

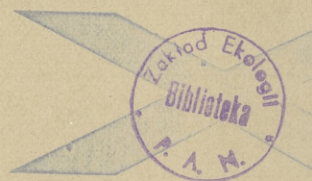
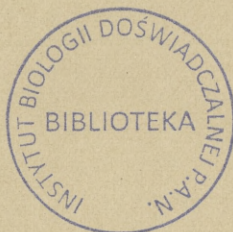
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Edward B. Poulton

**Mimicry in African Butterflies of the genus *Charaxes*,
with a classification of the species**



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E. B. Poulton

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Mimicry in African Butterflies of the genus *Charaxes*, with a classification of the species.

By Professor E. B. Poulton, F. R. S., Oxford.

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Introduction.

When the idea of mimicry between the butterflies of this genus was first suggested to me in a letter ¹⁾ written from Natal, 21 February 1897, by my friend Dr. G. A. K. Marshall, C. M. G., D. Sc., F. R. S., I found it then and for many years very difficult to entertain. Mimicry between these alert and powerful butterflies was so different from the well-known superficial resemblance to models like the *Danainae* or *Acracinae*, bearing in their habits and appearance the indications of distastefulness, or from the likeness between the species belonging to such groups, — so different indeed that it seemed at first impossible to bring them within the limits of the same general theory. My friend, the late Roland Trimen, F. R. S., felt the same difficulty (p. 528) and I believe that it will be felt by all naturalists when they encounter the subject for the first time. I am

¹⁾ Quoted in Trans. Ent. Soc. Lond., 1902, p. 505. See also pp. 528, 545 of the present paper.

convinced, however, that these difficulties will disappear when the whole of the evidence is considered. Thus my friend Dr. G. D. H. Carpenter wrote in 1915, after thinking over some of the facts which require explanation: "I don't know why I should have objected to the idea of mimicry in *Charaxes*, but now that it has worked its way in a bit, I cannot see how, accepting one form of mimicry, I can reject it here."

Dr. Jordan's suggestion that bionomic subjects were insufficiently represented among the papers to be read before the Third International Congress of Entomology, gave rise to the thought that this little-known department of mimicry in butterflies would make an interesting communication, especially if it could be accompanied by a paper recording Mr. Swynnerton's researches on the defences of *Charaxes*, and by one describing the proof by breeding that certain very different forms, mimicking different models, were the polymorphic females of a single species of this genus. Mr. Swynnerton kindly agreed and spent many hours of his short and strenuous leave in order to prepare his paper (p. 478). Dr. V. G. L. van Someren, with equal kindness, sent to me for exhibition at the Congress and record in these Proceedings (p. 507), some of the families illustrating the important discovery, made by his brother, Dr. Robert van Someren and himself, together with certain interesting families of dimorphic and polymorphic species of other genera, with their female parents.

As a brief introduction to the subject, I venture to quote, with a few slight alterations and some additions, the substance of an account given in the abstract of a Friday Evening Lecture at the Royal Institution, on 5 March 1915 (Proc. R. I., 1915, p. 372). For full details and experimental evidence Mr. Swynnerton's paper (p. 478) should be consulted.

In the genus *Charaxes* we are introduced to a novel aspect of butterfly mimicry; for both models and mimics are regarded by Mr. C. F. M. Swynnerton, who has observed and experimented with birds and their insect prey for many years, as among the most palatable of insects. Yet there can be no doubt about the fact that the large species of this genus are mimicked by the smaller ones, and that some of the larger species mimic each other. Mimicry in the African *Charaxes* has been chiefly studied by my friend Dr. Karl Jordan, who very kindly suggested most of the examples described

in this memoir, and has helped me in many ways from the stores of his wide and deep experience. Without his assistance I could not have attempted to undertake the work.

In their great monograph on the genus *Charaxes* (Nov. Zool., VII, 1900, p. 281) Rothschild & Jordan, writing on p. 477 of the female form of *C. etheocles* which resembles that of *ethalion* and is similar to the females (e. g. of *ameliae*) and males of other larger *Charaxes*, conclude that its pattern "is the normal one from which the other patterns have been derived; it is very variable. If the more or less great similarity between the *females* of this form and other *Charaxes* is due to all these insects having preserved a pattern which approaches the ancestral one, the agreement between the other forms of *etheocles* ♀ respectively with *bohemani*, *tiridates*, etc., must accordingly be the outcome of parallel development caused, as one is wont to say, by the protection which similarity in colour affords the individuals that associate together. Such an association of *etheocles* ♀ with other similarly coloured *Charaxes* is a fact observed first by Selous [see p. 540]; but we have very little further information on this point."

In the quarter of a century which has passed since these words were published a large amount of information has accumulated, making up a great mass of evidence in favour of the conclusion arrived at by these far-seeing naturalists. In the pages of this memoir I have made a point of bringing together all available records which prove that forms of *Charaxes* with similar patterns live in the same localities and may be seen flying together. The great amount of kind help which I have received will be acknowledged in its place, but I wish in this introductory section to express the most grateful thanks to the following naturalists who have supplied the much-needed evidence, have carried out breeding experiments, or given kind help in the determination and affinities of obscure forms: Dr. G. D. Hale Carpenter, D. M., M. B. E.; the late C. O. Farquharson, M. A., B. Sc.; Capt. A. L. Kent-Lemon; W. A. Lamborn; Dr. G. A. K. Marshall, C. M. G., D. Sc., F. R. S.; Dr. S. A. Neave, M. A., D. Sc.; The Rev. Canon K. St. Aubyn Rogers, M. A.; The Rt. Hon. Lord Rothschild, D. Sc., F. R. S.; Dr. Robert van Someren, M. D.; Dr. V. G. L. van Someren, M. B. O. U., F. L. S.; C. F. M. Swynnerton; Major C. A. Wiggins, C. M. G. and Lt. Col. R. S. Wilson.

Except for a number of Oriental species and a single Palaearctic subspecies, *jasius*, the genus *Charaxes* is confined to Africa and the

adjacent islands. The species of *Charaxes* are strongly built and extremely powerful in flight, the thorax, containing the wing muscles, being specially capacious. They are greatly attracted by fruit, exuding sap, and putrid or excrementitious substances, becoming after a time almost entirely engrossed in their occupation, although up to this point remarkably alert. Their habits before and when engaged in feeding and at other times are described in detail in Mr. Swynnerton's paper (p. 478), and have been confirmed by Dr. Carpenter's observations in other parts of Africa. Thus he wrote, 9 August 1915, of his experience at Kakindu, about 1° S. Lat. and 30 miles W. of the Victoria Nyanza:

"*Charaxes* most certainly *do* use the anterior, serrated border of the forewing for striking sharp blows, and I have seen one feeding at a pet crack on a tree-trunk and another alight, and manoeuvre with outspread wings so as to try and get the anterior rough edge under the wings of the other, when, I suppose, a sharp sudden closure would literally throw the enemy off its feet. It was very interesting to see them pushing each other about, and manoeuvring. Twice I saw a newcomer alight. He drove off the original, and then was himself driven off by the second arrival. Also, when sitting with wings closed, they drove off others by a sharp downstroke. (The two I saw fighting were of the reddish-brown, black-marked species (*C. cynthia*) with silvery stripe below which is very common here). I have, too, noticed often how they fly about at first and display the upper surface, and, if not quite absorbed in their food, when you approach they lower the hind wing a little (wings together over back) and this often brings into view a mark on the posterior edge of forewing, formerly concealed under the hindwing. If they do this, one is almost certain to fail to catch them, as it means they are very much on the alert. When still more nervous, they display the *upper* surfaces."

Two years later, at Lulanguru, near Tabora, Tang. Terr., Dr. Carpenter was offered further favourable opportunities for studying *Charaxes*, and in his recently published „Naturalist in East Africa“ (Oxford, 1925), he has stated his conclusions (pp. 24, 25) and given figures (Pl. I) of the principal models and mimics observed in both localities. His observations are quoted in detail in later pages.

The injuries so often seen along the border of the hind wings and to the „tails“ support the conclusion that the observed movements of these butterflies serve to divert attention from the vital parts²⁾.

²⁾ Specimens of three species of *Charaxes*, collected in 1898 and 1899 at Salisbury, Mashonaland, by Dr. G. A. K. Marshall, and represented in figs. 5, 10, 13,

When a *Charaxes* is seized its great strength enables it to struggle violently, and the effect is almost certainly intensified, in the larger species, by the serrated costa of the forewing. Swynnerton found that the chitinous exoskeleton is so tough that an insectivorous bird will often abandon a *Charaxes* after spending perhaps twenty minutes in the vain attempt to remove the wings. Repeated observations have convinced him that, with alertness and power of flight, „fighting weight“, and toughness of integument, *Charaxes*, in spite of its palatability, gives to its smaller enemies such an unpleasant experience that they will tend to avoid a repetition of it, except under stress of hunger, and that on this account the mimetic resemblance is advantageous. It should be added that the behaviour of large and powerful insectivorous birds shows that *Charaxes* is undoubtedly palatable. Furthermore, Swynnerton found that the thorax, after removal of its integument, is much appreciated by the smaller birds.

Mimicry in *Charaxes* is generally confined to the upper surface of the wings, and is principally, although by no means exclusively manifested by the females. The fact that some of the larger species, which act as models for smaller, are themselves mimics of other large species, and that one sex of a species may be a mimic while the other sex is a model, supply evidence that the resemblance is an advantageous advertisement of protective qualities held in common, although often in different degrees, by models and mimics, — that it is Synaposematic or Müllerian Mimicry. The same conclusion is supported by the great abundance of many of the mimetic species (p. 565).

The examples of *Charaxes* mimicry recorded in this paper are, I am convinced, far from complete. Probable associations other than those here described will occur to every student of the group, but they await the evidence which would justify their inclusion in these pages. The increase in knowledge during recent years justifies our confident hopes for the not distant future.

In order to understand the significance of the resemblances which form the subject of this paper, it is necessary to know the affinities of the forms which enter the various associations. Many species and

14, 15, 20 on pl. XI of Trans. Ent. Soc. Lond., 1902, are excellent examples of such injuries to the „tails“ and the part of the hindwing near them. Dr. V. G. L. van Someren also informs me that two specimens of *pelias saturnus* in his collection, from Fort Hall, Kenya Colony, had been attacked and the hindwings injured by a Drongo Shrike. This evidence, supplied by other naturalists in other parts of Africa, confirms the abundant proofs brought forward by Mr. C. F. M. Swynnerton (p. 494).

subspecies have been discovered since Lord Rothschild and Dr. Jordan published their great memoir, and many new facts have become known about the structure, affinities, and distribution of the forms recognised in it. In all this increase of knowledge the monograph itself has played the leading part. Therefore, with the kind help of Dr. Karl Jordan, a new classification of African *Charaxes*, embodying the additions to knowledge made in the last quarter of a century, has been prepared for the present memoir. This, it is hoped, will not only assist the student of mimicry to appreciate the meaning of the resemblances but will also be of value to the systematist in the arrangement of his specimens. The authors of species etc., when given in the classification or in lists, are not repeated in the text.

Mimicry in the genus *Charaxes* is of a kind hitherto unknown in Lepidoptera. Among other Orders, however, analogous examples are found in the mimetic resemblance of Longicorn beetles to other Coleoptera protected by their hardness and also in some instances by their strength³). Here, too, it has been pointed out, as Swynnerton has observed with *Charaxes*, that the defence is only effective against the smaller birds.

Among the Lepidoptera the facts are so interesting and stand so far apart from other examples of mimicry, and are at present restricted to a compact group of such moderate size, that it seemed advisable to attempt to give a full account of the present state of our knowledge on the subject. This result could only be achieved by greatly exceeding, in this paper and Mr. Swynnerton's, the limits usually observed in communications to the International Congress of Entomology. There would be serious objections to this course if the volume of Proceedings were swollen to an inconvenient size, or the finances of the Congress unduly depleted. The size of the volume is of course left to editorial decision, and, with regard to the second difficulty, I shall be pleased to authorize a grant in aid of publication from the Fund to promote the Study of Evolution presented to the University of Oxford by my friend Professor James Mark Baldwin.

A. The *varanes* Group of *Charaxes* as models: mimicry within the group.

I first concluded that *C. varanes* acted as a model for other *Charaxes*, in 1916, when looking through Dr. S. A. Neave's collection

³) See R. Shelford in P.Z.S., 1902, pp. 245—47, pl. XX, figs. 1—10 a. Also G. A. K. Marshall and E. B. Poulton in Trans. Ent. Soc. Lond., 1902, pp. 521—525.

from Uganda and Kenya Colony (1911—1912) in the British Museum. I was much struck by the remarkable similarity of the upper-side pattern of *C. lactetinctus* to that of *C. varanes vologeses*.

1. *C. lactetinctus* a mimic of *C. varanes*: *C. candiope* and *Palla ussheri interposita* ♀ in mimetic association with *C. fulvescens monitor*.

Dr. Neave's collection contained two female *C. lactetinctus* from the Nasisi Hills (4800 ft.) in Kenya Colony. The species, he informed me, was found in open country, while *C. varanes* itself also occurred everywhere in woodland and among clumps of trees in the open country as well as in the forest.

An allied association of 2 *candiope* and 3 *fulvescens monitor* in his collection was noticed at the same time. All were taken 18-21 June 1911, at Ilala, 14 miles E. of Mumias, Kenya Colony.

The association of *candiope* (Group B) with *fulvescens* (Group A) is paralleled by the upper surface resemblance between two Madagascar species of these groups — *analava* (A) and *antamboulou* (B). Dr. Jordan, who drew my attention to the likeness, pointed out the complete difference between the two under surfaces.

Both these continental associations have been independently observed in the field by Dr. V. G. L. van Someren who has also added the female of the Uganda race of *Palla ussheri*⁴) as another mimic of *fulvescens monitor*. His evidence is especially valuable, as it was obtained from observation of the living insects. He kindly wrote October 2-4, 1923:

„The association, so far as I have observed, is as follows — *fulvescens* with the female *ussheri* in the forests and clearings, and *varanes* with *lactetinctus* in the open Acacia park-like country.

“I have five specimens of *lactetinctus*. It is a beautiful butterfly and gave me great pleasure when I got my first specimen. I had to shoot two of them. They kept about 20 feet up and refused to come down, so in sheer desperation I took my collector's gun (.410), and, having reduced the shot-charge in a couple of cartridges (No. Dust.) I fired straight at them as they sailed out in the sun. They are hardly

⁴) *Palla ussheri interposita* Joic. and Talb. — Described from ♂ in Ann. Mag. Nat. Hist., Ser. 9, Vol. XVI, 1925, p. 646. The female of this Uganda race of *ussheri* is at once distinguished from the more western females by the clouding over of the dark basal area of upper surface of both wings by pale bluish-white scales, thus largely obliterating the sharp distinction between this patch and the adjacent pale yellow surface, and promoting the mimetic resemblance to *Ch. fulvescens monitor*.

damaged, yet they dropped at once! I have frequently adopted this method of capturing a high-flying insect of large size — *Charaxes*, *Papilio*, or *Planema*. They seldom get spoilt.

“To return to this association, the four together make up the group, but of course you must understand that, although I say *fulvescens* is a forest insect, it is sometimes found on the edges of forests, so also one finds *varanes* within the edges of forests. *Candiope* might come into this association also, as an outlying member.”

Further north in Uganda Dr. G. D. H. Carpenter saw a pair of *lactetinctus* flying together on Mt. Otze, about 10 m. W. of Dufile, in the W. Madi Province, in September 1921, and at the same time observed *varanes* on the same mountain. A month later he saw the two species flying on a little kopje at Arua Station, the H. Q. of the W. Nile District; on 11 October he caught *lactetinctus* and on the following day in the same spot the *varanes vologeses* he had seen flying with it.

On 22 and 23 May 1925 Dr. Carpenter again visited Mt. Otze and again saw many examples of both model and mimic. On 27 May he wrote as follows: „I was upon Mt. Otze again this time and though butterflies were extremely scarce on the whole, I saw about 8 *Ch. lactetinctus* and nearly broke my neck by gazing at them! They would settle out of reach, or, if within reach, would not allow me to strike at them! And I had no bait. They are most wonderful fliers: even among *Charaxes* they are *primi inter pares!* Two will go soaring away into the blue sky, buzzing round and round each other, till lost to view. Their white is very bluish — if they are ‘milky-tinted’, it is the bluish-white of much-watered skimmed milk! The brown also is deeper than that of the model (which, by the way, was fairly plentiful at the same time and place — on the summit of Otze and of small hillocks near the summit).“

Lord Rothschild has also received several specimens of these two butterflies in the same collection from the Bahr-el-Ghazal.

There is thus plenty of evidence that *varanes vologeses* and *lactetinctus* are associated in life in the hilly open country in N. Uganda and to the north of it.

On the west side of Africa *lactetinctus* is said to be not uncommon in Togoland. A single female in the British Museum was taken between the Scarcies R. and the R. Niger, in about 10° N. lat. I do not know of any evidence that it flies with *varanes vologeses* in these localities, but the latter is known to occur „all over West Africa from Senegambia to Angola“ (Nov. Zool., VII, 1900, p. 359).

Dr. Jordan considers that the western *lactetinctus* does not differ in any way from the eastern, but that the two form a single geographical race.

2. The female *C. azota* Hew. a probable mimic of *C. varanes*.

The study of Dr. Carpenter's collection of *Charaxes*, made between 23 October and 25 November 1917, on the summit of a granite kopje at Lulanguru, 17 miles W. of Tabora, Tang. Terr., suggested to me that the tawny, white-marked upper surface of the female *azota* is probably mimetic of *varanes vologeses*.

Although the white area is not basal as in the model, its position is such that the two would give a very similar impression when on the wing. During his stay at Lulanguru Dr. Carpenter caught 7 *varanes vologeses*, 7 females and 11 males of *azota*. Four female and two male *azota* were taken 19 and 20 November, together with three examples of *varanes* (Proc. Ent. Soc. Lond., 1917, p. cxxi.) The two species are also present among the *Charaxes* collected by Mr. Swynerton at Chirinda, S. E. Rhodesia, and one *azota* (a female) with two *varanes* were included in F. C. Selous's collection from Manicaland (P. Z. S., 1894, p. 14).

3. Two forms of the *zoolina* group of *Charaxes* probable mimics of *varanes*.

We have not the same evidence concerning the dry season forms *ehmkei*, of *C. zoolina ehmkei*, from the Cameroons-Congo-Angola area, and *homeyeri*, of *C. kahldeni*, from Angola⁵⁾, but I think there can be no doubt that their tawny and white upper surface is mimetic of *varanes vologeses* which is common in the same localities. Both forms are much smaller than *varanes*, but such differences between model and mimic are by no means uncommon.

B. *Charaxes saturnus* as both model and mimic of other *Charaxes*.

The historic interest of the *saturnus*-centred association has already been pointed out (p. 519), its discovery by Dr. G. A. K. Marshall being the first recognition of mimicry within the genus *Charaxes*. In the following sections *pelias saturnus* is spoken of by its familiar name, *saturnus*, and the races or subspecies of *pelias* will

⁵⁾ The wet season form *kahldeni* is known from a much wider range (p. 572).

be called the races or subspecies of *saturnus*. The strictly correct names are given in the list on p. 570.

1. *C. saturnus*, with male and female alike, as the model for the females of other *Charaxes*.

Dr. Marshall, in a letter written 21 February 1897, after referring to *xiphares* as a mimic of a Danaine model (p. 545), continued: „I believe there are more instances of mimicry in this genus, e. g. *achaemenes* and *guderiana*, of which the females are very scarce (though the male of the former is one of the commonest *Charaxes* in Mashonaland) and very differently coloured from the males, being remarkably like the common widespread *C. saturnus*.“ (Trans. Ent. Soc. Lond., 1902, p. 505) On pl. XI of the above paper are represented *saturnus* (fig. 13), *achaemenes* female (fig. 10), and *guderiana* female (fig. 13), all captured on the same day, 6 March 1898, at Salisbury, Mashonaland, by Dr. Marshall. These and other specimens of *saturnus* (figs. 14, 20) and the male of *guderiana* (fig. 5) are good examples of injuries inflicted during life to the hindwing and the „tails“.

The likeness between the two mimics and another species was noticed even earlier by Roland Trimen, but at that time without any suggestion of mimicry. He wrote to me on 30 January 1915, the year before his death: „My figures of the three uppersides of the curiously similar females of *C. lasti*, *achaemenes*, and *guderiana* (by a mistake of Butler's or the draughtsman's, the important undersides, so dissimilar, were not given) are in P. Z. S., 1894, Pl. V., in my account of Selous's Manica butterflies. It would be very interesting to know whether the mimetic species of *Charaxes* display the upperside, instead of having the usual habit of holding the wings closed and erect.“ The doubt expressed in the last sentence is fully answered by Mr. Swynnerton's paper (p. 478) and Dr. Carpenter's observations (p. 522).

Trimen's comments on these resemblances in the paper itself⁶⁾ are even more striking. Thus, he wrote of *achaemenes* on pp. 41, 42: „Although the upperside of the male and underside of both sexes are so completely unlike the pattern and colouring of *C. saturnus*, yet the upperside of the female is so remarkably similar to that of *saturnus* as

⁶⁾ „On Butterflies from Manica, South-east Africa“, P. Z. S., 1894, p. 14, pls. IV—VI. The collection described in this paper was made by F. C. Selous in 1892.

to be with difficulty distinguished from the latter without close comparison."

Furthermore, speaking of the female *guderiana*, which he described in the paper here quoted, Trimén remarked on p. 42 that, as this species „is unquestionably a member of the *ephyra* [= *etheocles*] and *ethalion* group of *Charaxes*, it is very unexpected to find the female, as in the case of *C. achaemenes* just mentioned, on the upperside closely resembling *C. saturnus*, and so differing widely from the aspect of her nearest congeners“.

Although, as Trimén said in his letter (p. 528), the female of *C. lasti* (= *boueti lasti*) belongs to the same association as the females of *achaemenes* and *guderiana*, it is not nearly so close a mimic of *saturnus* as either of them. Selou's Manica collection included a pair of *b. lasti* together with twelve *saturnus*.

The model and two more perfect mimics of this interesting association are beautifully represented in figs. 1—3 of the coloured plate XII, of Nov. Zool., VII, 1900, and the resemblance is referred to on p. 463. It is also noted by Aurivillius in Seitz, vol. XIII (Engl. Transl.), pp. 129 and 135.

Dr. Marshall's observations and conclusions in Mashonaland were independently repeated and confirmed by Dr. Carpenter in Tanganyika Territory, as recorded in Proc. Ent. Soc. Lond., 1917, pp. cxviii—cxxi. His table of *Charaxes* captured on the kopje at Lulanguru (p. cxxi) shews that both the mimetic females and a male of *saturnus*⁷⁾ were taken on the same day — 17 November 1917. The specimens bear his note “?mimetic relation: same spot and time“. Dr. Neave also took the three species together in Northern Rhodesia and adjacent territories (P. Z. S., 1910, pp. 39, 40).

As regards the relative abundance of the three, Dr. Carpenter's table records that fewer *saturnus* (7 males, 3 females) than of the other species were taken on the kopje at Lulanguru, the numbers of *achaemenes* being 7 males, 5 females, and *guderiana* 14 males, 21 females. Thus *guderiana* was apparently the commonest of the three in this locality (cf. p. cxix), whereas the males of *achaemenes* were the commonest in Dr. Marshall's Mashonaland experience (p. 528). Dr. Neave (ibid. p. 39) found *achaemenes* „one of the most abundant

⁷⁾ The members of this association, from Lulanguru, are represented by Dr. Carpenter on pl. I of his "Naturalist in East Africa", 1925: — a male *saturnus* in fig. 10, the female of *achaemenes* (fig. 12) and its male (fig. 9), the female of *guderiana* (fig. 11) and its male (fig. 8). The difference between the mimetic females and their respective males is very clearly shewn.

species of *Charaxes*, occurring throughout the whole country. The females are, however, very rare in my experience". Of *guderiana* he wrote „this species occurs everywhere and at all seasons. It is probably the most abundant species of *Charaxes* throughout this part of Africa." *Saturnus* was „a very common species throughout N. E. Rhodesia, less so in Katanga." All these facts suggest that the mimetic resemblance of the two females is Müllerian or Synaposematic, a conclusion confirmed by Dr. Jordan's observation that the male of *achaemenes* is itself mimicked by the *daria* female form of *etheocles* (p. 538).

An exceedingly interesting addition to the mimics of *saturnus* was discovered by Canon St. Aubyn Rogers who observed that a female form of *etheocles* taken by him at Taveta, Kenya Colony, differed from the ♀-forms *kirki* and *albifascia* n. ♀-f. in the hindwing bar becoming orange-ochreous instead of white, thus approaching the appearance of *saturnus*, which is common at Taveta (Trans. Ent. Soc. Lond., 1908, p. 507 note). At this time Canon Rogers had captured only two specimens, but later on he succeeded in taking several at Dabida, about 100 miles W. N. W. of Mombasa. The white of the discal bar in the hindwing of two specimens is entirely replaced by orange-ochreous, a change which, with the extended orange-ochreous of the forewing, renders this *rogersi* female f. a good mimic of *saturnus*. The whole series exhibited a transition from *rogersi* to the female form *albifascia*⁸⁾ with a white H. W. bar, of which a single example was included (Proc. Ent. Soc. Lond., 1918, pp. lxxxii, lxxxiii). One of the intermediates from Taveta was captured *in cop.* with a male *etheocles* of the form *chanleri*.

2. Races of *C. saturnus* as mimics of other *Charaxes*.

Canon Rogers pointed out, in the note referred to above, that *saturnus* was not among the *Charaxes* collected by Major C. A. Wiggins, C. M. G., in Uganda, and recorded by Dr. S. A. Neave in Nov. Zool., Vol. XI, March 1904, p. 323. On the other hand, 21 examples of *epijasius* from Nyangori, near the N. E. corner of the Victoria Nyanza, are given in the list on pp. 352, 353, and it was in Kavirondo that Mr. A. H. Harrison obtained a single specimen of the form of *saturnus*, which became the type of a new race, *pelias harrisoni*. This form, with the orange-brown of the wings darkened almost to black and surrounded by an orange border, and the

⁸⁾ The form referred to as *kirki* in Proc. Ent. Soc., 1918, is a new female form described on p. 553 of the present paper as *albifascia*.

H. W. blue spots greatly increased in size, is an evident modification of *saturnus* in mimicry of *epijasius*, as Dr. Jordan pointed out to me many years ago. Both model and mimic, extending doubtless across the intervening area, reappear in the extreme west of Uganda, on Ruwenzori, where they were taken together, 26 April 1906, on the S. E. of the mountain (3500 ft), by the Hon. G. Legge and Mr. A. F. R. Wollaston. The specimens are in the British Museum.

Dr. Jordan concludes that *jasius jasius*, the only European *Charaxes*, and *jasius epijasius* are two races of a single species⁹⁾ undoubtedly derived from a *saturnus*-like ancestor, and that a similar more recent darkening of the upperside and enlarging of the marginal pattern in the northern forms of *saturnus* has produced the race *harrisoni* in mimicry of *epijasius*, which originated in a similar change at an earlier date. It may be objected that, if the first change took place without mimicry, why should mimicry be invoked for the second. But we do not know the conditions under which the earlier change occurred. It too may have been a direct or indirect outcome of mimicry, a hypothesis discussed in another section (p. 533). In such a subject as this we can only speculate about what may have happened in earlier times under different conditions. One thing we do know that the change, however produced, has resulted in the powerful race *epijasius*, widespread in the open woodland country of North Africa, south of the Sahara, and mimicked by the female forms *viola* and *vansomereni* (p. 532) of the distantly related *etheocles* as well as by the closely related *harrisoni*.

One of the steps by which *harrisoni* arose from *saturnus* is suggested by the form *laticinctus*, known from several E. African localities. This variety of *saturnus*, with its broad pale margin, presents the most characteristic feature of *harrisoni*, *jasius* and *epijasius*. Other steps are suggested by four male *saturnus* in the Tring Museum — one with the label Usambara, although this locality requires confirmation, and three from Lake Baringo, Kenya Colony. Dr. Jordan informs me that these specimens, which exhibit considerable individual differences, especially in the blue markings, appear to reproduce various stages in the evolution of *harrisoni* from a form resembling *laticinctus*. It is interesting to know that *epijasius* itself was also received from Lake Baringo.

Another interesting form of *saturnus* is mimetic of a species

⁹⁾ Dr. Jordan points out that the remarkable development of blue in the race described from Liberia and Abyssinia bridges over the gap between *jasius* and *epijasius*.

further removed from it than *epijasius*. This interesting example, which I also owe to Dr. Jordan, occurs far to the south-west in N. Angola, where *brunnescens*, a local race of *saturnus*, has been developed in mimicry of *castor*. The darkening of the upperside is here less extensive than in *harrisoni*, and leaves a tawny bar resembling the corresponding marking of the huge model. *Castor* and *brunnescens* occur mixed in collections from N. Angola.

In view of the above example of mimicry, with *castor* as a model, it is interesting to record that Dr. Neave took a specimen of this species (at Mumias, Kenya Col.) which suggests that it may be following *saturnus* in the N. E. and producing a *harrisoni*-like form mimicking *epijasius*. This interesting variety of *castor* exhibits an increase of blue in the H. W. and reduction of the most prominent marking, the pale bar crossing both wings, which is nearly obsolete except for a triangular remnant in the H. W. The specimen is in the collection of the British Museum.

3. *Charaxes jasius epijasius* as the model of the female
C. etheocles viola and *C. e. etheocles* nov. ♀-f. *vansomereni*.

The mimetic resemblance of the *viola* and *vansomereni*¹⁰⁾ females of *etheocles* to *epijasius*, already briefly referred to on p. 531, was suggested to me by Dr. Jordan. Although at first a little doubtful I was soon convinced by the geographical association of both with their model, and by the evidence that model and mimic fly together and resemble each other on the wing. Thus Col. R. S. Wilson wrote, 7 February 1920, of his experience of the two species in the Nuba Mountains Province of the Sudan: „The *viola* form of *etheocles* flies with *epijasius*, and is almost indistinguishable from it on the wing except for its smaller size. I was out with Capt. Kent-Lemon at Talodi when I took my first specimen of the former butterfly, and we both thought it was an *epijasius*, until it was netted. Afterwards it was possible to distinguish it with care when on the wing, owing to the difference in size. We both took several *epijasius* round the same tree that day, and later on several occasions took them together. The tree particularly favoured was called Arrada (plur. Arrad) locally, viz. *Albizzia amara*, Boirin. . . . All the *Charaxes* I took in the Nuba Mountains Prov. are partial to it, viz. *varames*, *epijasius*, and *etheocles*.“ (Proc. Ent. Soc. Lond., 1920, p. xxiv.)

¹⁰⁾ Described on p. 553; represented on pl. 15, figs. 1, 2. See p. 508 for proof by breeding at Jinja that the male of *vansomereni*, *carpenteri*, and *cedreatis* is the form *picta*.

Capt. A. L. Kent-Lemon also took the same two species on the same day (25 May 1919), at Torit, Mongalla Prov., S. Sudan (*ibid.*, 1919, p. lxxvii); and Dr. Neave wrote of his experience in 1911-12: "As far as I recollect — and such of my material as is in the B. M. seems to confirm it — I only took the *viola* [*vansomereni*] form in the open country in Northern Uganda. It occurs on both sides of the Victoria Nile, but chiefly on the east. In that region apparently nothing but this form occurs, and it is more or less *all* open country. *C. epijasius* is common there, but owing to its being hard to catch and still harder to find in good condition, its numbers in collections probably do not represent its real incidence" (*ibid.*, 1919, pp. lxxvi, lxxvii. On the latter page localities of the two species in the Tring Museum, additional to those in Nov. Zool., Vol. VII, are quoted).

Among the *vansomereni* in the British Museum collected by Dr. Neave, S. of Elgon and E. of Jinja, are four unusually large specimens, suggesting, as did an example of *cedreatis* (p. 544) the possibility of incipient evolution of a mimic more nearly approaching the size of its model.

4. The possible influence of *Euvanessa antiopa* L. upon the evolution of two Northern races of *Charaxes* — *jasius* and *epijasius* — from *saturnus*.

The only occasion on which I have seen *jasius* in life was more than twenty years ago, in Majorca. It was sailing rather high up over some bushes and low trees, and I was at once struck with its *antiopa*-like appearance. Later on I examined the resemblance in detail and found that it was not only due to the general effect of the simple, striking and unusual pattern, but to the details of certain markings and to the modification of outline in both wings.

The very variable shape of the wings in *jasius* produces an effect suggestive of the angulated, irregular outline of the Vanessid far more completely than in *epijasius*. This resemblance is an exception to the general rule in being carried further in the males. On the other hand, the orange margin is on the average paler and nearer to the tint of *antiopa* in the females. In this respect, but not in others, *epijasius*, with a much paler margin, exhibits a closer likeness. Two features of *saturnus*, lost or modified in the intervening *epijasius*, are retained in the more distant *jasius*. Both promote a likeness to *antiopa* and may for this reason have been preserved. The postdiscal orange bar of *saturnus*, generally lost in *epijasius*, but sometimes indicated by a faint streak, is quite distinct in *jasius*, especially so on the F. W. costa where

in flight it may suggest the pale costal marks of *antiopa*. The blue, submarginal H. W. spots of *saturnus*, retained in *jasius*, are very *antiopa*-like, although developed towards the anal angle of the wing instead of towards the apical angle as in the Vanessid. In *epijadius* the blue spots fuse and spread into a prominent H. W. patch quite unlike anything in the pattern of *antiopa*.

As this paper was being prepared, and old notes on the *antiopa*-like outline of *jasius* came to light, I was haunted by the fear of some possible bias when the comparison was made and by the desire for re-examination. Opportunity being wanting at the time, I wrote to Capt. N. D. Riley, who kindly replied: "Of the three *Charaxes* you mention, *jasius*, *epijadius*, and *saturnus*, *jasius* undoubtedly bears the closest resemblance in outline to *V. antiopa*."

Considering the geographical distribution of *antiopa* in relation to this problem, the remote possibility should be borne in mind that the Palaeo-Nearctic Vanessid may formerly have spread about as far south in the Old World as it now ranges in the New, have overlapped the present range of *epijadius* and perhaps the northern limit of *saturnus*.

Specimens of *antiopa* from Guatemala exist in the British and Tring Museums, and it is well known in Mexico. Röber in Seitz states that it occurs in Venezuela, but confirmation is needed. The existing southern limit in the Old World appears to run along a line from north and central Spain to central Italy, Dalmatia, Greece (but not coastal), Asia Minor, Himalayas, W. China, and Japan. Seitz gives N. Africa, but here again confirmation is wanting. It is recorded by Mann from Sicily, but has apparently not been found by any subsequent collector. There is no doubt that *jasius* and *antiopa* occur together in the Pyrenees, S. France, Dalmatia, and Greece. In determining the southern limits of *antiopa* much kind help has been given by Dr. Jordan, Capt. Riley, and Mr. Talbot.

It is not necessary, however, to assume that the influence of *antiopa* upon *saturnus* was dependent upon a more extended southward range. If the enemies were common to its area and that of *saturnus*, if they remembered and applied in the southern area the experience learnt in the northern, the development of a southern mimic with a northern model would become quite intelligible. And the extremely simple, arresting pattern of *antiopa* renders it especially easy to remember. It may well be significant that in another example which seems to demand the same hypothesis for its interpretation, the pattern is also extremely simple and arresting. I refer to the upper- and

underside resemblance of the male *Athyma punctata* Leech and *Limnitis albomaculata* Leech in W. China to the male *Hypolimnas misippus* with a more southern range, apparently never overlapping that of its mimics („Essays on Evolution“, Oxford, 1908, pp. 217, 218, 381, 382).

Less striking but significant are the examples of African forest Lycaenids undoubtedly mimicking Acraeas of the more open country outside.

The fact that birds do remember patterns and do apply their experiences has been demonstrated by Prof. Lloyd Morgan („Habit and Instinct“, London, 1896). Nor is there doubt about the retentive memory which an animal of lower grade may possess; for a simple experiment has proved that a chameleon, after a single trial, remembered for many months the sober appearance of the hive-bee („Colours of Animals“, Internat. Sci. Ser., 1890, pp. 198, 199).

Unpublished experiments conducted many years ago shewed me that *Vanessa io* L. and *Vanessa urticae* L., although at first eaten, were soon rejected by the highly insectivorous Marmoset and by lizards, both these animals being kept in confinement and excessively eager for insect food. *Antiopa*, with its far more conspicuous pattern appearing on the under as well as on the upper surface, is probably more distasteful than these close allies. Carefully conducted experiments on a large scale with insectivorous birds are urgently needed.

Apart from the above considerations, it must be remembered that *jasius* and *epijasius* are considered to belong to a single species (p. 531) and that the effects produced by mimicry in the more northern race may, by interbreeding, have influenced the more southern.

Before leaving the subject it is of interest to enquire whether there is any evidence of *antiopa* acting as model in other parts of its range. In the Old World it may have influenced the pattern of the dark, white-bordered Satyrine butterfly *Satyrus (Nytha) parisatis* Koll. found in the W. Himalayas and Persia. *Antiopa* is known from Sikkim and Bhutan, and seems to skirt all round the area of *parisatis*, but has not been shewn to enter it. In the New World its possible effect is far more remarkable. The Acridian (grasshopper) *Dissosteira carolina* L. known as the „Black-winged or Carolina Locust“, ranges over an area „practically coextensive with America north of Mexico“¹¹⁾. These grasshoppers, „when flushed move in a noiseless, zigzag, seemingly aimless manner for quite a distance, the flight being

¹¹⁾ This and the other quoted statements concerning *D. carolina* are from „Orthoptera of Northeastern America“, Indianapolis, 1920: by W. S. Blatchley.

often more like that of a butterfly than of a locust" (p. 273). Speaking of the „curious aerial hovering“ of these insects, the author (p. 274) quotes the words of *Somes* — “From a distance this performance of *D. carolina* resembles the hovering of the ‘Mourning Cloak’ butterfly *Euvanessa antiopa*, more than the actions of a grasshopper“¹²).

In Canada, during and after the Toronto meeting of the British Association in 1897, I often had the opportunity of observing this grasshopper in flight, when, with its broad, black, pale-bordered hind wings unfurled, the resemblance to *antiopa* was very striking. The abundance of the *Vanessid* was to be inferred at the time of my visit from the numbers of pupae hanging from the fences around Toronto. My friend, Dr. F. A. *Dixey*, D. M., F. R. S., informs me that he had the same experience of *D. carolina* at the Toronto meeting of 1924. Furthermore, a distinguished Zoologist, not himself convinced that the theories of mimicry are sound, directed his attention to these flying grasshoppers as specimens of *antiopa*!

The experienced systematist has come to the conclusion that the northern *jasius* arose from a *saturnus*-like ancestor which has lost nearly the whole of its internal pattern and developed a pale border, studded internally with blue over part of its length. I have attempted to suggest conditions under which this remarkable change may have taken place.

C. *Charaxes brutus* as a model for many species of *Charaxes*.

The black, white-banded races of *brutus*, always with sexes alike, found over nearly the whole Ethiopian Region, are models for probably all the species of *Charaxes* with a similar pattern which fly with them — the females of *ethalion* and *etheocles* bearing the ancestral black-and-white pattern (viz: the female forms *ethalion* and *etheocles*); the female of *ameliae* which is a secondary model, and the female of *baumanni*¹³) the mimic of the female forms *ethalion* and *etheocles*; the white-barred female of *etesipe*; both sexes of *hansali baringana*

¹²) M. P. *Somes*, „Bull. Div. Ent. Minn. Agr. Exp. Sta., No. 141; St. Paul; 1924“, p. 53.

¹³) Dr. G. A. K. *Marshall* has observed that the female of *whytei* *Butl* (= *baumanni*) bears on the wing a strong resemblance to *Neptis agatha* *Cr.* (*Trans. Ent. Soc. Lond.* 1902, p. 505). Mr. *Swynnerton* states that he has often been deceived by the likeness of the *ethalion* ♀-f. *rosae*, to large specimens of the same *Neptis* (p. 493).

and of *hildebrandti*; the male of *achaemenes* and its mimic the *daria* female of *etheocles*. There is, furthermore, some evidence for an association with the white-barred Papilios of the *Zenobia* group, the resemblance between *brutus* and the male *P. echerioides* Trim. in Chirinda Forest, S. E. Rhodesia, being recorded by Mr. Swynnerton on p. 483.

The pattern of the butterflies of this combination is very simple, and, if we had no other evidence, it might be fairly urged that the resemblances are in part accidental, in part a mere expression of affinity. When, however, we follow the model into Abyssinia and find that the yellow-barred geographical race *brutus junius* is accompanied by the yellow-barred race *hansali hansali*; and again find that the female of the Madagascar race *brutus andara*, having the anterior (costal) part of the bar in the forewing, orange-tinted, is accompanied by the female of *etesipe cacuthis* with a similar bar, it is obvious that the theory of a true mimetic association is strongly supported. In Abyssinia the sexes are alike in both model and mimic; in Madagascar the female mimic resembles the female of the model. Dr. Jordan, who, ten years ago, suggested these two associations to me, together with most of those with the white-banded pattern, believes that *brutus* is the primary model for all the *Charaxes* members of this combination. In Abyssinia it is commoner than its mimic, there being 15 examples in the Tring Museum to 7 of *hansali*. I have recently received several *brutus somalicus* closely resembling *b. junius*, but not a single *hansali* in a collection from S. W. Abyssinia, kindly sent by Mr. Arnold Hodson. In Madagascar the two species appear to be about equally frequent.

Although *brutus*, so far as we know at present, always acts as a model, its mimics, on the other hand, exhibit very complex relationships, some of them acting both as models and mimics, some having males which are models for associations with very different patterns. The details will be found under other headings.

The bionomic significance of this white-banded pattern in *Charaxes* mimicry has been experimentally tested with positive results, at Chirinda, by Mr. C. F. M. Swynnerton (p. 490) who also recognised the reality of the mimetic association by observation of the members which fly in the patch of primitive forest at this S. E. Rhodesian locality. His conclusion that the *ethalion* ♀-f. (indistinguishable from the *etheocles* ♀-f.) is an undoubted mimic of *brutus* is confirmed by the independent observations of the Rev. Canon K. St. Aubyn Rogers who wrote 9 May 1916, from Dabida,

Kenya Colony: „There is also an interesting form of *Ch. etheocles* ♀ which is new to me. I have taken several but none in good condition. I enclose one so that you may see what it looks like. I have no doubt that it is a mimic of *Ch. brutus* which it greatly resembles.“ Canon Rogers also observed the mimetic resemblance of the *baumanni* ♀ to the *etheocles* ♀-f. in the same locality. The *daria* ♀-f. of *etheocles*, mimicking the male of *achaemenes* was described from Abyssinia, but neither it nor its model have acquired the yellow bar of *brutus junius*. A ♀ closely resembling *daria* has been taken at Handari far to the south in Tanganyika Territory where *achaemenes* is common, by Canon Rogers¹⁴).

D. The *C. tiridates* group as models and mimics.

1. *Charaxes cithaeron* as a model.

This eastern species is nearly related to *smaragdalis*, its western representative, and Dr. Jordan anticipates that transitional forms will be found in some intermediate geographical area. The male and female of *violetta* mimic the corresponding sexes of the commoner *cithaeron*. *C. pythodorus*, occurring in parts of the areas of both *cithaeron* and *smaragdalis* appears to mimic the males of these forms — the latter more closely than the former.

In the *etheocles* Group the *swynnertoni* ♀ of *ethalion* mimics the male of *cithaeron*, while its *rosae* ♀ mimics the female *cithaeron*. All these fly together in Chirinda Forest, S. E. Rhodesia, where *etheocles* appears to be absent. Ten uniform Chirinda males examined by Dr. Jordan, four being dissected, were all *ethalion*.

Females resembling *swynnertoni* and *rosae* occur with *cithaeron* further north on the E. coast, reaching Kenya Colony, and it has always been assumed that they are *etheocles*. The established facts at Chirinda throw some doubt on this interpretation; for *ethalion* exists with *etheocles* in these more northern localities (see also pp. 550, 551).

Rothschild and Jordan point out that the females of *cithaeron* from Mombasa differ from the Natal examples in the greater breadth and closer approach to the margin of the principal mark on both wings, and, on the underside of the F. W., in a thin line of scattered scales taking the place of a dark bar separating the outer end of the white band from the yellow lunule near the anal angle (Nov. Zool., VII, pp. 381-82). They suggest that these differences may be constant, an anticipation entirely confirmed by the fine series collected

¹⁴) ♀-f. *handari* nov., cf. p. 555.

in Kenya Colony by my kind friend Canon St. Aubyn Rogers. The females captured by him at Rabai, 14 m. N. W. of Mombasa; Ndzovuni 25 m., and Kaya Kauma about 35 m. N. of Rabai, exhibit not only the features described by Rothschild and Jordan but also a persistence, more complete than in the southern *cithaeron*, of the upper postdiscal white spots in F. W. In addition to the 2 uppermost, prominent in both races, 3 or 4 additional spots are more or less distinct, whereas in *c. cithaeron* these are usually absent, or if present obsolescent¹⁵). The correlation between these elements is seen in a single ♀ captured by Canon Rogers at Taveta which resembles *c. cithaeron* in the narrower bands and the lack of additional postdiscal spots in F. W. A female from Zanzibar (without data) agrees with the Kenya coastal series.

A female taken by Dr. S. A. Neave, 25 June 1905, on the banks of the Loangwa R., N. E. Rhodesia, Lat. 4.50 S., (about 1700 ft.), resembles the Kenya examples in every respect except that the F. W. bar is even wider and the blue patch of H. W. even larger, extending nearly to the base. This interesting specimen suggests the possibility that the coastal race extends south-westward through Tang. Terr. into N. E. Rhodesia. The 6 females from Chirinda Forest in S. E. Rhodesia (Swynnerton) are all *c. cithaeron* as in Natal, &c.

The much greater development of the upper section of the postdiscal spots in F. W. is also characteristic of the northern *xiphares nandina* ♀ as compared with the southern *x. xiphares*, but is far more emphasised in this close ally of *cithaeron*.

The specimens of *C. violetta* from Kenya localities closely resemble Kenya *cithaeron*, the females having a rather more highly developed postdiscal series in F. W., and it will be extremely interesting to observe whether the southern *violetta* follows *c. cithaeron* in the reduction of this series, and whether the *rosae* ♀ f. exhibits any modification of pattern corresponding with its models. A *rosae* ♀ in the British Museum, taken by Dr. Neave with a *cithaeron*, at Kibwezi, Kenya Colony, resembles the model in the breadth of the H. W. patch, but with so extremely variable a ♀ f. as *rosae*, a long series will be required before safe conclusions can be reached.

¹⁵) *Charaxes cithaeron kennethi*, n. subsp. — I suggest this name for the northern coastal race of *cithaeron* of which the females are distinguished from those of *C. c. cithaeron* by the characters described in the text. Type: A female from Ndzovuni, Kenya Colony, captured 25 Jan. 1911 by Canon Kenneth St. Aubyn Rogers. In Hope Dept., Oxford Univ. Museum, with paratypes, in the Oxford and British Museums, from the localities mentioned in the text.

2. *Charaxes bohemani* as a model for female forms of *C. etheocles* and the allied *C. fulgurata*.

The mimetic resemblance of these female forms to both sexes of the model is beautiful and convincing, being confirmed by the geographical coincidence, so far as data are available. It is also of much historic interest as supplying the earliest record of the association in life between models and mimics — although not at the time interpreted as such — in the genus *Charaxes*. This record appears in Roland Trimen's paper on F. C. Selous's butterflies collected in 1892 in Manica, S. E. Africa (P. Z. S., 1894). The author writes, on p. 44, of the *manica* female of *etheocles* "so closely resembling that of the much larger female of *C. bohemani*, that they might well pass for dwarf specimens of the latter species"; and he quotes, evidently from Selous, the note that one *manica* was taken, on 29 March, in the Mineni Valley, "on the same individual tree on which so many *C. bohemani* were captured". This tree is referred to in Selous's introductory notes (p. 16) and his observation recorded by Trimen is the earliest evidence of association referred to above, and the foundation of the statement in Nov. Zool., VII, 1900, p. 477, quoted on p. 521. Selous's collection contained 19 males and 17 females of *bohemani*, and of the female *etheocles*, 1 *phaeus*, mimicking *bohemani* ♂, and 3 *manica* mimicking its ♀.

Dr. S. A. Neave's experience of these butterflies in N. Rhodesia and adjacent Territories was the same as Selous's. He found *bohemani* „the most dominant of the larger *Charaxes*“, and „not uncommon throughout the wooded areas in all parts of the country“. The extreme wariness and powers of flight which he describes no doubt account for its numbers in collections being sometimes smaller than we should expect considering its influence as a model. Although the males of *etheocles* were taken over a wide area at all seasons he only captured five females, of which two were *phaeus* and three *manica*. His words — „These two forms of the female appear to mimic the male and female respectively of *Ch. bohemani*“ — contain, I believe, the first published recognition by a field observer of mimetic resemblance in the females of *etheocles* (P. Z. S., 1910, pp. 39, 40).

Dr. G. D. H. Carpenter's captures of *Charaxes* on a granite kopje at Lulanguru, 17 miles W. of Tabora, Tang. Terr., are recorded in tabular form in Proc. Ent. Soc. Lond., 1918, p. cxxi. In October and November 1917 he took 15 male and 11 female *bohemani* and 7 male and 6 *manica* female *etheocles*. He also independently recog-

nised the mimicry, having noted that the female *bohemani* „is resembled by a much smaller species“, and adding „? mimic“ to four out of the six *manica* females, and „? model“ to one of two female *bohemani* taken on 20 November, with one of these four *manica* (*ibid.*, p. cxix)¹⁶). The absence of the *phaeus* female from his collection is surprising, but it is possible that *manica* predominates where *bohemani* is specially abundant and its female — more conspicuous than the male — commonly seen. Where this large species is scarcer, the male may become a more advantageous model than the more rarely seen female. Although Dr. Carpenter did not take the *phaeus* female at Lulanguru, it is recorded from Tabora and Mamboya in Tang. Terr.; as also from the Ruanda country near Kigale (*ibid.*, pp. lx, cxx).

The late Mr. Hereward Dollman's collection from N. W. Rhodesia contained 14 *C. bohemani*, 20 male *etheocles* of the form *cytila*, 19 *manica* females and 1 *phaeus*. The proportions of mimics to models are not significant as the specimens were mostly bred. Mr. Dollman's notes describe *etheocles* as common and widely distributed in N. W. Rhodesia.

In addition to *etheocles* Mr. Dollman captured a few and bred many of a closely allied form at Solwezi, about 100 miles from the Katanga boundary. This *Charaxes*, described by Aurivillius as *fulgurata*, has been generally looked upon as a form of *etheocles*. Mr. Dollman believed, however, that its habits, food-plant, and larval characters provide sufficient evidence of specific distinction. His collection contained 16 males and 15 females, all of the form *coryndoni*, corresponding to *phaeus*. A second female form, *lunigera*, corresponding to *manica*, exists but was not taken or bred by Mr. Dollman. The male (of the form *cytila*) with both females of *etheocles* and the male and *coryndoni* female (under the name *mima*) of *fulgurata* are figured in Capt. N. D. Riley's interesting paper on the Dollman Collection (Trans. Ent. Soc. Lond., 1921, p. 234, pl. VI, figs. 1-5).

Looking at the two female forms *phaeus* and *manica* and comparing their patterns it would be reasonable to suppose that *phaeus* arose first and was transformed into *manica* by the appearance of the oblique white bar in the forewing, or conversely that *phaeus* was evolved from *manica* by the disappearance of the bar. Dr. Jordan has, however, shewn that each of these forms arose independently

¹⁶) Dr. Carpenter has figured Lulanguru examples of the male and female of *bohemani* and the *manica* female on pl. I of his „Naturalist in East Africa“. *Phaeus* is replaced by the *coryndoni* (= *mima*) female of *fulgurata* in fig. 6.

from the *etheocles* ♀ f. The two sets of transitional varieties, leading in the two directions, exist in the Tring Museum.

3. The predominance of the female forms of *C. etheocles* or *ethalion*, mimicking, respectively, the male and female of *cithaeron* and *bohemani*, determined by the relative abundance of the models.

In Chirinda Forest, S. E. Rhodesia, *bohemani* occurs, but is very rare as compared with *cithaeron* which is further strengthened by its mimic *violetta*. Two female forms of *ethalion* mimicking the sexes of *cithaeron* (p. 538) are common, but no mimic of *bohemani*. At Chirinda we are near the southern limit of *bohemani*; in Kenya Colony we strike its northern limit, and here Canon St. Aubyn Rogers has observed that it does indeed occur, but is very rare. Neither *phaeus* nor *manica* has been seen, and they are absent from a photograph of female forms of *etheocles* and *ethalion* sent to me by Dr. V. G. L. van Someren, although the mimics of both sexes of *cithaeron* and *violetta* were present.

Considering now the localities where it has been shewn that *bohemani* is abundant and its mimics occur but the mimics of *cithaeron* were not taken, we find that their models was either wanting from the collections (Dr. Carpenter's and the late Mr. Dollman's) or very scarce as compared with *bohemani*. Dr. Neave captured a single female *cithaeron* and saw one or two others (P. Z. S., 1910, p. 40). Selous's *Manica* collection also contained a single female.

The comparison between the numbers of the models and the presence of the mimics is very striking. Here are two closely related E. African *Charaxes*. Their patterns are very different and that of each male is also different from its female. Each is mimicked by two female forms of *C. etheocles* or *C. ethalion* — one form resembling the male, one the female of the model. One model, *cithaeron*, predominates to the north and to the south of the range of the other, and when the mimics have been taken in these north or south areas, they were only the mimics of *cithaeron*. Between these areas, in localities where *bohemani* has been shewn to be predominant and *cithaeron* absent or rare, only the mimics of *bohemani* were captured. It is unreasonable to believe that these local resemblances are merely coincidences, but I do not know of any hypothesis which can explain them except the one which assumes that they are advantageous and have been developed and fixed by natural selection.

4. The male *Charaxes tiridates* as a model for other *Charaxes*.

The upper surface patterns of *tiridates* and most of its mimics are entirely different in the two sexes. The male is a rich dark blue, with lines of light blue spots, and the pattern is surrounded by a pale yellow and black border along the outer margin of both wings.

The males of *Charaxes tiridates*, *numenes*, *bipunctatus*, and *mixtus* form a powerful association, the members of which would be indistinguishable upon the wing, and are probably models for other black, blue-marked *Charaxes* — *doubledayi*, *laodice*, *zelica*, and the males of *ameliae* and *imperialis*; also for some of the male-like females of *etheocles* and possibly sometimes for the males (pp. 559, 560). There is of course in this latter group nothing approaching the perfection of the resemblance of the *cedreatis* female to the female *tiridates*, &c., but, during rapid movement and in the passage through alternating light and shade, it is probable that some advantage would be gained by the rough likeness to this powerful male combination. It must also be borne in mind that there are probable mimetic resemblances between some of these blue-marked *Charaxes*, such as that between *doubledayi* and *ameliae*, the latter doubtless acting as the model.

5. The female *tiridates* as a model for other *Charaxes*.

The female pattern resembles that of *Danaida chrysippus* L., and the *chrysippus*-like species of the Geometrid genus *Aletis*, but the surface of both wings, except for the marginal pattern of the hindwing and the black, white-barred apical half of the forewing, is a peculiar olive-brown instead of the well-known tawny orange or orange-brown of the common *Danaida*.

The resemblance of *C. numenes* in both sexes to its commoner ally *tiridates* with a similar range, must have been noticed as soon as the species were recognised, but was probably explained as an incidental result of affinity. The *cedreatis* ♀-f. (pl. 15, fig. 3) of the smaller distantly related *Charaxes etheocles*, closely resembling the females of *tiridates* and *numenes*, obviously requires some other interpretation and at once suggests the theory of mimicry. The coincidence in distribution is very striking. *Etheocles* occurs over nearly the whole of Africa, but it is not until we enter the range of these two larger species that the *cedreatis* female appears. Travelling westward from the E. Coast in the equatorial region, the boundary of this range is first crossed near the eastern limits of Uganda. *Tiridates* and *numenes*, with the *cedreatis* ♀-f., also occur on the W. Coast and doubtless range eastward through the intervening forest, into Uganda.

Cedreatis has been proved by breeding (p. 507) to be one of four female forms of the same species in Uganda, having as their male the form described as *picta* Rothsch. Of the female forms one, *proto-cedreatis*, is probably a stage in the evolution of *cedreatis*, while the other two, *vansomereni* (p. 532) and *carpenteri* (p. 548), mimic *Charaxes* with patterns entirely different from each other and from that of the female *tiridates*.

The unusual size of one of the *cedreatis* females in Dr. Neave's Uganda collection in the British Museum, suggests that it would be interesting to compare a long series of this with the other female forms in order to test whether the immense size of the models, especially the female *tiridates*, has had any effect upon the size of its mimic.

In addition to these well-known members of the association a less common ally of *tiridates* and *numenes*, viz. *bipunctatus*, closely resembles them in both sexes and flies with them in Uganda and on the W. Coast. The male of another and much rarer ally, *mixtus*, probably with the same range as *tiridates* and *numenes*, almost exactly resembles their males, but a single example of the excessively rare female, taken by Dr. G. D. H. Carpenter at Kakindu (Proc. Ent. Soc. Lond., 1923, p. lxxvii), although possessing the *pattern* of the other females, is of an iridescent blue-black where they are olive-brown and non-iridescent.

6. The female *C. tiridates* pattern mimetic of species of *Euphaedra*.

The upper surface appearance in this female association was for long a puzzle to me. Why should a *chrysippus*-like pattern be accompanied by the peculiar olive-brown colouring? Why should it not have developed into true mimicry of *chrysippus*, following the example of many African species in many groups? That the appearance was definite and complete in itself and not a mere stage towards something else was rendered evident by the numbers and the different degrees of affinity of the constituent species. So the problem remained until it was solved by Dr. V. G. L. van Someren, who has done so much to help us in answering difficult questions of insect bionomics. He explained to me that in flight, and especially when winding their way through forest and undergrowth, the appearance strongly resembled that of the common Uganda species of *Euphaedra* with sexes alike. The pattern is similar, and, under the conditions described, the oblique white bar, the subapical spots and olive-brown of the *Charaxes* are very liable to be mistaken for the pale yellow bar, the white apical spot and somewhat different olive-brown of the *Euphaedra*.

A few weeks after our conversation on the subject Dr. van Someren wrote, 1 December 1922: „I am glad you do not disagree about the *cedreatis* form and the female *tiridates* and *numenes* as possible mimics of *Euphaedra losinga inaequalis*, and *spatiosa* and that group. I came to this conclusion when I was still very sceptical about the Mimetic theory, and it struck me at the time that if there was anything in it, then this must be an example!“

A list of the Uganda members of this association recognised by Dr. van Someren is given in the following passage from a letter dated 23 August 1923:

“Regarding the mimetic association, I consider that the following are concerned: female *tiridates*, female *numenes*, female *bipunctatus*, female *cedreatis* — possibly this new female f. *protocedreatis* (p. 556) with males and females of *Euph. spatiosa* Mab., *E. losinga inaequalis* Thureau, and one other near *E. uganda* Auriv., but with much less purple and with an olive bloom which gives the insect, when in flight, an appearance like the other two. It is a species which Dr. Jordan tells me is not yet named.“

The distribution entirely supports Dr. van Someren's conclusion, the *Euphaedras* appearing with the other members near the eastern border of Uganda, and *spatiosa* and *losinga* extending with them to the W. Coast.

In addition to the species of *Euphaedra* mentioned above Dr. van Someren has sent me from Uganda the female of *E. preussi olivacea* Grünb., which evidently falls into the same association as *spatiosa*, &c. Dr. Jordan informs me that the same race is represented in the Tring Museum from Unyoro.

7. The females of *C. xiphares xiphares* and *C. x. nandina* mimics of the Danaines *Amauris echeria* Stoll and *A. albimaculata* Butl.

The mimicry of *xiphares* was first observed by Dr. G. A. K. Marshall, who wrote 21 Febr. 1897, from Natal: “I do not remember ever having seen it suggested that the female of the handsome *Charaxes xiphares* mimics *A. echeria*, but I have little doubt that such is the case. It is a fairly common species at the Karkloof....“ (Trans. Ent. Soc. Lond., 1902, p. 505). Dr. Marshall's conclusion was accepted by Roland Trimen who wrote to me on 30 January 1915: “Except in female *C. xiphares*, not one of the eight congeners known to me in life has the upperside apparently mimetic.“

Dr. V. G. L. van Someren is convinced that the northern geographical race of *xiphares* — *nandina* — is similarly mimetic of the

same Danaine models. He wrote to me from Nairobi, 23 August 1923, as follows:

“Another *Charaxes* which undoubtedly comes into a mimetic association is the female of *Ch. x. nandina*. This certainly comes into the *Am. echeria* and *albimaculata* association. Although it is a much larger insect than its models, yet it must derive some protection from nearness in size to the *cenea* female of *Papilio dardanus* (which I think must be distasteful to a certain degree). I have a very fine series of male and female — some 42 specimens. I saw a female laying one evening high up on a tree (same food-plant as *cithaeron*). I couldn't get them that evening, but visited the place next day with ropes and tackle and had the tree cut down and gently lowered. The eggs were there all right but none hatched, as they were all parasitised.”

The fact that the food-plant is the same as that of *cithaeron* confirms the systematist's conclusion that the two species are nearly related. It is interesting to find that, of these two close allies, the female of one is a mimic of Danaine models, while both male and female of the other are the models for different species of *Charaxes*.

E. The *Charaxes zoolina* group, with conspicuous forms mimicking *Pierinae*, and dead-leaf-like forms with upperside mimicry of other *Charaxes* and of *Nymphalinae* outside the genus.

The second of the two great sections of African *Charaxes*, the Leptodontiae, contains for the most part much smaller, weaker butterflies, without the formidable saw-like edge to the F. W. costa. The under surface of several species is well concealed by Special Protective Resemblance to dead leaves. The mimetic forms mostly resemble the more powerful species of the Hadrodontiae, but some mimic butterflies of other genera. The few models in the Leptodontiae — each of them probably also joining an association centred by Hadrodontiae — are resembled by other species of their own section.

The *Zoolina* Group, with species exhibiting a remarkable dimorphism, is placed first among the Leptodontiae.

The fundamental discovery that *zoolina* and *neanthes* were forms of the same species was made by Mr. G. F. Leigh of Durban, who, in August 1908, bred 6 male and 1 female *neanthes* and one female *zoolina* from eggs laid on May 18 by a female *neanthes* (Proc. Ent. Soc. Lond., 1908, p. lxiv). A little later Mr. Leigh repeated the experiment with a female *zoolina* as the parent, the offspring being

4 male, 2 female *zoolina*, and 6 male, 9 female *neanthes* (*ibid.*, 1909, p. xlix; 1910, p. xli).

This interesting discovery led Dr. Jordan to examine all the forms in the *zoolina* group, and finally to determine that *kahldenii* and each of two geographical races of *zoolina* appeared in two forms corresponding to those of the third race — *zoolina* and *neanthes* (*ibid.*, 1908, pp. lxxviii-lxx, lxxxvi, lxxxvii). His arrangement of the group is quoted in detail in the classification of *Charaxes* on p. 572.

Although the *zoolina*-like forms are conspicuous, like so many wet season forms, and the *neanthes*-like well-concealed, like so many dry, an analysis of the material in the Hope Department shewed that, if they are seasonal, they are by no means confined to their respective periods of the year (*ibid.*, 1908, pp. lxxv-lxxviii).

The upper surface of the *zoolina* form is mimetic of the well-known appearance of many Pierine butterflies. Thus Dr. G. D. H. Carpenter has taken this form drinking at rain-puddles in company with Pierines near Ndala, Tanganyika Territory, and recorded the Pierine-like appearance of its upperside (*ibid.*, 1918, pp. cviii, cix). Mr. Swynnerton also came to the same conclusion from his observations at Chirinda, S. E. Rhodesia (p. 482).

The tawny and white upperside of the *neanthes*-like forms — *ehmkei* of *zoolina ehmkei*, and *homeyeri* of *kahldenii* — are doubtless mimetic of *varanes vologes* (p. 527); and Mr. Swynnerton suggests that the same surface of *neanthes* itself may be to some extent mimetic of *Atella phalantha* Drur. and *columbina* Cram. (See also p. 568.)

The underside of all the forms corresponding to *neanthes* is dead-leaf-like. In *neanthes* the midrib-like stripe is given the most convincing appearance of a strongly projecting ridge, by the representation of high light along one side and deep shadow along the other. I believe it will be found that the butterfly rests in a position such that the bright side is turned towards the source of light. Its habits have been described by Dr. Carpenter: „... a very dead-leaf tailed brown Nymphaline.... It flitted from bush to bush, taking especial care to settle on or near clusters of wrinkled dead leaves“ (*ibid.*, 1918, p. cviii)¹⁷). Compare also Mr. Swynnerton's record of the habits of this form (p. 501).

¹⁷) The habits of *neanthes* and the Pierine-like appearance of *zoolina* are also recorded in Dr. Carpenter's "Naturalist in East Africa", Oxford, 1925, p. 98.

F. The male and female of *C. etesipe* as both models and mimics of other *Charaxes*.

It was suggested in Proc. Ent. Soc. Lond., 1918, p. lxxxii, that the male *etesipe* is the model for the dark, blue-marked *carpenteri* ♀-f. of *etheocles* (pl. 15, fig. 4). Both species were taken in the same forest near Kakindu, Tang. Terr. (31° 30' E., 1° 10' S.) by Dr. Carpenter in 1915¹⁸⁾. Since then I have learnt from Dr. V. G. L. van Someren that both are well known in the Jinja district of Uganda, and that he had himself recognised the *carpenteri* female as a mimic of the male *etesipe*, observing that „it is quite deceptive on the wing“.

It is probable that the male *etesipe* is also, under favourable conditions, an outlying member of the association of blue-marked *Charaxes* with the males of *tiridates* and its allies as the central members (p. 543).

The white- or cream-marked female of *etesipe* is a member of the *brutus*-centred combination (p. 536), being especially associated with the female of *ameliae* and the *etheocles* ♀-f. of *etheocles*. In the neighbourhood of Jinja, Uganda, the female *etesipe* appears in two forms, one mimicking *castor*, the other *brutus*. Thus, Dr. V. G. L. van Someren wrote on 13 September 1923: „I have bred quite a number of *C. etesipe*. The female is dimorphic with two marked forms — (1) with a white bar, mimetic of *C. brutus*; (2) with a yellow bar mimetic of *C. castor* — excellent mimics both of them.

„The yellow extends throughout the whole length of the bar as seen when the wings are expanded, but it is deepest in the forewing. The spots are also yellow. One does, of course, get certain examples with most of the yellow in the hinder part of the bar in F. W.“

Since the receipt of this interesting information I have, through the kindness of Dr. Robert van Someren, had the opportunity of studying seven female *etesipe*, mostly bred specimens, from the Jinja district. It appears from this material that in this area *castor* is more powerful as a model than *brutus*. Not one of the females is white-barred and probably all but one would resemble *castor* more closely than *brutus*. There is, however, an extremely gradual transition from the specimen with the darkest F. and H. W. bar to the

¹⁸⁾ Both model and mimic from Kakindu have been recently figured by Dr. Carpenter in his „Naturalist in East Africa“, Oxford, 1925, pl. I, figs. 1 and 2.

one with the palest. The undoubtedly *castor*-like forms appear to be undescribed¹⁹).

The mimicry of *brutus* by the *etesipe* females with a white or cream-coloured bar and the corresponding changes in the Madagascar races of both model and mimic have been described on pp. 536, 537.

G. *Charaxes* of the *etheocles* group as mimics
and the male of *etheocles* as a model.

1. *C. ethalion* with females mimicking other *Charaxes*.

This species is very closely related to *etheocles* and probably all its female forms are similar to some among the far more numerous females of the latter. *Ethalion* is an East African species, ranging from Cape Colony and Natal to Kenya Colony. *Etheocles* is found all over Africa south of the Sahara, except Cape Colony and Natal.

Four female forms of *ethalion*, indicated by letters *a* to *d*, are distinguished in Nov. Zool., VII, 1900, p. 479.

The ancestral *brutus*-like female (*a*) bears a white bar, more or less edged and shaded with blue, crossing both wings and formed of a double series of spots, discal and postdiscal, in the fore wings. In the female (*b*) the upper spots of the two F. W. series are of a buff colour. It is probable that this variety is even more ancestral than the white-marked form, and that at one time the model *brutus* was orange-tinted in the same part of the pattern, as its female and the mimetic female of *etesipe cacuthis*, still are in Madagascar (p. 537). In another form (*c*), also *brutus*-like, the lower spots of the two series in the fore wing are more or less fused (Nov. Zool., VII, 1910, pl. XII, fig. 4).

Two other female forms mimic respectively the male and female of *C. cithaeron*, and are co-mimics with *violetta*. The mimic of the male is the form (*d*) *swynnertoni*, with blue F. and H. W. markings, described from Chirinda, S. E. Rhodesia (Proc. Ent. Soc. Lond., 1918,

¹⁹ *Charaxes etesipe etesipe* n. ♀-f. *castoroides*. — The principal marking, viz. the bar crossing both fore- and hindwing varies from orange-ochreous to pale yellow, resembling in this respect the different depths of tint exhibited by *Charaxes castor*. The paler tint of the H. W. section of the bar is also characteristic of many *castor* in the Jinja district. The admarginal red of the hind wing is retained more completely than in the white-barred *brutus*-like females, probably resembling on the wing the submarginal orange-brown markings of *castor*.

Type, bred at Jinja, June 1924, by Dr. R. van Someren, in Hope Dept., Oxford University Museum. Paratypes in the British, Oxford, Tring and Witley Museums.

pp. lxxix-lxxx). A similar female from Taveta, Kenya Colony, is represented in Nov. Zool. VII, 1900, pl. XII, fig. 6. Two of these mimetic forms (*d*) have been bred by Mr. Swynnerton, together with a male, and a female of the form (*b*) — all four from the eggs of a female parent (*b*). Another large family from a *swynnertoni* parent included 17 males and 14 *swynnertoni*. (For both these families see Proc. Ent. Soc., 1918, p. lxxx.) It is probable that a similar form exists among the females of *etheocles*, but where the two species exist together, as in Kenya Colony, a satisfactory decision can only be gained by breeding and examining the structure of the males in the families (p. 538).

The last female form of *ethalion*, with white markings, mimicking the female of *cithaeron*, is similar to the ♀-f. *rosae*, described from Delagoa Bay and hitherto considered to be a female *etheocles*, but evidence is much wanted (p. 538). The bearing of the Chirinda female forms upon the relationship of *ethalion* to *etheocles* was discussed by Dr. Jordan in a letter of 28 January 1915:

“The question of the status of *etheocles* and *ethalion* is encountered in very many instances. We are here on the border-land between species and subspecies. Originally *ethalion* was the southern subspecies and *etheocles* the tropical subspecies. The former having spread north and the latter south, the two overlap. I do not believe they interbreed, but should not be surprised if their *stations* in the districts where both occur were, as a rule, different. If we had no males of *ethalion* from Kenya Colony, the district S. of Kilimanjaro, and other parts of Tanganyika Territory, where *etheocles* also is found, i. e. in the tropics, I should be less reluctant to believe in the two insects interbreeding. On the other hand the occurrence of *rosae* at Chirinda with *ethalion* males suggests the conclusion that in this locality it is a female form of this species. I am afraid, we cannot solve the problem without more abundant material, there being apparently no structural differences between the females of *ethalion* and *etheocles*. The fact that female *rosae* has not been also evolved in Natal is perhaps explained by its southern position (monomorphism being often observed in outlying districts), and also by the absence of two models, the females of *cithaeron* and *violetta*, which occur further to the north at Chirinda, and other localities.”

Dr. Jordan's opinion remained the same five years later when he again wrote on 17 March 1920: “I am convinced that the four males from Chirinda which I have labelled *ethalion* are all the same insect as the Natal ones. We have such males from various places north of

the Zambesi, as well as one from the south shore of the Victoria Nyanza. I think there can also be no doubt that the four kinds of females (*a*, *b*, *d*, and *rosae*-like) you received with these males are *ethalion*. That one of these, with a white curved band on the forewing (♀-f. *rosae*), is unknown in Natal is strange, but is no argument against the assumption that the female of *ethalion* is polymorphic in the more tropical parts of eastern Africa."

These interesting letters emphasise the importance of breeding from known females, not only in Chirinda, but in localities such as Kenya Colony, where *ethalion* and *etheocles* are known to fly together. Sound conclusions can only be reached by these means.

2. *C. blanda kenyae* n. subsp. entering associations with *ethalion* and *etheocles*.

This new geographical race of *C. blanda* Rothsch., described below, was kindly sent to me in 1923 by Dr. V. G. L. van Someren, who wrote: "I have four males and three females. They all come from the Sokoke Forest at the coast of Kenya Colony, between Takaungu and Malindi, N. of Mombasa. I have taken *C. guderiana* in the same area. The shape of this new form is quite unlike that of *etheocles*, but they undoubtedly enter into association with it." A later letter also gave Rabai (14 m. N. W. of Mombasa) as a locality. Dr. Jordan, to whom I shewed the specimens, at once recognised them as a more northern race of *blanda*, from Mikindani, Tang. Terr. It is of great interest that Dr. van Someren has obtained the female, *blanda* ♀ being unknown.

C. b. kenyae certainly enters into association with *etheocles*, as Dr. van Someren states above. The male, in flight or resting with open wings at a little distance, would probably be indistinguishable from the *swynnertoni* ♀-f., while the female would as strongly resemble the *etheocles* ♀-f. or *ethalion* ♀-f. *a*. Thus the central model of the male is *C. cithaeron* ♂ with *violetta* ♂ (p. 538), that of the female, *brutus* (p. 536).

Dr. van Someren has received the following female forms from the localities of *C. b. kenyae* and also from Dalgube on the Kenya coast, just above Shimoni and Vanga: *rogersi*, *kiriki* (*albifascia*), *etheocles* and *rosae*. With these was a hitherto unknown form of male with silvery underside. *Rosae* mimics the female *cithaeron* (p. 538), while *kenyae* ♂ mimics its male.

Charaxes blanda Rothsch., n. subsp. *kenyae*.

Male. *Forewing*. — Apex even more falcate than in *blanda*, the bay in the outer margin being rather deeper. The 6 upper post-discal spots much larger and white, whereas in *blanda* they are blue with white centres in the 5 uppermost. The two discal spots beyond the end of cell are much larger and whiter. The 2 postdiscal blue spots in area 1 *b.* are fused and much larger, that in 1 *a.* twice as long. The blue spot in cell larger. The iridescent blue of F. and H. W. paler.

Hindwing. — The broad blue disco-postdiscal bar gives off a branch near the base of vein 6, the dark ground-colour forming a V between it and the bar. A very faint trace of this branch can be detected in *blanda*. The submarginal spots are much smaller.

Underside. — Very similar to *blanda*.

Female. — Much larger than male. Pattern similar, but much whiter and the blue when present much paler. All markings larger with outlines less defined. H. W. bar divides at vein 7. The underside resembles the male but with less contrast between the tints.

Length of F. W. — Male, 33.0 mm. female, 39.0 mm.

The male is the same size as the type of *b. blanda* kindly lent to me for comparison by Lord Rothschild. (The measurement of the specimen was erroneously given as 31.0 mm. instead of 33.0 mm.)

Type ♂ and paratype ♀ in Hope Dept., Oxford Univ. Museum, from Sokoke Forest, February, 1921: V. G. L. van Someren.

3. Descriptions of new female forms of *C. theocles theocles*

a) ♀-f. *aubyni* nov.

In this form of female all the principal markings are similar to those of the *etheocles* ♀-f., but of a very pale yellow or cream-colour.

Type in Hope Dept., Oxford Univ. Museum, from Dabida Mountain (3700 ft.), 2 July 1916: Canon Rogers.

♀-f. *aubyni*, which would resemble *brutus* on the wing (p. 536), appears to be common on Dabida Mountain, about 100 miles W. N. W. of Mombasa, and also occurs on Sagalla Mountain in the same district. It is a stable form; for Canon St. Aubyn Rogers has bred two such females and a male from the eggs of a similar female parent, taken in this locality. Furthermore, the pattern of the captured specimens is remarkably constant. Dr. Jordan kindly examined the male genitalia and found it to be a form of *etheocles* nearest *chanleri*.

A list of the males and female forms from Dabida is given on p. 555.

The stability of this pale-yellow-patterned form being proved and the male which was bred in the same family identified, it has stronger claims to a name than most ♀ forms of *etheocles*, and I dedicate it to the kind friend who obtained the evidence.

b) ♀-f. *vansomereni* nov.

This female differs from the ♀ *C. e. viola* in the F. W. being broader and its outer margin straighter; the white bar and the submarginal black of the H. W. broader. In the n. ♀-f. *albifascia* this submarginal black is broader still, the white bar narrower even than that of *viola*.

Type from Buyala, near Kampala, Uganda, Febr. 1924, Dr. R. van Someren: in the Hope Dept., Oxford University Museum. Paratypes from the Jinja district eastward to the N. E. corner of the Victoria Nyanza, in British, Oxford, Tring and Witley Museums.

This Uganda ♀-f. is probably transitional eastward into the ♀-f. *albifascia* in W. Kenya Colony. North of Uganda it is replaced by *viola*.

The pattern of this interesting ♀ form is very like the *ethalion* ♀-f. *c.* figured in Nov. Zool. VII, pl. XII, fig. 4, and could be derived from this by very slight and simple changes. The essential similarity will be realised by comparing the above fig. 4 with figs. 1 and 2 on pl. 15 of these Proceedings, remembering that the two figures represent butterflies belonging to the same bred family.

The fact that *vansomereni*, *protocedreatis*, *cedreatis*, and *carpen-teri*, are females of the male f. *picta* was demonstrated by Dr. V. G. L. van Someren and Dr. Robert van Someren (p. 478), and I have much pleasure in naming this form in commemoration of their valuable work.

c) ♀-f. *albifascia* nov.

Differs from *vansomereni* in the more extensive suffusion of the dark ground colour of F. W. with orange brown, especially towards the apex; the H. W. bar narrows from above downwards and there is a characteristic projection of its outer border in the angle between vein 3 and the cell, in area 3. This feature is common to the closely related forms *albifascia*, *kirki*, and *rogersi*. The breadth of the dark marginal zone of H. W. and narrowness of the bar have been mentioned under *vansomereni*.

Type, from Dabida Mountain, Kenya Col. (abt. 3700 ft.), 26 Jun. 1916, Canon Rogers, in Hope Dept., Oxford University Museum. This is the specimen described as "fully the ♀-f. *kirki*"

in Proc. Ent. Soc. Lond., 1918, p. lxxxii. The second example referred to as "very nearly" *kirki* was taken on 21 Jun. 1916.

Paratype from Itimba distr., Tang. Terr., Rev. G. Wood, in Brit. Museum. This ♀-f. is erroneously referred to as *kirki* in the above-quoted paper (pp. lxxxii, lxxxiii). The type of *kirki* is from Mamboya, Tang. Terr., and bears on the anterior half of the H. W. bar a very distinct and extensive brownish-orange flush, particularly between veins 5 and 7. Being unable to visit London at the time, I owe this description of the type to the kindness of Capt. Riley. It is therefore clear that the specimens described as transitional between *kirki* and *rogersi* (l. c.) are in reality *kirki*, while the forms with a white H. W. bar unshaded by orange are not *kirki*. As, furthermore, they play an important part in the evolution of other mimetic forms it is desirable that they should receive a name, and the one proposed, *albifascia*, emphasises the distinctive feature.

When a sufficiently long series of *etheocles* females has been collected in E. Uganda and W. Kenya Col. I believe it will be found that the white H. W. bar becomes narrower on the average from W. to E. From these comparatively narrow-barred more eastern specimens it is probable that the *albifascia* ♀-f. arose as a mimic of the male *C. ansorgei* in W. Kenya Colony. Evidence that *vansomereni* can give rise to *albifascia* is provided by a specimen taken by Dr. Neave on the Semliki Plains, near the S. shore of Lake Albert (2200 ft.), 25-27 Nov. 1911. This female, now in the British Museum, exhibits a pattern which is very nearly that of *albifascia*, the chief difference being the strong development of blue in the H. W. bar. If such a variety as this can arise in W. Uganda it is reasonable to suppose that it may have appeared in the more eastern area where, meeting with its model, the male *ansorgei*, it would become subject to selection.

Further eastward still in Kenya Colony *albifascia* came under the influence of the predominant *saturnus*, and the white H. W. bar became overspread in varying degrees by orange-brown, producing *kirki*, a mimic of the paler varieties of the model in Kenya and far to the south in Tang. Terr. Increase in the orange-brown finally displaced the white of the H. W. bar, thus leading to *rogersi*, mimicking the darker coloured *saturnus* in eastern Kenya. Although, I believe, that the three female forms arose in these areas respectively, all of them — *albifascia*, *kirki* and *rogersi* — fly together in E. Kenya and the first two in Tang. Terr. The presence of a co-mimic, the ♀ *guderiana*, would encourage the *kirki* forms which closely resemble

it. So far as our present knowledge goes this female, intermediate between the other two, appears to be commoner than either of them.

Varieties of *kirki* sometimes revert to the ancestral *etheocles* ♀-f. in the separation of the upper postdiscal and discal spots of the F. W., thus forming two rows instead of a broad bar. Such a specimen was collected by Dr. Neave on the Nandi Plateau, Kenya Col., 30 May—4 June 1911. A similar variety is present among the *kirki* females taken by Canon Rogers at Dabida.

It is of interest to record the males which were taken with *albifascia*, *kirki*, and *rogersi* by Canon Rogers, in the various localities:

Taveta. — 25 ♂ all *chanleri* (also 7 male *ethalion*), 1 *rogersi* (from Maketao between Taveta and Voi), 2 *kirki*—one of them, near *albifascia*, in cop. with *chanleri* ♂.

Dabida. — 3 ♂ near *chanleri* but with reduced pattern, 4 *aubyni*, 1 ? *aubyni* (worn), 1 ? *etheocles* (worn), 1 *aubyni* with infusion of *kirki* or *albifascia* (worn), this from Mlamba W. of Dabida, 1 *rosae*, 1 *albifascia* (type), 4 *kirki* (1 very near *albifascia*), 1 *rogersi* (type). Also the parent *aubyni* with 2 ♀ offspring of same form and 1 ♂ near *chanleri*.

Sagalla. — 4 ♂ of which 1 is *chanleri* and 3 are transitional to *picta* in the presence of 4 or 5 postdiscal spots in F. W.; 1 ? *aubyni* (worn), 1 *etheocles*, 1 *rogersi*.

Nairobi. — 1 *kirki*.

Kongwa (Tang. Terr., abt. 40 m. W. of Dar-es-Salaam). — 3 ♂ *ethalion*, 1 *kirki* very near *albifascia*.

d) ♀-f. *handari* nov.

Similar to f. *darja*, but on F. W. above the upper discal series more widely separated from the postdiscal, especially so at the third postdiscal spot which is more distally placed, and the series consequently more elbowed than in *darja*. Outside the F. W. band and inside the two last patches, also on both sides of the H. W. band, a blue scaling replaces the dull greenish blue of *darja*. On underside of F. W. a well-marked black patch in front of a double patch before tornus, and in H. W. the four black dots from anterior tail to anal angle are larger and more prominent than in *darja*.

Type from Handari (about 3500 ft.), about 10 miles E. of Mvumi and 250 m. W. of Dar-es-Salaam, Tang. Terr., in Hope Dept., Oxford Univ. Museum.

The only known example of this ♀-f. was taken by Canon St.

Aubyn Rogers, 8 May 1917. Two males of the form *chanleri* were captured in the same locality.

This female appears to belong to the *brutus*-centred combination, within which it is especially associated with the male of *C. achaemenes* (p. 536).

Being at the time unable to compare this ♀-f. with the type of *daria* I owe the above account of the differences in pattern and colour to my kind friend Dr. Jordan.

e) ♀-f. *protocedreatis* nov.

This interesting form exhibits the upperside pattern of *cedreatis* with certain ancestral features retained and the nearly uniform tawny olive replaced basally by a very dark brown with a tawny tinge, distally, in the H. W. and in areas 1 a. and 1 b. of F. W., by a pale olive zone which in two specimens out of three is more tawny than in *cedreatis*. This zone is palest in area 1 b. of F. W. over the site of the two white marks in *cedreatis*. In the hindwing of the two specimens mentioned above, the zone forms a postdiscal band with its upper section defined but its lower transitional into the dark internal surface of the wing. This band is faintly but unmistakably indicated in some specimens of *cedreatis*²⁰⁾ by a paler shade of olive. The third specimen more nearly approaches *cedreatis* in the olive tint of the zone and in its much greater and very gradual invasion of the internal surface along its whole length, especially in the H. W. The internal surface of both F. and H. W. is also rather more tawny and less dark. In all three specimens the external border of the zone is much less sharply defined than in *cedreatis*.

In the F. W. the 5 upper postdiscal spots of the *etheocles* ♀-f. are retained, blue (the uppermost white-centred) in two specimens, white with blue margins in the one which most nearly approaches *cedreatis*. In *cedreatis* the 2 uppermost are retained, much enlarged, as in *tiridates* and *numenes*, the other 3 having disappeared in most specimens, in others being represented vestigially by one or even two of the series. The 2 uppermost discal spots, blue or blue and white, are more distinctly indicated than in *cedreatis*. The oblique, white, central bar of the F. W. is faintly tinged with a tawny shade of which traces are sometimes seen in *cedreatis*.

The under surface does not differ from that of *cedreatis* more widely than specimens of *cedreatis* differ from one another.

²⁰⁾ It would be very interesting to determine the proportion of specimens which retain this pale band on the W. Coast as compared with Uganda.

The length of F. W. is from 41.0 to 44.0 mm. The ♀-f. *protocedreatis* is thus, like *cedreatis*, a very large female form of *etheocles*.

Type and two paratypes from the Jinja district, Uganda, 1923, V. G. L. van Someren: in the Hope Dept., Oxford Univ. Museum. The type (July) is intermediate between a relatively ancestral specimen (June 13) with a more clearly defined H. W. postdiscal band, and the one (June) which is most transitional towards *cedreatis*.

This ♀-form of *etheocles*, which I had never seen before and was also new to Dr. Jordan, was kindly sent to me in 1923 by Dr. V. G. L. van Someren, who agreed that "it is undoubtedly transitional to *cedreatis* of which form one gets many in the Jinja district. They occur in about equal numbers. I have had both forms emerge from pupae found on the food-tree." The ♀-*protocedreatis* has also been bred in the same family with the male *picta* by Dr. R. van Someren (p. 509). The pattern of *protocedreatis* is very similar to that of *vetula* Rothsch., from the Ogové R. (Nov. Zool., p. 488, pl. XII, fig. 8).

The pattern and the development of the tawny tint suggest that *protocedreatis* might readily develop into a member of the *Danaida-chrysippus*-centred association. It is possible that this colour may indicate the transference of allegiance from one association to another, but whatever be its past history, *protocedreatis* undoubtedly represents a stage towards the evolution of *cedreatis*. It is of the highest interest that this ancestral form should survive in considerable numbers in Uganda, close to the eastern limits of *cedreatis*, while it is unknown in the metropolis of *cedreatis* on the W. coast.

4. The female forms of *etheocles*: the mimics tabulated with their models.

The mimetic females of *etheocles*, joining different associations, are so scattered in these pages that it will be convenient to bring them together in one list, and the male forms in another; also to attempt to set forth in a scheme the lines of their evolution from the primitive pattern more or less represented by the *etheocles* ♀-f. and *ethalion* ♀-f. *a* and *b*.

Rothschild and Jordan in their great monograph (p. 477) group the mimetic females of *etheocles* as follows:

- "(1) similar to the ♂♂ or ♀♀ of the many other *Charaxes*, for instance, *ameliae* and *imperialis*;
- (2) similar to the male *etheocles*, the white markings of the upper-side having almost entirely disappeared;

- (3) similar to the ♀♀ of *Ch. violetta* and *cithaeron*;
 (4) similar to the ♀ of *Ch. bohemani*;
 (5) similar to the ♀♀ of *Ch. tiridates* and *numenes*;
 (6) similar to the ♂ of *Ch. bohemani*."

Aurivillius, in Seitz's Vol. XIII, Eng. Transl., points out on p. 136 that the females of *etheocles* "exactly mimic" other species of *Charaxes*; and he specially mentions on pp. 136-137 the following ♀ forms, *etheocles*, *regalis*, *manica*, and *cedreatis* with their respective models the females of *ameliae*, *imperialis*, *bohemani*, and *tiridates* (with *numenes*). He also, on p. 135, specially refers to the importance of breeding the forms.

In the following table the mimetic female forms are arranged in groups determined in part by the affinity between their patterns, in part by their geographical distribution.

Models Species of <i>Charaxes</i>	Mimetic females of <i>etheocles etheocles</i> and the female of <i>etheocles viola</i> .	Distribution.	Notes.
<i>C. tiridates</i> ♂ and <i>C. numenes</i> ♂	<i>alladinis</i> Butl., <i>virilis</i> Rothsch. and probably other ♂-like forms.	W. Africa.	Male-like patterns not necessarily derived directly from ♂
<i>C. etesipe</i> ♂	<i>carpenteri</i> Poulton.	Uganda and immediately adjacent Tang. Terr.	
<i>C. ameliae</i> ♀ See also <i>brutus</i> - centred association (p. 536).	<i>etheocles</i> Cram.	A member of the <i>brutus</i> -centred association over the whole range of <i>e. etheocles</i> . Within this association its chief model is the ♀ of <i>ameliae</i> .	The primitive female pattern so far as it exists.
<i>C. cynthia</i> ♀	<i>ochracea</i> Rothsch.	Tropical W. Africa.	Derived by simple changes from primitive female.
<i>C. imperialis</i> ♀	<i>regalis</i> Rothsch.		
<i>C. tiridates</i> ♀ and <i>numenes</i> ♀	<i>protocedreatis</i> nov. ♀-f.	Uganda.	<i>protocedreatis</i> a stage towards <i>cedreatis</i> . For details see p. 556, 557.
<i>C. tiridates</i> ♀ and <i>numenes</i> ♀	<i>cedreatis</i> Hew.	Tropical W. Coast to Uganda.	

Models Species of <i>Charaxes</i>	Mimetic females of <i>etheocles etheocles</i> and the female of <i>etheocles viola</i> .	Distribution.	Notes.
<i>C. epijasius</i>	<i>viola</i> ♀ of <i>etheocles viola</i> .	Hinterland of N. W. tropical Africa, Senegambia to Niger; Lado Enclave, Bahr-el-Ghazal, S. Sudan.	The only known ♀-f. of the subspecies. Derived from a ♀ such as Nov. Zool. VII, pl. XII, fig. 4.
<i>C. epijasius</i>	<i>vansomereni</i> nov. ♀-f.	N. Uganda.	} For evolution from W. to E. see pp. 553-555.
<i>C. ansorgei</i> ♂	<i>albifascia</i> nov. ♀-f.	Kenya Colony and Tang. Terr.	
<i>C. saturnus</i> model of transitional forms (<i>kirki</i>).	<i>kirki</i> Butl.	Kenya Colony and Tang. Terr.	
<i>C. saturnus</i>	<i>rogersi</i> Poul.	Kenya Colony and Tang. Terr.	
<i>C. achaemenes</i> ♂	<i>daria</i> Rothsch. and Jord.	The only ♀-f. known from Abyssinia.	Simply derived from primitive ♀
<i>C. achaemenes</i> ♂	<i>handari</i> nov. ♀-f.	Tang. Terr. (Handari, about 250 m. W. of Dar-es-Salaam.)	
<i>C. cithaeron</i> ♀	<i>rosae</i> ²¹) Butl.	E. Africa.	Transitional vars. connect <i>rosae</i> with the primitive ♀
<i>C. bohemani</i> ♂	<i>phaeus</i> Hew.	E. Africa from Tang. Terr. to Manicaland. N. Rhodesia, Angola.	Derived independently from primitive ♀ (p. 541), <i>manica</i> through a <i>rosae</i> -like stage.
<i>C. bohemani</i> ♀	<i>manica</i> Trim.		

The dark, nearly patternless *etheocles* females *alladinis* and *virilis* upon the wing are probably outlying members of the association with the male *tiridates* as its centre (p. 543). The ♀ *alladinis* with its purplish sheen is a better mimic than *virilis*. Male-like females of *etheocles* are generally rare in collections; but Mr. W. A. Lamborn sent me three with four males bred in 1913 from larvae collected indiscrimi-

²¹) The *swynnertoni* ♀ mimicking *cithaeron* ♂ is not included, as it has not yet been proved by breeding to be a ♀ form of *etheocles* as it has of *ethalion* (p. 550).

nately on *Adenantha pavonina* at Moor Plantation, near Ibadan, S. Nigeria. Furthermore, the late Mr. C. O. F a r q u h a r s o n sent me five females and three males bred in 1915, from the same food-plant in the same locality (Proc. Ent. Soc. Lond., 1918, p. lxxxiii; Trans., 1921, p. 402). Dr. J o r d a n, after seeing these specimens, suggested the possibility that they had been affected by artificial conditions. But two of Mr. Lamborn's larvae had only been in confinement seven and six days respectively before they became female pupae, while the size of all the eight females seems to prove that the conditions were perfectly healthy. Apart from these eight I have never received any females from this locality, and, on the whole, it seems to be probable that the majority or perhaps all the females are there male-like and mimics of the male *tiridates*²²). These *etheocles* females are nearer to *virilis* than *alladinis*, but they vary so greatly among themselves that I have hesitated to describe them. Until more material has been received it is better to regard them as forms of *virilis*. Their very variable and elusive markings are described in Proc. Ent. Soc. Lond., 1918, p. lxxxiv, where it is pointed out that, „although developed to a much fainter degree they greatly resemble those of *carpenteri*, a form which could probably be easily derived from variable male-like females such as these“.

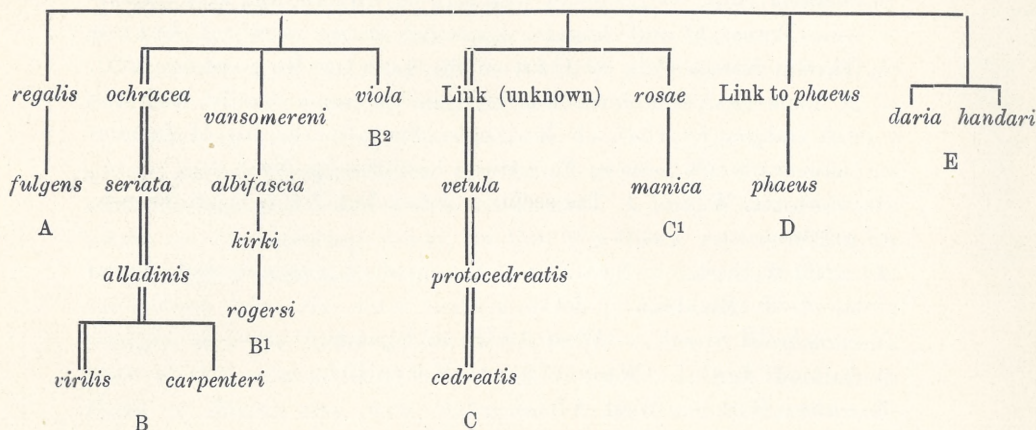
A male-like female near *carpenteri* occurs with this latter in Uganda. Dr. V. v a n S o m e r e n is inclined to think that it is distinct but breeding experiments are required.

5. Probable lines of evolution of the female forms in different parts of the range of *C. etheocles*.

The following scheme, drawn up with the kind help of Dr. J o r d a n, attempts to set forth the lines of evolution of the mimetic females of *etheocles* in the different geographical areas. The 16 female forms recorded in Nov. Zool. VII, pp. 486—88 are included in the scheme, with the exception of *lunigera* and *coryndoni* now considered to be the females of *fulgurata* (p. 541), and omitting *dewitzi*, of which our knowledge is insufficient.

²²) Male-like females of *etheocles* seem to be especially characteristic of the West Coast. In the Hill Museum, 2 *virilis* are from the Ivory Coast; of 2 *alladinis* one is certainly and the other possibly from the Upper Kasai River, while a fifth female from Coomassie is nearer to the eight S. Nigerian specimens and like them is not far from *carpenteri*.

Common ancestor an *etheocles* ♀ more or less like *ethalion* ♀ *c* (Nov. Zool., VII, 1900, pl. XII, fig. 4).



A. — West African forest region, the country of *Ch. imperialis*, model of *regalis*.

B. — West African forest region to Uganda and Tanganyika Terr. immediately S. of it.

B¹. — N. Uganda E. through Kenya Col.; then S. into Tanganyika Terr.

B². — Open country from Senegambia E. to Nile.

C. — West African forest region E. to Uganda. The single *vetula* from Ogové R.

C¹. — Corresponding forms of E. and S. Central Africa. A series in Brit. Museum, from Zimbiti, Port. E. Africa, clearly exhibits the transition from *rosae* to *manica*.

D. — E. and S. Central Africa. Absent with their models from W. Africa.

E. — *daria* is the only ♀-f. known in Abyssinia; the similar form *handari* is from Tang. Terr.

6. The male forms of *C. etheocles*.

The male forms of *e. etheocles* recognised by Rothschild and Jordan (ibid., pp. 483—85) are as follows, omitting No. 2 (*fulgurata*) which is treated as a distinct species (p. 541), and including 3a, *contraria*, from Aurivillius in Seitz. It will be seen that only Nos. 1, 3 and 4 can be associated with female forms on satisfactory evidence.

1. *picta* Rothsch. — E. Africa westward to Uganda. Proved by breed-

ing (p. 507) to be the male of the *carpenteri*, *vansomereni*, *proto-cedreatis*, and *cedreatis* females in the Jinja district.

3. *chanleri* Holl. — E. Africa westward to Unyoro, and S. to Rhodesia, Transvaal and Angola. Captured *in cop.* with ♀-f. *kirki* at Taveta, Kenya Col., by Canon St. Aubyn Rogers (p. 555). A male near this form was bred in the same family with the ♀-f. *aubyni* by Canon Rogers. See also the list of females taken with this male in E. African localities (p. 555).
- 3a. *contraria* Weym. — Tang. Terr. (Seitz, Vol. XIII, Engl. Transl., p. 136).
4. *cytila* Rothsch. — Nyasaland. Accompanying *manica* and *phaeus* in N. W. Rhodesia (p. 541).
5. *catachrous* Staud. — West Africa to Uganda.
6. *hollandi* Butl. — West Africa to Kenya Col.
7. *carteri* Butl. — West Africa.
8. *ephyra* Godt. — West Africa.
9. *lutacea* Rothsch. — Congo basin and Unyoro.
10. *violacea* Rothsch. — West Africa.

7. The male of *C. etheocles* as the model for the male of *C. opinatus* on Ruwenzori.

It is, I think, the most interesting fact in the whole subject of *Charaxes* mimicry that a male of the great train of mimetic female forms should itself act as a model. It is, in my opinion, hardly possible to imagine a stronger indirect proof that *Charaxes* mimicry is Müllerian or Synaposematic. I well remember the astonishment and delight with which I first looked at the three male specimens of *C. opinatus* in the British Museum and realised that they were evident allies of *C. anticlea* with the pattern so modified as to produce a strong superficial resemblance to the male of *etheocles*. In the words of Aurivillius (*ibid.*, p. 134), the male *opinatus* is "almost exactly like that of *etheocles* in shape and size."

The males of *anticlea* are black with a broad orange-brown margin to the hindwing, produced, gradually narrowing for a variable distance into the forewing. In the male *opinatus* the outer edge of this margin is retained, forming a narrow border to the hindwing, a border which, although extending further down the wing and entering the tails, obviously resembles the red border along part of the hindwing which is such a characteristic feature in many males of *etheocles*.

A series of submarginal, dark, white-centred spots on the hindwing of the male *anticlea* is represented in *opinatus* by a longer series of

blue, white-centred spots within the narrow orange border, closely resembling the series occupying a similar position in the male *etheocles*.

The tails of *opinatus* are long and slender, like those of *etheocles*, and quite unlike the short and stumpy appendages of *anticlea*.

Opinatus is of the same size as *etheocles* and considerably larger than *anticlea*, its expanse of wing being about one-fifth greater.

Believing that *C. opinatus* has been derived by selection from a species with a pattern similar to that of *anticlea* there remains one other inconspicuous feature of much interest. A line of obscure brown marks on the hindwing would, on this hypothesis, represent the internal edge of an orange band nearly as broad as that of *anticlea* but equidistant from the outer margin of the wing instead of nearly straight, as in the latter species. The question arises — Why should a trace of this internal edge have been retained? It may be that in flight or during rest with expanded wings, under certain conditions of light and shade, this obscure line promotes the resemblance to those males of *etheocles* which bear a row of semi-lunar blue marks in nearly the same position. In certain specimens these marks are brownish. Two male *etheocles* taken on Ruwenzori by the expedition which captured *opinatus* exhibit on the hind wing these blue marks²³) as well as the narrow red margin distinctly developed.

The colour and pattern of the under surface at once shows the close affinity of *opinatus* to *anticlea* and its true difference from *etheocles*. Nevertheless, this example of mimicry is so important and interesting that I did not wish to depend solely on colour and pattern, however clear the evidence given by them appeared to be. And I was all the more anxious to test the affinity by some other and more trustworthy criterion because my old friend Mr. F. A. Heron, in describing the species in *Trans. Zool. Soc.*, Vol. XIX, p. 156, has written — “Above, the species has the appearance of a member of the *C. ethalion* group, and below, resembles some ally of *C. anticlea*, thus apparently forming a link between these two divergent groups.”

With the consent of the authorities of the British Museum one of the specimens was submitted to Dr. Jordan who very kindly

²³) Resemblance in a male mimic to the pattern but not the colour of a model, preceding resemblance in colour as well as pattern by its more advanced female, has been described in the sexes of *Pseudacraea dolomena albostrigata* Lathy., f. *mim. dolabella* Hall (*Proc. Ent. Soc. Lond.*, 1924, pp. clxi, clxii). It must also be remembered that, although numerous forms are recognised among the males of *etheocles* (pp. 561, 562), the difference between their upperside patterns is not sufficient to prevent any one of them from acting as an appropriate model for *C. opinatus*.

examined the male armature and reported — "*opinatus* is close to *anticlea* in structure." We may therefore conclude that the resemblance to the male *etheocles* is superficial and not an incidental consequence of affinity.

The three males of *opinatus* were collected on the E. slopes of Ruwenzori in 1906, by the Hon. H. G. Legge and A. F. R. Wollaston — one (the type) at 5-7000 ft. on 2 March; two at 6-13000 ft. on 3 February. These are the only known examples of the species. The female is almost certain to be mimetic; for a non-mimetic female with a mimetic male is excessively rare in Lepidoptera. The fact that a western female of *anticlea* is a co-mimic with a female form of *etheocles* renders it probable that the female *opinatus* also resembles one of these forms, or, it may be that, like its own male, it mimics the male *etheocles*. Its capture will answer one of the most interesting questions which await solution in this genus and indeed in all African butterflies.

8. The male of *C. anticlea* mimicking the male of *C. protoclea*, and its female the female of *C. cynthia* in W. Africa.

The "remarkable upperside resemblance" borne by this small *Charaxes* to the large *C. protoclea*, to which it is "not nearly related" was pointed out as one of a series of such likenesses, by Rothschild and Jordan in 1900 (*ibid.*, pp. 285, 286). Reference to the classification will shew that the model belongs to the first and the mimic to the second of the two main sections into which the African *Charaxes* are divided. Furthermore, the rare female of *anticlea anticlea* on the tropical W. coast, becoming a co-mimic with the *ochracea* ♀ f. of *C. etheocles* (p. 558), mimics the female of *C. cynthia* and *lucretia*, two rather large species in the first section. A female *anticlea adusta* from the Cameroons in the Adams Collection (British Museum) has a broadened F. W. bar like that of a ♀ *cynthia* from the same area. When, however, we reach the eastern part of its range in Uganda and Kenya col. the bar of *a. adusta* ♀ is broader still, while that of *cynthia* and *lucretia* (in Uganda) remains narrow. So far as it is possible to conclude from the small number of specimens available, the *adusta* ♀, except perhaps in the Cameroons, ceases to mimic other *Charaxes* but appears to resemble rather strongly both sexes, but especially the female, of *Vanessula milca* Hew. The arrangement of the dark and light areas on the underside is also such as to promote a general resemblance between these two Nymphalines. Mr. Talbot has kindly examined the 7 *a. adusta* females from Angola, Congo and

Kenya Colony, in the Witley Museum and finds the bar variable in breadth but very wide as compared with that of *a. anticlea*. It is probable, as he suggests, that *adusta* ♀, *Vanessula milca*, and a few *Precis*, &c. are members of a rather elaborate association with certain species of *Planema* and *Acraea* at its centre.

The question arises — Why should the male *anticlea* or some form closely allied to it, have modified a pattern which mimicked the male *protoaclea*, utilising its fragments to promote the resemblance now borne by the male *opinatus* to the male of *etheocles*, a species in the same section as itself although belonging to another subgroup? We cannot answer the question with confidence, but further material may supply it. In the meantime it may be suggested that, as the change appears to have occurred on the slopes of Ruwenzori and probably other mountains surrounded by forests in which the model *protoaclea* exists, there is some condition associated with the station, it may be a direct or indirect effect of elevation, which prevents the entrance of this model but allows *etheocles* and *opinatus* to thrive unchecked.

H. The majority of the commonest species of *Charaxes* are mimics as well as models.

The consideration of *anticlea*, of which the male is a very common butterfly, and yet a mimic, naturally leads to the enquiry whether such resemblances are often observed among the commonest species of *Charaxes*. Some evidence on this subject will be found scattered through the preceding pages. As a further test I asked Dr. Jordan if he would tell me which, on the whole, are the commonest species in collections received by the Tring Museum. He kindly replied:

“In the Congo district *lucretius*, *brutus* and the male *etheocles* are the commonest species in collections; then follow *tiridates*, *varanes*, *candiope*, *protoaclea*, *castor*, *pollux*. On the east side of the continent the male *etheocles*, the male *achaemenes*, *saturnus*, *varanes* and *candiope* are generally in collections, even if nothing else. The male *etheocles* appears to be much in evidence everywhere.”

The outstanding abundance of the male *etheocles* has also struck me and I suppose everyone who receives collections from Africa between the Sahara and Natal. Breeding proves that the females are really as abundant as the males (p. 508) and their comparative rarity must be due to retiring habits which would render them much less often seen than the males by their natural enemies as well as by man. Nevertheless the numbers of the males seen on the wing and the fact

that the male acts as a model leads to the conclusion that the females also possess powers of resisting the attacks of enemies probably similar in kind although differing in degree from those of their models. The same considerations apply to *achaemenes* of which the male is very common and acts as a model for the *daria* female of *etheocles*. Among the other most abundant species the female of *protoclea azota* is probably a mimic of *varanes* (p. 527); *candiope* is an outlying mimic in the *fulvescens monitor* association (p. 525); *saturnus*, usually a model, mimics *castor* in Angola, and has developed into the race *harrisoni* mimicking *epijasius* in Uganda (p. 530); the female of *tiridates*, a central model for the females of other species, is itself a mimic of *Euphaedras* (p. 544). Thus the majority of the commonest African *Charaxes* may act as mimics as well as models — a conclusion which emphasises the Müllerian character of the associations into which they enter.

I. Protective resemblance on the under surface of African *Charaxes*: their mimics and models outside the genus.

It is interesting to note that Special Protective Resemblances are rare on the under surface of the larger African *Charaxes*. Doubtless many species are concealed when at rest by obliterative pattern or colouring, but special resemblances, *e. g.* to dead leaves, are only known in relatively few such as the *Varanes* Group (p. 503). When, however, we turn to the smaller, feebler species included in the Leptodontiæ many examples of such procryptic resemblances are found. The beautiful dead-leaf-like underside of the *neanthes* form of *zoolina* has already been described (p. 547); in *eupale* there is resemblance to a green leaf with indications of the high light on one side of a projecting midrib; in many, such as *porthos*, *zelica*, *laodice*, *lichas*, *paphianus*, *nichetes* and others, procryptic likeness, in various degrees of perfection, to dead leaves.

Among all the butterflies outside the genus I only know of one which can be safely looked upon as a mimic of *Charaxes*, and this is barely an exception, for it belongs to the closely related genus *Palla* (p. 525).

Salamis duprei Vins., the Madagascar Nymphaline, is remarkable for possessing two long tails to the H. W. — one the produced anal angle, the other a tail like that of other species of its genus, but greatly lengthened. Another feature is the exaggeration of the falcate

apex of F. W. It would be interesting to learn from naturalists on the spot whether there exists such an association between this species, *C. analava* and *antamboulou* that influence, perhaps reciprocal influence, is possible.

In the next category, that of *Charaxes* mimics of outside models, the resemblances of *C. baumanni* female and the *ethalion* ♀-*rosae*, to *Neptis agatha* (pp. 493, 536) are not included, as there is no reason to suppose that the presence of this butterfly has influenced their patterns. For the same reason *Papilio echerioides* ♂ and the similar pattern of its male allies in relation to *C. brutus* and *C. achaemenes* ♂ (p. 537) are omitted.

Charaxes acraeoides Druce, ♂ — Cameroons. When my friend the late Mr. Herbert Druce shewed me his specimen (at that time unique) I was at once struck with its close resemblance to *Pseudacraea clarki* which also occurs in the Cameroons. Aurivillius has recorded the likeness (*ibid.*, p. 138). Dr. Jordan informs me that "the pattern of the F. W. beneath is similar to that of *jahlusa* and *zingha* in the presence of internervular lines, as in many other *Nymphalinae*, but not in other *Charaxes*. In structure, however, *acraeoides* is different and was probably derived from the *jasius-saturnus* group and thus belongs to Section I, whereas *jahlusa* and *zingha*, structurally near together, are placed in Section II". Dr. Jordan also notes the mimetic resemblance, but adds — "The white subapical band of *acraeoides* is normally absent from *clarki*. Both have dark internervular lines on forewing, like *Acraea egina*."

C. acraeoides ♂ is apparently a member of an association of black and red male butterflies of which *Acraea egina* is the centre. Other members are *Ps. clarki* (especially the *f. egina* Auriv.), *Ps. boisduvali* Dbl., and *Papilio ridleyanus* White.

A list of *Charaxes* mimics of models outside the genus is given in tabular form below:

Species of <i>Charaxes</i>	Models
<i>C. j. jasius</i>	<i>Nymphalinae</i> <i>Euwanesa antiopa?</i> (p. 533)
<i>C. tiridates</i> ♀ <i>C. numenes</i> ♀ and their <i>Charaxes</i> mimics	<i>Nymphalinae</i> Species of <i>Euphaedra</i> (p. 544)

Species of <i>Charaxes</i>	Models
<i>C. x. xiphares</i> ♀ <i>C. x. nandina</i> ♀	<i>Danainae</i> <i>Amauris echeria</i> " <i>albimaculata</i> (p. 545)
<i>C. lydiae</i> ♀ ²⁴⁾ Female unique, male unknown	Day-flying moths of the Lymantrid genus <i>Nyctemera</i> , <i>Cymothoe beckeri</i> H.-Sch. ♀ (Nymphalinae) being a co-mimic
<i>C. acraeoides</i> ♂ Male very rare, female unknown	<i>Nymphalinae</i> <i>Pseudacraea clarki</i> Butl. <i>Acraeinae</i> <i>A. egina</i> Cram. ♂
<i>C. zoolina</i> , f. <i>a. neanthes</i> (p. 547) <i>C. lichas</i> } Probably with their <i>C. jahlusa</i> } allies ²⁵⁾	<i>Nymphalinae</i> <i>Atella phalantha</i> Drury " <i>columbina</i> Cram. <i>Lachnoptera ayresi</i> Trim.
<i>C. zoolina</i> , forms <i>b</i> , of the species and races of this group	<i>Pierinae</i> Common type of Pierine pattern (p. 547)
<i>C. zingha</i> ♂ ²⁶⁾	<i>Acraeinae</i> One of the larger red and black Acraeas such as <i>egina</i> ♂, but only dring uflight
<i>C. anticlea</i> ♀	<i>Nymphalinae</i> Although a mimic of <i>C. cynthia</i> ♀ in the west, the ♀- <i>anticlea</i> appears to mimic <i>Vanessula milca</i> and its associates in the eastern part of its range (p. 564)

24) Dr. Jordan kindly called my attention to this remarkable example and has written the following note upon the two co-mimics and their models; "I do not think that *Char. lydiae* has been independently influenced by *Cym. beckeri*; the forewings of the two exhibit only a very superficial resemblance. *Char. lydiae* occurs in the area of *Nyctemera phanax* Jord. and *N. vesperina jonesi* Sharpe; it resembles the females and the white form of the males of both. *Cym. beckeri* has a more extended range, occurring in the areas of the above two species of *Nyctemera* as well as in the area of *N. hesperia* Cr., which does not go south beyond the Niger; this *N. hesperia* is similar in both sexes to *beckeri* ♀."

25) Dr. V. G. L. van Someren has observed the strong likeness of *jahlusa* to *Lachnoptera ayresi*. Dr. Carpenter has taken *lichas bebra* drinking at mud in company with two *Atella columbina*, in Tang. Terr., a little S. of Uganda.

26) The pattern is not *Acraea*-like. The Acraeoid colouring is recorded by Rothschild and Jordan (*ibid.*, p. 455). Dr. V. van Someren informs me that the female on the wing resembles *C. pollux*.

K. Classification of the African Species of
Charaxes, with the single Palaearctic subspecies
C. jasius jasius.

The number and page, thus [22. a, p. 357], after the name of species or subspecies in the following list, give the reference to Nov. Zool., VII; 1900, where the literature and geographical distribution as then known will be found. Localities *after* the bracket record more recent information.

The date of publication, and distribution, thus "(1903) — Tang. Terr.", are appended to species or subspecies described since the appearance of Nov. Zool., VII. It has not been considered necessary to indicate the localities of aberrations.

African species of *Charaxes*, with the single Palaearctic subspecies
C. jasius jasius L.

I. HADRODONTIAE. Costal margin of forewing coarsely serrate.

A. *Varanes* Group²⁷).

1. *varanes varanes* Cram. (= *austrinus* Rothsch.)
[22. a, p. 357].
ab. *brachycauda* Le Cerf. (1923).
— *vologeses* Mab. [22. b, p. 358].
2. *fulvescens fulvescens* Auriv. [23. a, p. 361].
— *monitor* Rothsch. [23. b, p. 361].
— *saperanus* n. n. (= *comoranus* Auriv. 1909: nec Rothsch.
1903). — Mayotte I.
— *acuminatus* Thureau (1903) — Tang. Terr.
3. *balfouri* Butl. [24, p. 361].
4. *analava* Ward [25, p. 362].

B. *Candiope* Group.

5. *candiope candiope* Godt. [26. a, p. 366].
— *velox* Grant [26. c, p. 368].
— *thomasius* Stgr. [26, b, p. 367].
6. *antamboulou* Luc. [27, p. 368].
7. *cowani* Butl. [28, p. 370].

²⁷) This group is closely related to the Oriental species. Apart from the secondary whitening of upper surface and the leaf-like modification of the under, the pattern is ancestral, as is to be seen in the lines on the basal half of the hindwing under surface which run across the cell towards the abdominal margin.

C. *Cynthia* Group.

8. *protoclea protoclea* Feisth. [44, p. 403].
 ab. *marginepuncta* Holland (1920).
 ab. *nigropunctata* Neustett. (1916).
 — *nothodes* Jord. (1911). — W. of L. Tanganyika.
 — *azota* Hew. [43, p. 401].
 ab. ♂ *aequidistans* Gaede (1918).
 ab. *nyasana* Butl. [43, p. 403].
9. *boueti boueti* Feisth.²⁸⁾ [46. b, p. 410] Also N. Nigeria.
 — *lasti* Gr.-Sm. (= var. *alticola* Grünb. 1912) [46. a, p. 409].
 — *rectans* Rothsch. and Jord. (1903). — Abyssinia.
10. *cynthia* Butl. [45, p. 405].
 ab. *wawamba* Grünb. (1912).
 ab. *kinduana* Le Cerf (1923).

D. *Lucretius* Group.

11. *lucretius* Cram. [47, p. 410].
 ab. *caliginosa* Le Cerf (1923).
 ab. *lucida* Le Cerf (1923).
 ab. ♀ *albofascia* Le Cerf (1923).
12. *odysseus* Stgr. [48, p. 413].
13. *lactetinctus* Karsch [49, p. 414].

E. *Jasius* Group.Subgroup α .

14. *jasius jasius* L. [61, p. 446].
 — *epijasius* Reiche [62, p. 450].
 ab. *murina* Le Cerf (1923).
 ab. *feisthameli* Le Cerf (1923).
15. *pelias pelias* Cram. [60. b, p. 445].
 — *liberiae* Le Cerf (1923). — Liberia.
 — *pagenstecheri* Schultze (1913). — S. Abyssinia.
 — *saturnus* Butl. [60. a, p. 444].
 ab. *laticinctus* Butl. [60. a', p. 444].
 — *brunnescens* Rothsch. (1899) [60. b', p. 455].
 Congo, Angola.
 — *harrisoni* E. M. Sharpe (1904). — Kenya Col.²⁹⁾
 Uganda.

²⁸⁾ The relation of the races of *Ch. boueti* to each other and to *Ch. cynthia* requires further investigation.

²⁹⁾ The type is labelled "Kamagombo, S. Kavirondo: 24. Jan. 1903. A. H. Harrison".

16. *hansali hansali* Feld. [59, p. 440].
 — *baringana* Rothsch. (1905). —
 L. Baringo, Kenya Colony.
17. *castor castor* Cram. [58. b, p. 439].
 ab. ♀ *antiqua* Le Cerf (1923).
 — *flavifasciatus* Butl. [58. a, p. 438].
 — *comoranus* Rothsch. (1903). — Grt. Comoro.

Subgroup β.

18. *brutus brutus* Cram. [57. d, p. 433].
 — *natalensis* Stgr. [57. e, p. 433].
 — *angustus* Rothsch. [57. c, p. 432].
 ab. *fractifascia* Le Cerf (1923).
 — *andara* Ward [57. f, p. 435].
 — *junius* Oberth. [57. a, p. 431].
 — *somalicus* Rothsch. [57. b, p. 432].
19. *ansorgei* Rothsch. [56, p. 428].
20. *pollux pollux* Cram. [55. b, p. 426].
 — *geminus* Rothsch. [55. a, p. 427].
21. *phoebus* Butl. [54, p. 424].

Subgroup γ.

22. *druceanus druceanus* Butl. — [50, p. 415].
 — *kivuensis* Jord. (1925). — L. Kivu.
 — *proximans* Joic. and Talb. (1922). — C. and E. Africa.
23. *phraortes* Dbl. [53, p. 422].
24. *andranodorus* Mab. [52, p. 420].
25. *eudoxus eudoxus* Drury [51. a, p. 419].
 — *mechowi* Rothsch. [51. b, p. 419].
 — *cabecus* Jord. (1925). — Uganda.
26. *fallax* Richelm. (1913). — Cameroons.

F. *Tiridates* Group.

Subgroup α

27. *violetta* H. Gr.-Sm. [30, p. 372].
28. *numenes numenes* Hew. [29, p. 371].
 — *neumanni* Rothsch. (1902). — Abyssinia.

Subgroup β.

29. *bohemani* Feld. [31, p. 374].
30. *cithaeron cithaeron* Feld.³⁰⁾ [33, p. 379].
 — *kennethi* n. subsp. — Coast region of Kenya Col.

³⁰⁾ The relation of the Nairobi and Uganda races to each other and to *Ch. brevicaudatus* requires investigation.

31. *brevicaudatus* Schultze (1914). — E. Africa.
 32. *smaragdalis smaragdalis* Butl. [34. a, p. 384].
 — *orientalis* Joic. and Talb. (1918). — E. Africa.
 — *butleri* Rothsch. [34. b, p. 385].
 33. *monteiri* Stgr. [35, p. 385].
 34. *tiridates tiridates* Cram. [36, p. 387].
 — *marginatus* R. and J. (1903). — Abyssinia.
 35. *mixtus* Rothsch. [38, p. 390].
 36. *bubastis* Schultze (1916). — Cameroons.
 37. *bipunctatus* Rothsch. [37, p. 390].

Subgroup γ .

38. *xiphares xiphares* Cram. [32, p. 376].
 — *nandina* Rothsch. (1901). — E. Africa.

Subgroup δ .

39. *ameliae ameliae* Doumet. [39, p. 391].
 — *amelina* Joic. and Talb. (1925). — Nyasaland.
 40. *imperialis imperialis* Butl. (40, p. 394).
 — *albipuncta* Joic. and Talb. (1921). — Cameroons S'ward.
 41. *pythodorus pythodorus* Hew. [41. a, p. 398].
 — *nesaea* H. Gr.-Sm. [41. b, p. 398].

The Nandi specimens are 41. a.

G. *Hadrianus* Group.³¹⁾

42. *hadrianus* Ward [42, p. 398].
 43. *lydiae* Holland (1917). — Cameroons.

H. *Nobilis* Group.

44. *nobilis* Druce [88, p. 512].
 45. *superbus* Schultze (1909). — Cameroons.
 46. *acraeoides* Druce (1908). — Cameroons.

II. LEPTODONTIAE. Costal margin of forewing finely serrate.

I. *Zoolina* Group.³²⁾

47. *kahldeni* Homeyer
 Form a. *homeyeri* (= *W-brunnea* Beth.-Bak.)
 [91, p. 520].
 ab. *bellus* Strand (1914).

Form b. *kahldeni* [90, p. 519].

Extends to Semliki Valley, W. Uganda.

³¹⁾ Closely related to the preceding group — a derivative from the *ameliae* Subgroup.

³²⁾ From Dr. Jordan's classification in Proc. Ent. Soc. Lond., 1908, pp. lxx, lxx.

48. *zoolina zoolina* Westw.Form *a. neanthes* Hew. [93. *a*, p. 523].ab. *obscuratus* Suff. (1904).,, *b. zoolina* Westw. [89. *a*, p. 517].— *ehmkei* Dew.Form *a. ehmkei* Dew. [92, p. 521].,, *b. phanera* Jord. (1908). — N. Angola.— *betsimiseraka* Luc.Form *a. betanimena* Luc. [93. *b*, p. 524].ab. *andriba* Ward (1873).,, *b. betsimiseraka* Luc. [89. *b*, p. 518].J. *Eupale* Group.49. *eupale eupale* Drury [87. *a*, p. 511].— *latimargo* Joic. and Talb. (1921). — Cameroons S'ward.— *dilutus* Rothsch. [87. *b*, p. 512].50. *subornatus subornatus* Schultze (1916). — Cameroons.— *minor* Joic. and Talb. (1921). — Ituri, Nairobi.K. *Jahlusa* Group.51. *jahlusa jahlusa* Trim. [86. *a*, p. 509].— *argynnides* Westw. [86. *b*, p. 509].— *kenyensis* Joic. and Talb. (1925). — Mombasa, Teita.L. *Lichas* Group.52. *lichas lichas* Dbl. [85. *a*, p. 506].ab. *othello* Suff. (1904).— *bebra* Rothsch. [85. *b*, p. 507].53. *paphianus paphianus* Ward [84, p. 502].— *subpallida* Joic. and Talb. (1925). — E. Congo and Uganda.M. *Zingha* Group.54. *zingha* Stoll [63, p. 452].N. *Etesipe* Group.55. *etesipe etesipe* Godt. [64. *d*, p. 459].— *abyssinicus* Rothsch. [64. *c*, p. 458].— *tavetensis* Rothsch. [64. *b*, p. 458].— *cacuthis* Hew. [64. *a*, p. 457].56. *penricei penricei* Rothsch. (= *peculiaris* Lathy) [65, p. 460].— *dealbata* Joic. and Talb. (1922). — Angola.57. *achaemenes* Feld. [66, p. 460].ab. *fasciatus* Suff. (1904).ab. ♀ *monticola* Joic. and Talb. (1925).

O. *Etheocles* Group.Subgroup α .

58. *anticlea anticlea* Drury [77. a, p. 494].
 — *adusta* Rothsch. [77. b, p. 494].
 59. *opinatus* Heron (1909). — Ruwenzori.
 60. *baumanni* Rghfr. [76, p. 491].
 61. *thysi* Capron. [75, p. 490].
 62. *hildebrandti* Dew. [68, p. 469].
 63. *blanda blanda* Rothsch. [69, p. 471].
 — *kenyae* n. subsp. — Coast region of Kenya Col.

Subgroup β .

64. *kheili kheili* Stgr. [71, p. 473].
 — *northcotti* Rothsch. [70, p. 472].
 65. *guderiana* Dew. [72, p. 473].
 66. *etheocles etheocles*³³) Cram. (= *kitungulensis* Strand)
 [74. a, p. 481].
 — *viola* Butl. [74. b, p. 488].
 — *pembanus* Jord. (1925). — Pemba I.
 67. *fulgurata* Auriv. [74. a, p. 483].
 68. *ethalion* Boisd. [73, p. 478].

P. *Nichetes* Group.

69. *nichetes nichetes* H. Gr.-Sm. [83. b, p. 502].
 — *leoninus* Butl. [83. a, p. 501].

Q. *Laodice* Group.Subgroup α .

70. *porthos porthos* H. Gr.-Sm. [80, p. 497].
 — *dummeri* Joic. and Talb. (1922). — Uganda.
 71. *zelica* Butl. [81, p. 498].
 72. *laodice* Drury [82, p. 498].

Subgroup β .

73. *mycerina* Godt. [78, p. 494].
 74. *doubledayi* Auriv. [79, p. 496].

Discussion:

W. R. Thompson asks: what will occur if the small species of *Charaxes* is attacked first, and how does one explain the lack of resemblances in the males? Either resemblance should be developed, which it is not, or resemblance is not essential and the explanation lapses.

³³) The numerous male and female forms are given on pp. 552-562.

A n s w e r. — It is hardly necessary to say that mimicry is of no value against an enemy which has not seen the model; but enemies are unlikely to remain without this experience for more than a small fraction of their lives. Mimicry is of course well known in the males of sexually monomorphic *Charaxes*. When, however, the patterns of male and female are different and are associated with sex, selection will act independently upon each of them and will exert greater pressure upon the female and also have more chances of exerting such pressure, because (1) a female is of greater value to the species than a male; (2) females are in greater danger than males, being less active because laden with eggs which, furthermore, they must pause to deposit; (3) females are more variable than males, as is proved by the prevalence of female polymorphism apart from mimicry.



