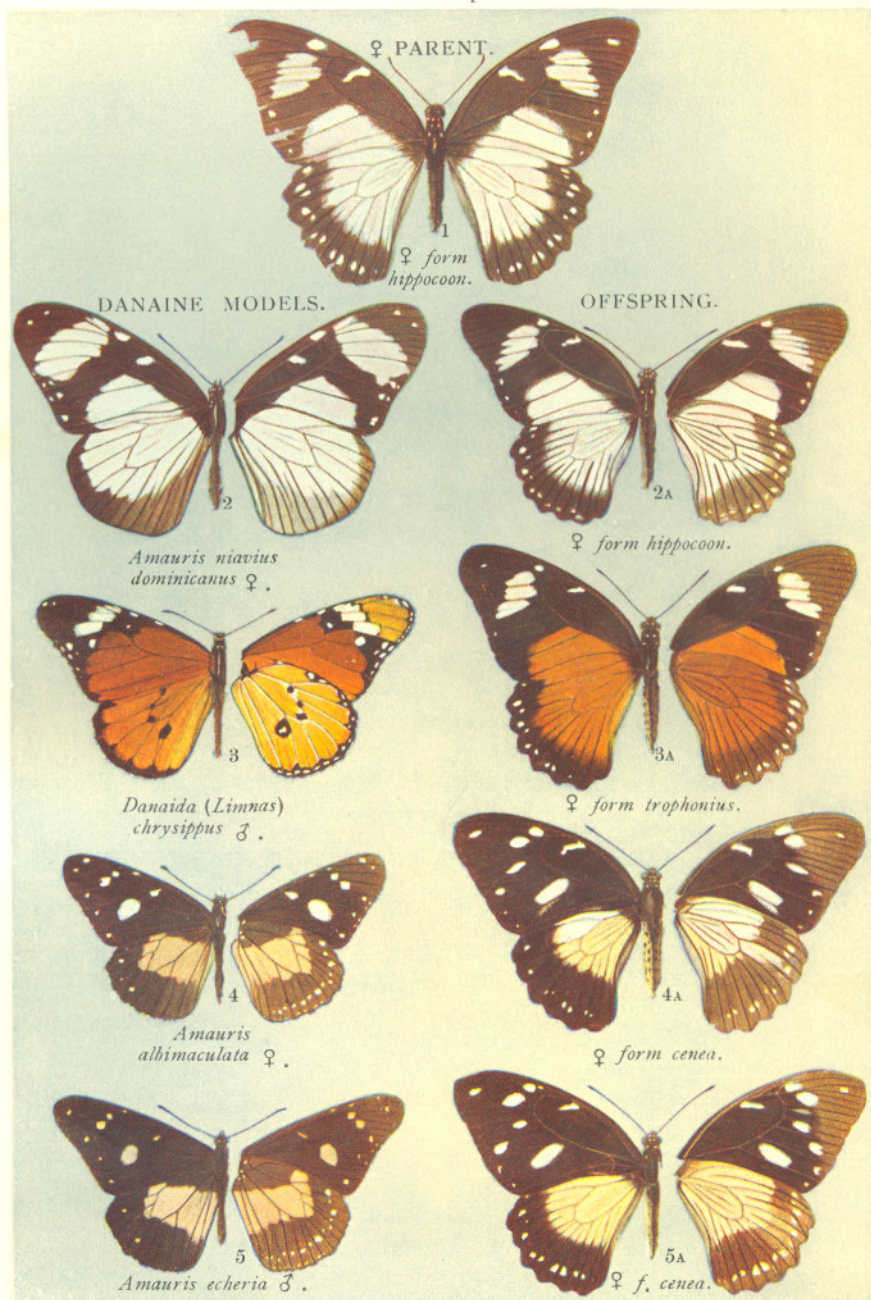


PLATE I.
Frontispiece.



Mrs. P. P. Whelpley, pnx.

André & Sleigh, Ltd.

All figures are about $\frac{2}{3}$ of the natural size.

Examples of the mimetic female forms of *Papilio dardanus*, subsp. *cenea*, bred in 1906 from a *hippocoon* form of female: Durban, Natal. The female parent and the Danaine models from the same locality are also figured.

PAPILO DARDANUS.

THE MOST INTERESTING BUTTERFLY IN THE WORLD.

by

PROF. E. B. POULTON, F.R.S.

(Illustrated.)

Naturalists at Nairobi are fortunate in that they live in a district which is pre-eminent in the light that is thrown on the past history and origin of the varied forms of this most remarkable butterfly. The importance and interest of the Kikuyu and Nairobi examples will, however, be best understood if introduced by an account of the finished product, to which they supply essential preparatory stages. Of the three plates by which this account is illustrated (1) originally appeared in the Transactions of the Entomological Society of London (1908, pl. XXIII.) and is here reproduced by kind permission of the Council, while (II) and (III) were first published in the Proceedings of the Second Entomological Congress at Oxford in 1912. "Trans." and "Proc." with no further addition, except the year and page, refer to the publications of the Entomological Society of London. Nearly every note, or paper, quoted in the following pages can be consulted in the volumes of "Hope Reports" in the possession of the East Africa and Uganda History Society.

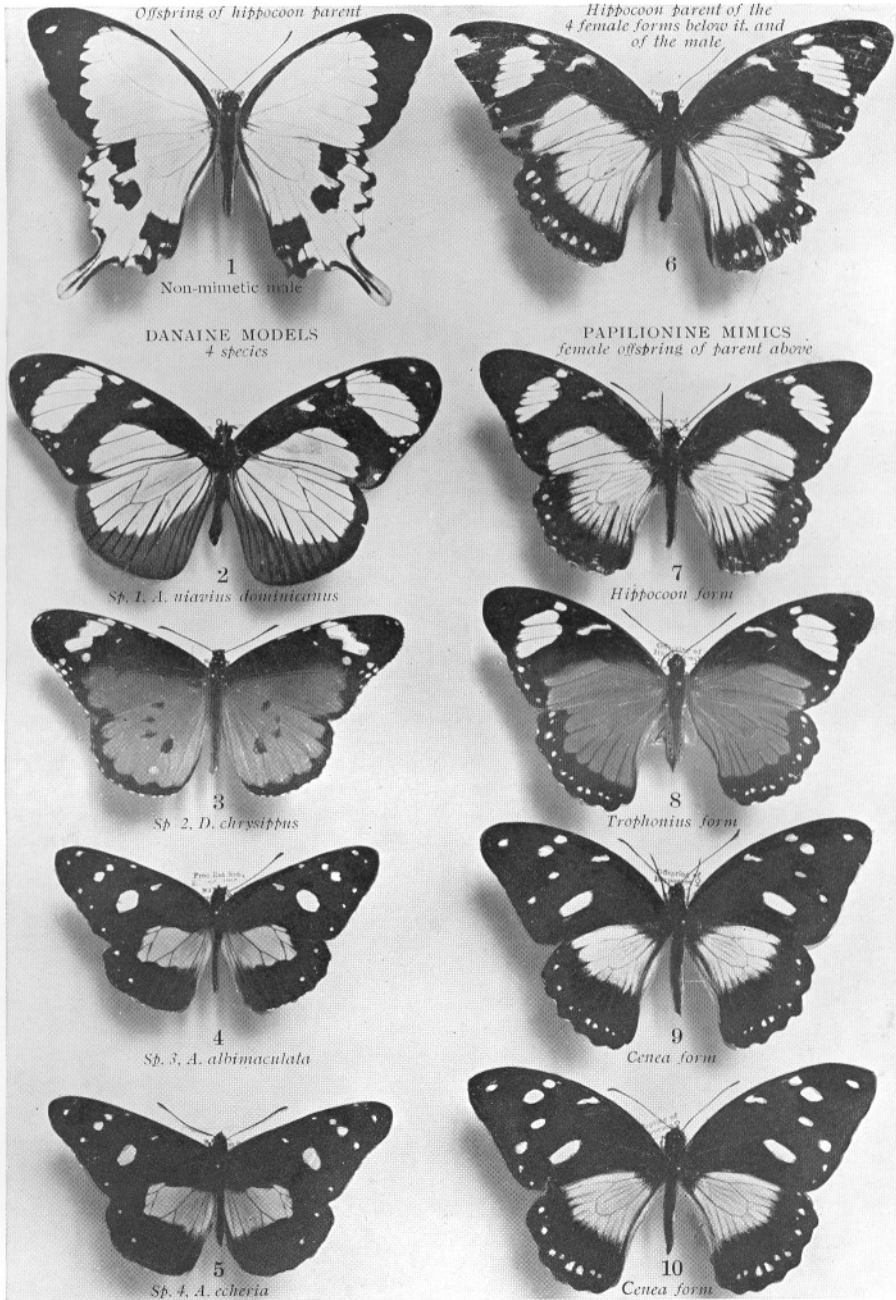
THE DISCOVERIES OF ROLAND TRIMEN.

Henry Walter Bates laid the foundation of the theory of mimicry in 1862 when his great memoir, with its curiously unrevealing title, "Contributions to an Insect Fauna of the Amazon Valley," was published by the Linnean Society (Trans., Vol. XXIII., p. 495).

A. R. Wallace, in the same Transactions (1866, Vol. XXV., p. 1) showed that Bates' interpretation of the complex resemblances between distantly related butterflies held good in the Oriental Region no less than in Tropical America. Finally Roland Trimen, in the same publication (1870, Vol. XXVI., p. 497) applied the theory to African butterflies and especially to the female forms of *Papilio dardanus*.

At the time when Trimen wrote this memoir the name *dardanus* was not recognised, the male butterfly resembling, but not exactly like the examples shewn on Pl. II., Fig. I., or Pl. III., Fig 3, being then known as *merope*, described from West Africa, by Cramer, in 1777.

PLATE II.



Alfred Robinson, photo.

Nearly $\frac{2}{3}$ of the natural size.

Andre & Sleigh, Ltd.

Papilio dardanus cenea, the S. E. African Sub-species of *P. dardanus* with the four Danaine models of its female forms. The proof by breeding that the mimics are one species. (Near Durban, Natal, 1906, G. F. Leigh.)

Later on it was found that this same male had been described and figured as *dardanus* in the previous year, by Brown. (III. Zool., p. 52, pl. XXII., 1776.) Although no locality is given, the excellent figure left no doubt that Brown's *dardanus* was described from a West African male, and that the name *merope* had to be sunk. Trimen was familiar with the South African form of *dardanus* and he also examined every specimen he could find in British collections. The result was always the same; the long-tailed swallowtail "merope" was always a male and there was no female to put with it.

Trimen similarly examined all the specimens he could find, of a tailless *Papilio* described by Stoll as *cenea* (Pl. I., figs. 4a, 5a, Pl. II., figs. 9, 10), a mimic of the Danaines, *Amauris albimaculata* (Fig. 4 on Pls. I. and II.), and *A. echeria* (Fig. 5 on Pls. I. and II.). The examination of all the *cenea* (about 25) then known in collections revealed nothing but females.

Trimen next studied the fourteen specimens, then known, of the tailless *Papilio hippocoon*, described from West Africa by Fabricius, and later as *westermanii*, by Boisduval. The S.E. African form of this black and white butterfly is represented on Pl. I., figs. 1, 2a; Pl. II., figs. 6, 7, and its Danaine model *Amauris niavius dominicanus* in Fig. 2 on Pls. I. and II. Here too only females of *hippocoon* were found.

He finally passed in review the seven specimens, which were all he could find, of the tailless *Papilio trophonius*, described by Westwood, and suggested as the possible female of *cenea*—shewn above to be itself a female. *Trophonius* is represented on Pl. I., fig. 3a; Pl. II., fig. 8, and its Danaine model *Danaida chrysippus*, on Fig. 3 of Pls. I. and II. All seven were females.

In arriving at the conclusion that *cenea*, *hippocoon*, and *trophonius* were three forms of "merope," modified in mimicry of three Danaine models—an astonishing suggestion at the time—Trimen was aided by a consideration of the Madagascar *Papilio meriones*, Felder, with a male very like "merope" (compare figs. 1 and 3, Pl. III.), and a tailed female (fig. 2) whose pattern resembles the male except for a pronounced black mark starting at the base of the fore-wing costa and almost crossing the cell. Concerning this feature he wrote:—

"In the broad black costal bar of the fore-wings which distinguishes the female in Madagascar, regarded in relation to the hind-marginal black border, it is not difficult to recognise the material upon which natural selection might gradually work, to the ultimate production of a "Danaidiform" butterfly like *Hippocoon* or even *Cenea*. . . ."

How entirely this prediction is justified will appear in later pages; and, indeed, it was not without confirmation at the time, confirmation provided by a fourth form of female, *dionysos*, of which three examples in Hewitson's collection were known to Trimen. This female form, well-known but rare on the West Coast, is very variable in that very feature of the female *meriones* which Trimen recognised as the foundation of the mimetic pattern; and as Trimen points out, the three specimens of *dionysos* exhibited two very different degrees of transition in this respect between the *meriones* female and the mimetic *hippocoon*.

Trimen's conclusions were received with incredulity. Thus W. C. Hewitson wrote:—" *P. merope*, of Madagascar, has a female the exact image of itself; and it would require a stretch of the imagination, of which I am incapable, to believe that the *P. merope* of the mainland, having no specific difference, indulges in a whole harem of females, differing as widely from it as any other species in the genus "; and he went on to compare *merope* with certain South American swallowtails of which the sexes had recently been recognised, reducing four supposed species to two. Of these pairs, at length united, he said: " Though much unlike each other, there is quite sufficient resemblance not to shock one's notions of propriety." A little later Hewitson received from Rogers, his own collector, then in the Island of Fernando Po, *Papilio merope* and *P. hippocoon*, taken by him in copulation; another illustration of the saying that " truth is stranger than fiction." (E.M.M., Oct., 1874, p. 118.)*

My distinguished predecessor, Prof. J. O. Westwood, was also at first incredulous, but became convinced when he received from Mr. Mansel Weale, the males and some of the female forms bred from larvae feeding together in his South African garden.

I well remember as an undergraduate nearly fifty years ago, Prof. Westwood pointing out the extraordinarily interesting comparison between the Madagascar and the African females of *dardanus*.

I must not dwell at too great length upon the historical aspect of the subject, but the continental race of *dardanus* with male-like females demands some attention.

* For an account of the controversy see Trans., 1874, p. 187.

THE ABYSSINIAN AND SOMALI RACE, *P. DARDANUS ANTINORII*, OBERTH.

Many years after the appearance of Trimen's original Memoir, two additional races of *dardanus* with male-like females were described by M. Charles Oberthur (whose recent death is such a grievous loss to Entomological science)—*antinorii* in 1883, and *humbloti*, from the Comoro Islands, in 1888. The former is of the highest interest in relation to the evolutionary history of *dardanus* on the mainland of Africa. With two exceptions all the known females of *antinorii* are male-like. These two astonishing specimens were described and figured by Kheil (Iris., III., p. 335, figs. 1 and 2, 1890). Both are mimetic but differ from all other mimetic females of *dardanus* in the possession of long "tails" to the hind wings. The pattern of one, named *ruspinae*, much resembles that of the *chrysippus*-like *trophonius* or rather *trophonissa*, of the other, *niavoides*, that of the *niavius*-like *hippocoon*. Coloured representations of both are given by Dr. Eltringham in Figs. 4 and 8, Pl. X of his "African Mimetic Butterflies" (Oxford, 1910). (This plate is entirely devoted to the forms of *dardanus* and should be consulted in connection with the present paper.)

The most probable explanation of the presence of these two extraordinary specimens, is, I believe, that they are hybrids between the female *antinorii* and a wandering male from further south, carrying the factors for the females *trophonissa* and *hippocoon*. (Dr. van Someren's recent discovery of a form of *dardanus* at Marsabit, S.E. of Lake Rudolph, with *hippocoon*-like and *cenea*-like mimetic females (Proc., 1924, p. xxv.) supports this conclusion, and suggests that collections from still further north, leading on into Abyssinia, would be of the greatest interest.) In one outstanding feature, the great size of the sub-marginal white spots of the hind-wing, the two specimens are alike, suggesting the probability that they were the offspring of the same female. Being unable to consult the paper at the moment, I have been kindly helped by Capt. N. D. Riley, who informs me that Kheil gives the locality as Korata on Lake Tana, and quotes Dr. Stecker's statement that the species was one of the commonest in the district, "so little shy that they could be picked off the flowers with the fingers." Nevertheless only four females were obtained—*ruspinae*, *niavoides*, and two male-like.

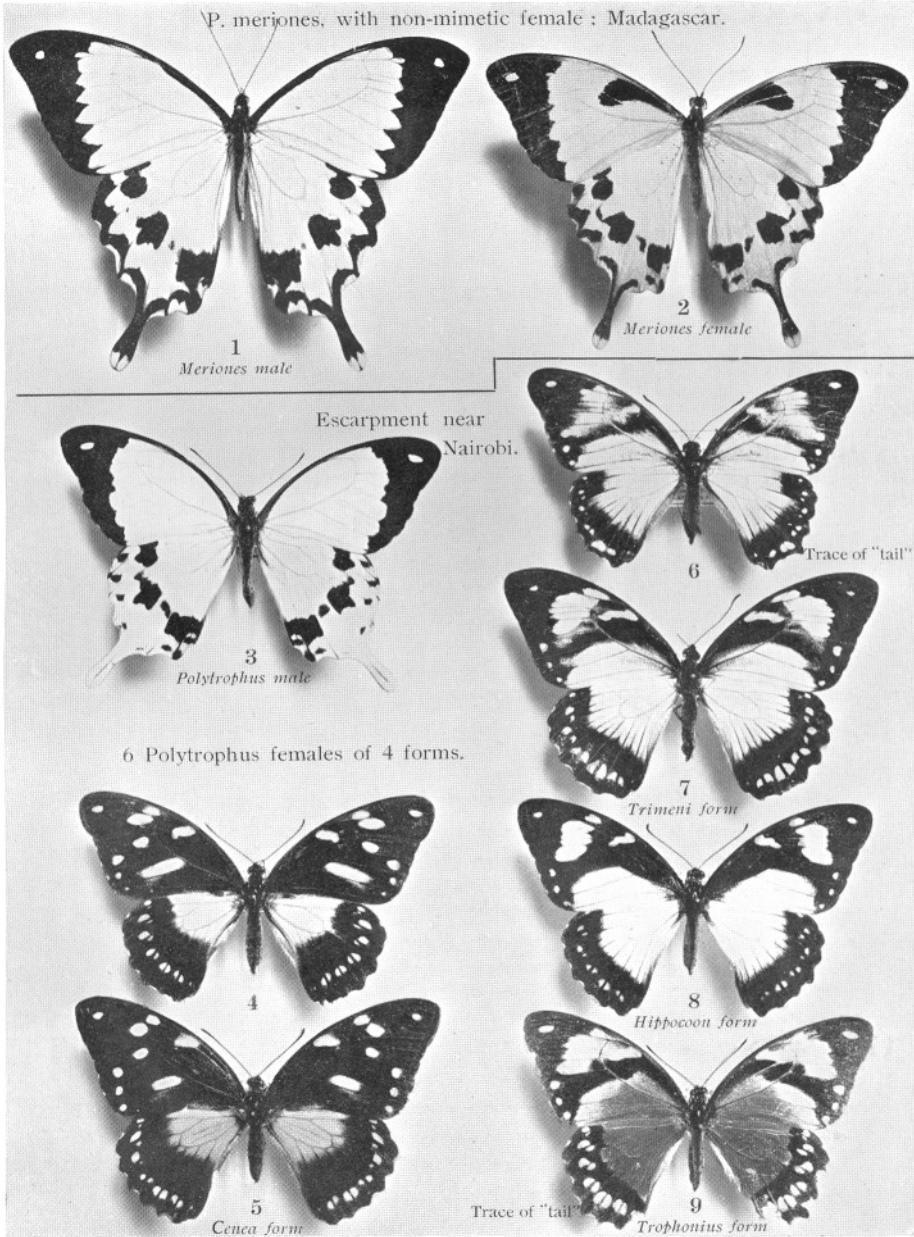
I have recently examined the females of *antinorii* in the British and Tring Museums, and found to my surprise that in a considerable proportion of them, the tails are much reduced. In one female out of seven at Tring this reduction is accompanied by an extension of the dark mark beyond the cell of the fore-wing, conspicuously into area 2, slightly into 3. Two interpretations suggest themselves. The reduced tails and prolonged costal bar may be traces of earlier hybridization with southern races diluted by prolonged interbreeding with pure *antinorii*; or these features may be due to the spontaneous appearance of variations such as that which led to the original development of a mimetic pattern. It is in favour of this latter hypothesis that M. le Cerf has recently described a Madagascar female in the Hill Museum, Witley, with a similar extension into area 3 on the undersurface (Bull. Hill Mus., Vol. I., No. 3, p. 379, Pl. I., fig. I.). He also describes on the same page a *meriones* female in the Paris Museum, with the right-hand tail reduced to a rudimentary projection, but as the left is normal I do not think that much significance can be attached to the specimen. There can be no doubt that such variations are extremely rare in the Madagascar race as compared with the Abyssinian. Extensive collections from various parts of Abyssinia and Somaliland would probably throw much light on this fascinating problem. *Antinorii* is evidently common in the Goolis Mountains, to the south of Berbera, a locality from which my friend Sir Horace Byatt sent me a fine series of males, but unfortunately no females. The comparison of these Somali females, if they could be collected, with those from Abyssinia would probably be highly instructive.

PLANEMOIDES, THE MIMETIC FEMALE FORM WITH AN ACRAEINE MODEL.

All the mimetic females hitherto mentioned resemble *Danaine* models, but a most interesting addition was made in 1903, when Dr. S. A. Neave recognised (Proc., 1903, p. xli.) in a collection made by Major Wiggins, C.M.G., at the N.E. corner of the Lake Victoria Nyanza, a female form mimicking the *Acraeina* butterfly *Planema poggei* (also a little further west, the male of *Pl. macarista*). This new form was named *planemoides* by Trimen in the same year (Proc. 1903, xxxviii-xl.), and was figured by Dr. Neave in Trans., 1906, Pl. X., fig. 8.

Planemoides and its model extend S.W. to Angola, and an Oxford specimen of the mimic bearing the label "Angola, Rogers: 1873" was probably received by Prof. Westwood from his friend Hewitson, to become thirty years later one of the types of Trimen's description. The other type, from the Kavirondo-Nandi district, has also been kindly presented to the Hope Collection by Mr. C. W. Hobley, C.M.G.

PLATE III.



Alfred Robinson, photo.

Rather over half the natural size.

Andre & Sleigh, Ltd.

The non-mimetic ancestor of *Papilio dardanus* (*merope*) from Madagascar, and transitional forms, shewing the origin of mimetic females, from the Kikuyu Escarpment, near Nairobi, British East Africa (6,500—9,000 ft.).

Indisputable proof of the soundness of Neave's and Trimen's inference that *planemoides* is one of the female forms of *dardanus* was obtained later on by breeding experiments, but before speaking of these and many others by which Trimen's original conclusions have been confirmed, it is necessary to describe briefly the distribution of the races of *dardanus* on the mainland.

THE AFRICAN GEOGRAPHICAL RACES OR SUB-SPECIES OF *P. DARDANUS*.

Five races in addition to *antinorii* are recognised by Dr. Karl Jordan (Zeitsch. f. Wissenschaft, Zool. Bd. lxxxiii.). The distinguishing characters relied on are the black markings of the male hind-wing and the form of the male genital armature. Dr. Jordan concludes that these differences of form are not such as to prevent interbreeding along the line where the area of one race meets that of another, and there is strong evidence that such interbreeding takes place.

The following are the races distinguished by Dr. Jordan, to each of which I have added the commonest and best-known female forms:—

1. *Papilio dardanus cenea*, Stoll. S. Africa, northwards to Delagoa Bay, completely transitional into the next subspecies, both geographically and in racial characters. The male and chief forms of female are represented, with the models of the latter on Pls. I. and II. The *hippocoon* female of this and the next subspecies, differing from the West Coast form described by Fabricius, has been named *hippocoonoides* by Haase, the chief distinction being the larger white area on the hind-wing, in mimicry of the eastern race of *Amauris niavius*, which also has a larger patch than the western race and has been called *dominicanus* by Trimen.

2. *Papilio dardanus tibullus*, Kirby. Delagoa Bay northward to the Mombasa district. Westward it is completely transitional into *polytrophus* in the Nairobi area, and northwards probably into *dardanus*, the fused races spreading to the Abyssinian border and perhaps interbreeding with *antinorii*. Typically *tibullus* has by far the most heavily marked male of any subspecies. The female forms are very similar to those of *cenea*.

3. *Papilio dardanus polytrophus*, Jordan. Aurivillius defines the area of this race as the high-lying districts of the interior of Tanganyika Territory and Kenya Colony at the South and East sides of Victoria Nyanza, extending as far north as Kavirondo. The great majority of the known specimens are from the Kikuyu Escarpment and Nairobi. Typically it is a small high mountain form with a male having the pattern of the subspecies to the west of it, but the armature of *tibullus*, to the east. Such a male from the Kikuyu Escarpment (6,500-9,000 feet) is represented on Pl. III., fig. 3, and some of its female forms from the same locality in figs. 4-9.

At Nairobi it is larger and the males often far more heavily marked, due without doubt to interbreeding with *tibullus*. The female forms are extraordinarily variable and include wonderful transitional stages leading from the male-like female to the fully-formed mimics. They will be considered in detail in a later paper.

4. *Transitional*.—Dr. Jordan here places the forms from Uganda and especially its eastern border, which, in the structure of the male armature are transitional between the eastern and western races, although in other respects—size and pattern—similar to the latter. Aurivillius in "Seitz" does not separate these transitional forms from *dardanus dardanus*, the succeeding race.

5. *Papilio dardanus dardanus*, Brown.—The transitional forms spoken of under 4 gradually die away as we proceed westward in Uganda and Tanganyika Territory west of the Victoria Nyanza, being replaced by *dardanus dardanus*, a race which spreads to the West Coast from Sierra Leone to Angola. These western specimens are larger than those of the other subspecies, the superiority being especially marked in the Congo area. Dr. Eltringham has shown that the pattern of the males from Fernando Po approaches that of the male *meriones* of Madagascar on the opposite side of Africa (Proc. 1916, p. xciii.).

The predominant female form of *dardanus dardanus*, especially on the West Coast, is *hippocoon*. The western form of *trophonius* has been named *trophonissa* by Aurivillius, being distinguished from the eastern form by the greater extent of orange in the fore-wing and its entrance into the cell. It is everywhere present in the area of this race, but everywhere relatively rare. Not uncommonly the orange colour appears in the subapical fore-wing bar, so that all the markings are orange—the form *niobe* of Aurivillius. The corresponding eastern form named *salaami*, by Suffert, is rarer relatively to *trophonius* than *niobe* to *trophonissa*, the latter being probably benefitted by its resemblance to an *Acracine* model *Planema tellus*. The *cenea* female is common in Uganda, where its models, especially *Amauris echeria*, are abundant, enters the eastern fringe of the Congo forest, but disappears at some unknown point, before reaching the coast, although a model is known but apparently not commonly, on its southern tropical section.

Planemoides is one of the chief female forms of Uganda, extending with its model to Angola. *Dionysos* is the interesting primitive form mentioned as hitherto only known from the West Coast.

6. *Papilo dardanus antinorii*, Oberth.—This race has been already sufficiently dealt with except in one point. The males are more lightly marked than in any other subspecies, in this respect approaching most closely to *dardanus dardanus* and *polytrophus*.

It is important to remember that each of the races 1—5, interbreeds with its neighbours in adjoining areas, as is clearly proved by the intermediate forms abundant along the common boundaries and often spreading far beyond them. Similarly a female form such as *planemoides* characteristic of one race and mimicing models found in the area of its distribution, may pass, by interbreeding, well into an area of another, where, far removed from its model but probably reinforced by fresh invasions, it may persist as a rarity.

It has been already pointed out that *antinorii* too, probably interbreeds with the race to the south of Abyssinia, and that the two extraordinary tailed mimetic-females may perhaps have originated in this way.

FAMILIES BRED FROM KNOWN FEMALE FORMS OF
DARDANUS IN VARIOUS PARTS OF AFRICA.

It will be convenient to review the breeding experiments which have been conducted with parents from different races, following the order already adopted, but deferring *polytrophus* and omitting *antinorii* in which such experiments have never been made.

1. *Breeding experiments with the South African P. dardanus cenea*:—

The first experiments of this kind ever made with *dardanus* were those of G. F. Leigh, beginning in the year 1902, when he bred three *hippocoonoides* females, twenty-four *cenea*, and eighteen males from a *cenea* female taken "in cop." with "*merope*" near Durban (Trans., 1904, p. 677, Pl. XXXI.). Later he bred several families from the same female form, as also from *hippocoonoides* and *trophonius*, nearly always obtaining a majority of *cenea* among the offspring and sometimes only this form. In 1923, however, he bred a majority of *hippocoonoides* in one family, while Miss Fountaine in 1909 obtained nineteen *trophonius*, two *cenea*, and sixteen males from the eggs of a *trophonius* female taken near Durban (Proc., 1912, p. cxxxiv.).

One of the most striking of G. F. Leigh's families, from a *hippocoonoides* parent is illustrated on Pl. I., showing the female parent and each female form present in the offspring, together with its model from the same locality. Of these females three were *hippocoonoides* (fig. 2a), three *trophonius* (fig. 3a), three *cenea*, with white spotted fore-wing (fig. 4a), five *cenea* with the chief fore-wing spot pale ochreous (fig. 5a). The same specimens are shown uncoloured on Pl. II. This interesting family, which included fourteen males of which one is represented on Pl. II., fig. 1, is described and figured in Trans., 1908, p. 434, Pl. XXIII.

Many families of the S. African race were bred in 1913 by C. F. M. Swynnerton at Chirinda in S.E. Rhodesia: Seventeen families from *hippocoonoides* parents yielded males and females like the parents; two from *cenea* parents, one from *trophonius*, and one from a form recently named *natalica* by M. le Cerf, all yielded males and a mixture of *hippocoonoides* with females of the parental form (Proc. 1914, p. lvii.). These results and W. A. Lamborn's in S. Nigeria (vide p. 13) strongly suggest a mendelian interpretation, the common *hippocoonoides* form being recessive and presumably mating most frequently with a male carrying factors for the same female form, the three rarer female parents, heterozygotes, (or hybrids), each combining its own dominant form with the common recessive *hippocoonoides*. Such females mating with the common form of male carrying factors for *hippocoonoides*, would give the observed mixture of female offspring (Proc., 1914, p. lvii-lxx.).

These conclusions were confirmed by Swynnerton's later experiments at Chirinda (Proc., 1919, p. xxx.). The fact that *cenea* is much the commonest female in Natal and the S. coast of Cape Colony is explained by the abundance of its models, and the rarity or entire absence of the black and white *Amauris niavius dominicanus*. At Chirinda, the black-and-white model is common, but much less so than the model of the *cenea* form, and the far greater effect of the former upon the proportion of the female forms is probably due to its extreme conspicuousness.

It is to be noted that the locally predominant form may be a Mendelian recessive, as *hippocoon* or *hippocoonoides* in most parts of Africa, or a dominant, as *cenea* (over *hippocoonoides*) in Natal and Cape Colony.

2. *Breeding experiments with the East African race P. dardanus tibullus.*

A hitherto unrecorded family received from W. A. Lamborn at Tanga, was reared from eggs laid by a *hippocoonoides* female, and contained, as at Chirinda, only females of this form and males. z

3. *Breeding experiments with the race P. dardanus polytrophus, at Nairobi.*

It has already been explained that the extraordinarily interesting breeding experiments of Dr. van Someren and Canon St. Aubyn Rogers at Nairobi will be considered in a future paper. It is, however, appropriate to point out that the Nairobi race of *dardanus* is by no means pure *polytrophus*, but often contains a strong element of *tibullus*, as is proved by the heavy marking present on the hind-wing of so many males.

4. *Breeding experiments with the transitional race of P. dardanus in E. Uganda, Etc.*

Two interesting families bred by Dr. Carpenter were reared from eggs of females taken in eastern Uganda and just south of it. The first, in 1912-13, from the eggs of a *planemoides* female captured on Bugala Islands in the Sesse Archipelago, Victoria Nyanza, yielded twelve males, seven *hippocoon* and three *planemoides* females, the latter bred for the first time (Proc., 1913, p. liii.; Trans., 1913, p. 656, Pl. XXXIX.). The second, in 1915, from eggs laid by a remarkable female combining the patterns of *planemoides* and *trophonissa*, taken near Kakindu Hill, 30 miles west of the Victoria Nyanza, and a little south of the Uganda border, yielded six males and two females, one of which was *planemoides* and the other *trophonissa*, the western form of the East Coast *trophonius*. The female parent thus produced the two constituents of its pattern (Proc., 1915, p. lxxxvi., *vide* also p. 9 of this paper).

It may be mentioned here that other, although much less extreme, instance of the fusion of two patterns are well known. Thus the *cenea* offspring of *trophonius* may exhibit traces of their parentage in the richer, redder tint of the hind-wing patch, and in modifications of the pattern (Trans., 1906, Pl. XVII., figs. 8 and 11, and description). Similarly, when bred from *hippocoonoides*, the *cenea* offspring may exhibit marked paleness in the same patch (Trans., 1908, p. 436, *vide* also Pl. I., fig. 4a of this paper). All specimens with such traces of fusion are probably heterozygotes exhibiting imperfect dominance, and would split up into their constituents in the later generations.

5. *Breeding experiments with the West African race, P. dardanus dardanus.*

Seven families were bred in 1911-13, by W. A. Lamborn in the Lagos district of S. Nigeria. All the parents were *hippocoon*, by far the commonest form on the West Coast, and the female offspring were of the same form. The seventh family, reared in 1913* contained besides fifteen males, nine *hippocoon* and eight *dionysos*, the latter an interesting and primitive form, well-known but always rare on the West Coast, and bred for the first time on this occasion.

The comparison of these two female forms in the same family provides strong indirect evidence of the influence of selection. The pattern of the nine *hippocoon*, resembling the well-known model, *Amauris niavius niavius*, is constant; that of the eight *dionysos*, unprovided with a model, extremely variable, ranging from a specimen like the type figured by Doubleday and Hewitson in which the oblique bar crossing the fore wing is altogether absent, through a graduated series to one in which it is well developed.*

* Proc., 1914, p. lxiii. The parent, 17 female offspring and one male, are represented on Pl. 1 of Proc., Linn. Soc., London, 1915-16. The parents of all female offspring of the first, fourth, and fifth families are shewn on Pl. XI. of Trans., Ento. Soc., 1913, and Proc., 1912, pp. xii. and cxxxi.

THE EVOLUTION OF THE MIMETIC FEMALES OF "PAPILIO DARDANUS":

Further reference to *dionysos* as a primitive form, in addition to that already mentioned (pp. 6 & 13), was made by Trimen in 1874 (Trans., p. 148), and nearly a quarter of a century later he drew attention to a far more significant specimen in the Hope Collection at Oxford—a female form of *tibullus* collected by Lt. Turner at Zanzibar in 1884. Comparing this with *dionysos* he describes it as "a much closer approximation to the masculine colouration. . . . The transverse trace of black in the fore-wing is even fainter . . . and the colour of the wide pale spaces and the hind-marginal spots in all the wings is almost exactly the pale creamy-yellowish tint of the male. . . . There can be no doubt that in this specimen we have a marked case of reversion to the original colouring of the female, but it is unaccompanied by any inclination toward the recovery of the lost tail of the hind-wings." (Proc., 1897, pp. lxxxviii., lxxxix.; Trans., 1906, Pl. XIX., fig. 1.)

VESTIGES OF HIND-WING TAILS IN SOME PRIMITIVE FEMALES AND THE MOST ANCESTRAL MIMETIC FORMS.

In the address from which I have just quoted, Trimen also expressed the reasonable hope that other transitional females would be discovered "at some point in the wide territories between Abyssinia and Zanzibar" (p. lxxxviii.). Only three years later the prediction was abundantly verified by the late W. Doherty, who made a large collection of female forms of *dardanus* on the Kikuyu Escarpment (Sept.-Nov., 1900, at 6,500-9,000 ft.). The great majority of these specimens are in the Zoological Museum at Tring, but a good series exists also at Oxford and at the Hill Museum, Witley. The most primitive of the Oxford specimens, the type of the female form *trimeni*, originally figured of the natural size in Trans., 1906, Pl. XVIII., fig. 1., is here represented on a reduced scale in Pl. III., fig. 6. It will be observed that there is a distinct trace of a "tail" to the hind-wing, and it is especially interesting to note that such rudimentary tails are more commonly found in *hippocoön* and *hippocoönoides* than in any other mimetic form.

In other words the ancestral rudiment is most frequently found in association with the most ancestral of the mimetic patterns.

That this is the most ancestral and most easily derived from a male-like pattern such as is borne by the Madagascar female will be made clear by comparing figs. 2, 6, 7, and 8 on Pl. III.

Two West Coast *hippocoon* in the British Museum possess rudimentary tails (Trans., 1906, Pl. XIX., figs. 2 and 3) which are especially prominent in a specimen from Gaboon, and in Lamborn's and Swynnerton's breeding experiments the artificial conditions appear to have often caused slight but distinct reversion in this female form. Out of Lamborn's six families, two included several *hippocoon* with these traces (Trans., 1913, Pl. XL., figs. 10, 15, 17, 21). One of the families was artificially cooled in the pupal state, but it is uncertain whether this condition produced any of the effect. Still more significant was Lamborn's seventh family mentioned on page 13. In this family none of the *hippocoon* offspring exhibited traces of a tail which nevertheless were slightly indicated in some examples of the more primitive form, *dionysos*. Here too Lamborn exposed some of the pupae to cold but there was no evidence of any effect.*

My distinguished friend Prof. van Beinnmelen of Groningen has contended in his interesting papers on the origin of the patterns of Lepidoptera, that these tail-less mimetic females, of tailed males are not derived from a form like that of the male, or the tailed female of Madagascar, etc., but are descended, unchanged in this respect, from the tail-less ancestor of the tailed Swallowtails. The facts mentioned in the preceding paragraph are very difficult to reconcile with such a hypothesis, and a discovery of Lamborn's furnishes a complete refutation. He has recorded that "the pupal wing-cases are the same in shape in both sexes, but whereas, in the male, the tails are readily visible on either side of the mid line on the night before emergence, in the female the space for their reception, though present in an equal degree, is unoccupied by wing-tissue." (Proc., 1914, lxvii.).

It will be observed that the vestigial tails often associated with primitive patterns and colours provide strong evidence against the conclusion that the two Abyssinian females with long tails and fully-developed mimetic patterns (p. 7) are ancestral or in any way represent stages in the evolution of the mimetic females of *dardanus*.

† The sex of the future butterfly can be ascertained by an examination of the wing-cases by the aid of transmitted light, from about the fourth day, if development is proceeding normally.—(Editor.)

* During recent experiments, it was found that in cases where the pupae had suffered a severe shock just when the larvae had changed to pupae and were still soft, the resultant butterflies showed distinct traces of male pigmentation varying from a small patch of yellow, to complete male colouration of one, two, three or all the wings. Also, that in cases where there was only slight male pigmentation, tails were present.—(Editor.)

THE PALE YELLOW PIGMENT OF THE MALE DARDANUS PROVED
TO EXIST IN THE PRIMITIVE FORM OF FEMALE.

Dr. E. A. Cockayne has shewn that the yellow colour of the male *dardanus* is due to a special pigment wide-spread in both butterflies and moths and one which can always be recognised by its fluorescence (Trans., 1924, p. 1). The parts of an insect's wing containing this pigment shine with a brilliant faintly bluish light, suggestive of moonlight, when exposed in a dark room to the dark ultra-violet light-rays, most conveniently obtained by the use of a mercury lamp.

Such parts stand out in startling contrast against the dark background of the other pigments of the wing. Although the chemical constitution of this pigment has not been determined it is certainly a definite substance; for it can be dissolved out of the wing by acetic acid and the solution fluoresces like the dry substance.

At Dr. Cockayne's suggestion and with his kind help, the pale yellow pigments of the primitive females of *dardanus* were tested, and Trimen's conclusions entirely confirmed. The yellow pigment of the female fluoresced like that of the male and is evidently the same chemical substance. When it has been transformed into white as in *hippocoon*-like females, or darkened into orange-brown as in *trophonius* and *trophonissa*, it is no longer the same substance and entirely ceases to fluoresce (Proc., 1921, p. xcix.).

In the note referred to above it is recorded that the pale-spotted *cenea* from the Kikuyu Escarpment fluoresced, while the very slightly darker pigment of the same forms from the lower elevation of Nairobi was non-fluorescent (*vide* also Cockayne in Trans., 1924, pp. 7 and 8). Later researches on the splendid material received from Dr. van Someren and Canon Rogers, has however shewn that fluorescent *cenea* commonly occur at Nairobi and in families bred from Nairobi parents, but it is still probable that such specimens occur in larger proportions at the higher elevation. Rogers has observed that the paler, more male-like, presumably fluorescent pigments of *cenea* appear in the pupa later than the somewhat darker non-fluorescing pigments of the same form, thus supporting the conclusions suggested by the physical test, that the two substances, although closely similar to the eye, are essentially different.

Until Dr. Carpenter conducted his experiments and twice bred *planemoides* from a known parent (p. 13), the only direct evidence that it is one of the female forms of *dardanus* was founded on a specimen taken in S.E. Uganda (1902) by Capt. T. T. Behrens, R.E.,

" the specimen was on the left side a gynandromorph, portions of the male markings and scattered patches of scales being, as it were, let into the female pattern (*vide* footnote, p. 15). When the butterfly is placed in the path of the ultra-violet rays, the little yellow patch, however small, shines out like a star on the dark background of the non-fluorescent female pattern." (Trans., S.E. Union Sci. Soc., 1923, p. 73; also Trans., 1906, p. 297, Pl. XVIII., fig. 4.)

FURTHER ANCESTRAL ELEMENTS IN TRIMENI AND OTHER PRIMITIVE
FEMALES OF DARDANUS.

The oblique black bar produced by the lengthening of the outer end of the costal mark in *meriones* (of Pl. III., figs. 2, 6, 7, 8) has already been mentioned. In the most ancestral *trimeni*-like form named *dionysoides* by Aurivillius, the mark is unlengthened as in the most primitive, and, as it happens, the type form of *dionysos*. The West Coast form may in fact be briefly summed up as follows: A fore-wing of *trimeni* pattern, with all its variations but the white pigment of *hippocoön*; a hind-wing of *trophonissa*, but with a paler tint. The developing parts of the pattern of both *trimeni* and *dionysos* have cloudy edges (dyslegnic) different from the comparatively sharp outlines (eulegic) of *hippocoön*.

Another ancestral feature of the pattern of *trimeni*, often retained by the fully mimetic females, is the trace of the two more or less complete gaps in the black band which is the most prominent feature of the male and un-modified female hind-wing. One of them is opposite to, but a little lower than the root of the tail, and between gap and tail is the largest pale area outside the black band; similarly occupying a corresponding position in *trimeni* and other primitive females, and often also in the mimetic females, is the largest pair of pale markings in the black border. Furthermore, the strong development of the whole series of these pale markings in the primitive females, *e.g.*, Figs. 7 and 9 of Pl. III., is clearly a much less reduced remnant of the area outside the black band of the male than that seen in the mimetic females, *e.g.*, figs. 7-10 on Pl. II. The fact that these markings are paired is due to the internervular streak passing through the remnant of pale ground-colour in each space and cutting it into halves, as is most clearly seen on the under surfaces shewn on the right side of figs. 2a-5a, on Pl. I.

Traces of the other gap, nearer to the costa or front edge of the male hind wing, are clearly seen on the under surfaces referred to above (*vide* especially figs. 2a and 4a) and on the upper surface of the *trimeni* shown on Pl. III., fig. 6.

THE EVOLUTION OF THE HIPPOCOON-LIKE FEMALE FROM TRIMENI.

It is now convenient to discuss the origin of each of the mimetic forms from the transitional females of the Kikuyu and Nairobi districts, following in the first place the order of figs. 2a-5a on Pl. I. The evolution of *hippocoon* will have already become clear from the previous account and the comparison of figs. 2, 6, 7, 8 on Pl. III. It will, I think, be convenient to speak of the transitional forms leading to it, but retaining the fluorescent yellow of the male, as *protohippocoon*, which will therefore include *dionysoides*, *trimeni*, and any other variety retaining the male yellow pigment and bearing a pattern intermediate between the Madagascar female and the black-and-white mimetic form.

THE EVOLUTION OF THE TROPHONIUS-LIKE FORM LAMBORNI.

The Kikuyu female figured as *trophonius* on Pl. III., fig. 9, is a *trimeni* with the chief pale yellow area, continuous from fore to hind-wing, almost completely over-spread with an orange flush. The specimen figured is seen to bear a vestigial tail, entire on the left side, broken on the right. All the pale colour is fluorescent. This form, which is well known in the Nairobi district and also occurs rarely in Tanganyika Territory, as far south as Kilosa (Proc., 1922, p. xlii.) has been named *lamborni* (Trans., 1917, p. 335). It bears the same relation to *trophonius* and *trophonissa* that *trimeni* bears to *hippocoon* and *hippocoonoides*; and it, and any of its varieties, which may be described as *protohippocoon* with the orange flush over most of the chief pale area, may be conveniently named *prototrophonius*.

THE EVOLUTION OF THE CENEA FEMALE FORM.

The history of this form of mimetic female is more difficult to understand than that of *trophonius* or *hippocoon*, but figs. 6, 4, and 5 on Pl. III., studied and compared in this order, suggest the line of development. The hind-wing pattern is derived from that of *trimeni* (fig. 6) by a broadening of the black border, the pale yellow pattern at first remaining fluorescent (fig. 4), but losing this property as it becomes ochreous in the hind-wing and ochreous or white (in the form *acene*, Suff) in the fore-wing (fig. 5). The spots near the margin also become smaller in the final product (Pl. II., figs. 9 and 10). The position of the spots in the fore-wing can be seen fore-shadowed in the *trimeni* on Pl. III., fig. 6. The lower border of the chief oval spot becomes defined by a band-like growth of the black ground-colour from base to anal or lower angle of the wing, while the five spots next in size are completed by the ground-

colour invading the pale area along the edges of which they are more or less clearly recognisable in fig 6. We thus arrive at such a primitive form of the *cenea* pattern as is represented on Pl. III., fig. 4, and from this pass by a change in the pale pigment to forms like Fig. 5. Forms of *cenea* which still retain, in any part of the pattern, the fluorescent yellow, may be conveniently called *protocenea*. At present these have only been proved to exist in the Kikuyu and Nairobi districts.

The possibility must not be lost sight of that such an example as *trimeni* as is shewn in fig. 6 may be a heterozygote, combining pure *trimeni* and some form of *cenea* or *protocenea*, and that the apparently foreshadowed fore-wing spots may not be truly ancestral. Such a view can only be confirmed or refuted by breeding experiments; but it is difficult to imagine how the patterns of figs. 4 and 5 could have arisen from one like fig. 2 except through a stage similar to that represented in fig. 6.

THE EVOLUTION OF THE PLANEMOIDES FEMALE FORM.

When I formerly discussed the development of this interesting form (Trans., 1906, pp. 293-7, Pl. XX., figs. 1-4) transitional varieties between it and *cenea* and between it and *hippocoon*, both from the N.E. of the Victoria Nyanza, were described and figured, also unfigured, a form combining the patterns of *planemoides* and *trophonius* (actually *trophonissa*), from Entebbe. It was argued that all these intermediates were probably "the result of first crosses between females of one form and males bearing the tendencies of the other female forms. We are compelled to believe that in later generations their female offspring would not remain intermediate, but would split up, in accordance with the Mendelian conception, into the parent forms; and we can thus understand the comparative rarity of intermediates." (*ibid*, pp. 295-6.)

The last mentioned intermediate, studied in 1906 from a beautiful drawing by Dr. Eltringham, was presented by him to the Hope Department and could thus be compared with two other examples taken by Dr. Carpenter at Kakindu, S. of the Uganda border. From one of these he bred, in 1915, the two female forms, *planemoides* and *trophonissa* (p. 12), thus confirming the conclusions arrived at nine years earlier.

It is in every way probable that the second intermediate, between *planemoides* and *hippocoon*, is also a heterozygote which would split up into its constituents in later generations; but as regards the first intermediate between *planemoides* and *cenea*, now known as *leighi*, further knowledge has proved that the conclusion was mistaken, that the form is stable over a vast area, extending

immensely beyond the range of *planemoides*, so that it is impossible to adopt the plausible interpretation of *leighi* as a hybrid between *cenea* and a male bearing the *planemoides* tendency, or *vice versa*. We are therefore driven to the hypothesis that the *leighi* form is a persistent definite stage in the evolution of *planemoides* (Proc., 1911, p. xli).

The *leighi* form which, as already explained, was first obtained from the N.E. corner of the Victoria Nyanza, and figured in Trans., 1906, Pl. XX., fig. 1, was four years later bred and captured in Natal. Eight specimens were obtained, most of them by G. F. Leigh, in 1910, and the form, although always proportionately extremely rare, has continued to appear (Proc., 1911, p. xxxiii.; 1912, p. cxxxv, 1913, p. vii).*

During the past year, 1923, Leigh has both seen it in the wild state and bred it. Nearly all the *leighi* forms have appeared always mixed with other Natal forms, in the families from eggs laid by *trophonius* females.

There can be little doubt that *leighi* arose from the *cenea* form probably with the addition of the pale, subapical, fore-wing bar of *hippocoön* or *trophonius*, or more probably retained from the ancestral *trimeni*. The other parts of the fore-wing pattern are nearly as in *cenea*, the chief difference being a shortening of the principal mark in area 2, and its growth downwards and outwards into areas 1a and sometimes also 1b. A tendency towards this growth is often to be seen in *protocenea* and *cenea* (e.g., Pl. III., figs. 4 and 5; Pl. II., fig. 9) although very faintly in the last figure.

The colour of all these fore-wing markings is the rich orange-brown of *planemoides*, and all that is required to produce the fore-wing of this latter form is the fusion of the oblique bar and all the spots except the sub-marginal into a single broad irregularly outlined bar. The apical spot, common to *cenea* and *leighi*, generally disappears while the other sub-marginal elements persist. A specimen of *planemoides* taken by a native collector in August, 1910, between Jilore and Malindi near the coast of Kenya Colony, supports

* The 1912 family containing *leighi*, and recorded on p. cxxxvi., is there spoken of as the second, but, as this form was bred three times in 1910, it must have been the fourth. A figure of the South African form of *leighi* is given by M. le Cerf on Pl. II., fig. 12 of his paper in Bull. Hill Mus., Vol. I., No. 3, p. 369. The author is mistaken in thinking that only three examples of the form are known. He agrees that the southern *leighi* corresponds to a stage in the evolution of *planemoides* in other parts of Africa (see p.).

the above interpretation. In this butterfly, presented to the Oxford University collection by Canon Rogers, the fore-wing bar is divided and thus approaches the pattern of *leighi* (Proc., 1911, p. xlii.). In the prolongation of orange along the inner margins of this specimen and the large size of the white patch of the hind wing, we probably witness the influence of the male parent carrying the factors of *hippocoonoides*, by far the commonest form of the female in this district (Trans., 1908, p. 499).

The hind wings of *cenea*, *leighi*, and *planemoides* have the same pattern, but the pale ochreous basal patch of the first becomes, sometimes darker, sometimes much paler, in fact nearly white, in the second, while in *planemoides* a pure white patch in mimicry of the *Planema* models is typical, and a darker one quite exceptional.

Following the lines already adopted, the *leighi* form and its varieties may be spoken of as *protoplanemoides*.

A SIMPLIFIED NOMENCLATURE FOR THE NON-SYSTEMATIC NATURALIST.

The origin and meaning of the forms of *dardanus* must certainly appeal to every naturalist who is interested in the problems of evolution; but the study is hindered at the outset by a complicated nomenclature, complicated indeed may be inferred from the fact that only a small part of its intricacy is here revealed. Thus many of the kaleidoscopic changes undergone by the pattern of the extremely variable female form *cenea* have received names and even the same form, when it appears in a different race, has been given a different name.

I have suggested in the preceding pages a simple and uniform modification of well-known names to indicate the primitive form from which each mimetic female arose; and, although from the strict systematist's point of view this procedure means further complication by the addition of synonymms, it is hoped and believed that the naturalist will be aided in his study of the subject.

In a somewhat similar manner, the various female forms in each race may be indicated by adding to each the initial letter of the race name. For this purpose race (4), founded on transitional characters in the male, may be disregarded, and the initial letters of the following employed—*cenea*, *tibullus*, *polytrophus*, and *dardanus*. The system of nomenclature, as applied to the principal form names, but capable of extension to others is as follows: Proceeding from the most primitive to the most specialised patterns:

- A. Mimics of the *Danaine*, *Amauris niavius*: (1) c, t, and p, *hippocoön* (= *hippocoönoides*), mimicking *A. n. dominicanus*; (2) d. *hippocoön*, mimicking *A. n. niavius*. Derived from a male-like female through t. and p. *protohippocoön* (= *dionysoides* and *trimeni*).
- B. Mimics of the *Danaine*, *D. chrysippus*: (1) c., and t. *trophonius*; (2) d. *trophonius* (= *trophonissa*). Derived from *protohippocoön* through t. and p. *prototrophonius* (= *lamborni*).
- C. Mimics of the *Danaines*, *Amauris albimaculata* and *A. echeria*: (1) c., t., p., and d. *acene*, mimicking the above *Danaines* with white spots in fore wing, completely transitional into (2) c., t., p., and d. *cenea*, mimicking the pale-ochreous-spotted form of *echeria*. Derived from *protohippocoön* through (p.) *protocenea*.
- D. Mimic of the *Acraeines*, *Planema poggei* and *P. macarista*: t., p., and d. *planemoides*. Derived from *cenea* or *acene* through c., p., and d. *protoplanemoides* (= *leighi*).

I have attempted in the preceding pages to give a condensed account of the chief forms of this most interesting butterfly and to trace the evolution of its mimetic females. In a future paper I hope to discuss the bearing upon this hypothetical history of the splendid series of families bred from known female parents at Nairobi by Dr. van Someren.

NOTES ON THE OCCURRENCE OF A SPECIES OF CHALICOTHERE IN UGANDA.

BY THE LATE C. W. ANDREWS, D.Sc., F.R.S. (British Museum).

In the number of *Nature* which appeared on November 10th, 1923, I published a short article entitled "An African Chalicothere," giving an account of the discovery in the neighbourhood of Albert Nyanza of the characteristic toe-bone of one of these curious animals. The specimen was sent to the British Museum (Natural History) by Mr. E. J. Wayland, Director of the Geological Survey of Uganda and was accompanied by numerous fragmentary remains of Hippopotamus, Phacochoerus, Crocodile, Chelomans and Siluroid fish together with some fresh-water shells. The beds from which these specimens were collected are probably of Pleistocene age.

The Chalicotheres (*Ancylopoda*) are one of the most peculiar groups of Mammals: they actually belong to the Perissodactyla, the uneven-toed Ungulates, of which the horse, rhinoceros, and tapir are