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**An investigation into the Defences of Butterflies
of the genus Charaxes**



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An investigation into the Defences of Butterflies of the genus *Charaxes*.

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(With plate 14.)

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Introductory Note.

An investigation into the *raison d'être* of the exceptionally interesting polymorphic mimicry (for so it seemed to be) of several of the larger species of *Charaxes* by the females of certain small species (*C. ethalion* Bdv. and *C. theocles* Cr.) was suggested to me in 1909 both by Dr. G. A. K. Marshall and by Prof. E. B. Poulton.

Flight so difficult as to become deterrent (after vain attempt) to attack by birds had been suggested as the quality in virtue of which the larger species were worth mimicking.

I had already devoted much attention to the food preferences of birds and, having used large numbers of *Charaxes* in the course of these experiments, I believed that their chief deterrent quality was known to me. It seemed well, however, to test by a few special experiments the validity of my conclusion, and, in general, to investigate somewhat more fully the defences of the available species in Chirinda Forest, South-Eastern Rhodesia, a most excellent locality for *Charaxes*, and including *C. ethalion*, one of the polymorphic mimics we were especially anxious to study.

I would like to take this opportunity of thanking Prof. Poulton

warmly for the great trouble he is taking in presenting this paper and seeing it through the press.

ENEMIES OF *CHARAXES*.

I have myself witnessed and made records of attacks on large *Charaxes* by a wild Roller (*Coracias caudatus* L.), wild Bee-eaters (*Merops apiaster* L.) and a Drongo (*Dicrurus ludwigi* Smith); by two Kingfishers, *Halcyon orientalis* Peters, and *Ispidina natalensis* Smith, the small size of the latter being made up for by its wide bill and consequent capacity for swallowing large objects whole; also by a very small Hawk, not quite certainly identified but probably the Pigmy Falcon, *Poliohierax semitorquatus* Smith.

The attacks by the three first-named species were on *Charaxes* in flight, when the upper surface would be fully displayed; but such attempts would hardly conduce towards their mimicry by *C. ethalion*, etc.; for even the larger *Charaxes* are not very appreciably protected in relation to these powerful birds. The attacks by the Roller and Hawk were of a systematic nature, and I have little doubt that the large species of *Charaxes* have many very formidable enemies, capable of contributing heavily to the production of the procryptic element in their under-sides and their habits.

I have also a record by a native — but I have reason to believe it trustworthy — of a successful attack by a very small Flycatcher (*Trochocercus albonotatus swynnertoni* Neum.) on a male *Charaxes ethalion*. This, if accepted, is of importance as showing that even the very smallest of our butterfly-eating birds may successfully attack this mimetic species.

The larger species amongst my captive birds used to attack all species of *Charaxes* with the greatest readiness, and there can be no doubt that birds, in East and South-East Africa, are extremely important enemies of the genus. Wild Bee-eaters (*M. apiaster*) readily attacked, although not always successfully, the *Charaxes* that I released for them. Wild lizards (large specimens of *Mabuia striata* Peters) to which I have offered dead *Charaxes* have attacked and eaten them, but I doubt whether lizards are, with us, of importance in this connection. The larger *Mantidac* are more serious enemies and I quote the following observation to show how even a relatively small species (*Phyllocrania paradoxa* Burm.) may successfully attack a *Charaxes* that is a good deal larger and stronger than itself. But Mantidae are of little importance in relation to mimicry in this genus.

Extract from notes on a wild Mantis

(Phyllocrania paradoxa).

The observation was made on 13th October 1909, when the *Mantis* was seen to stalk and attack a *Charaxes* feeding on a growing banana bunch:

"... I never thought that the Mantis would attack from here. Still less that it would succeed — the distance (which I afterwards measured) from its own centre of equilibrium to the butterfly's costa being exactly 2½ inches. Suddenly the butterfly was lying on its side, its wings grasped by the powerful claspers, and the Mantis was hurriedly eating through the costa. The whole thing happened so quickly and quietly that a *Charaxes candiope* Godt. that was touching its fallen companion was not disturbed in the least. Whether the Mantis now released its hold to seize lower down I do not know, but the butterfly, which had been prevented from struggling by the fact that both costae were seized at once, slipped from its grasp and fluttered feebly to some rank vegetation close by — its disablement the result of the eating through of the costal nervures of the forewing, an operation that had taken only a few seconds. The Mantis again went through the performance of 'cleaning its nails', an occasional turn of the head in the appropriate direction showing that it was keeping all the time a keen eye on all arrivals, movements and departures; but for a long time no butterfly came within reach. At last another *C. candiope* (a small specimen) settled where its predecessor had been, but heading slightly away from the Mantis. Nevertheless the latter had a try and again pulled the butterfly over on to its side. But it was only the hind wings that were caught. The claws at once pulled through them, producing the lacerated appearance one sometimes sees in captured butterflies, and the butterfly escaped. Its commotion and flutter roused the others and all went off."

Special Exposure to Danger when Feeding.

When feeding, *Charaxes* tend to be distinctly conspicuous. Often they are massed in numbers at highly exposed fruits, and even when only in ones or twos or threes at smaller, isolated fruits or at gum exuding from bark, their frequent shiftings of position, the continuous slight nodding movement as the proboscis is pushed up and down in the pulp, the arrivals and departures, the buttings and pushings and flappings to dislodge more fortunately placed neighbours, the effect of pushing by species of *Neptunides* and other strong Cetoniid beetles swarming over the same fruits, the openings and shuttings of the wings for balance as their owner clambers over the fruit should it be small, and the occasional vivid display of the more wary individuals, all tend to catch the eye. The white bar on the upper surface — or the under when light is strongly transmitted — of a non-heliotroping, feeding *Charaxes brutus* Cr. is sometimes a conspicuous object from a distance, and still more so is its owner when, as occasionally happens, one finds it hanging from some small fruit (as of *Rauwolfia inebrians* K. Schum.), in a blaze of sun with the wings half

or fully spread. In a special observation that I carried out in March 1911 on *Charaxes* feeding at the fruits of a huge *Rauwolfia* on the outskirts of the Chirinda Forest, I found that, turning round suddenly to look at the tree at fifteen paces from its outermost branches (far more than enough in relation to bird enemies), my eye was every time caught, here by the movements, there by the form and colours, of the butterflies at various points all over the tree, and that by continuing to look for a few moments I could see and recognise many more; but that, turning at as far away as fifty paces, I detected and recognised similarly only two feeding butterflies, a *C. brutus* and a *C. candiope*, both with the sun shining on them. The glossy flashing leaves of the *Rauwolfia* were however, the chief concealing factor here, and I could still recognise and easily distinguish from the Cetoniids the various butterflies as they flew out, and circled round or hovered over a new fruit. At 105 paces I could still see these movements, detecting the Cetoniids less easily than before, yet distinguishing them at once from the butterflies by their smaller size and less erratic flight. I found it hard to distinguish the *species* of the *Charaxes* at this distance excepting where once or twice the sun shone full on the upper surface of a *C. candiope* turned towards me.

All this, of course, in relation to their natural enemies, is the height of conspicuousness. It is true that when they happen to be feeding on excreta or fallen fruit, when these are amongst dead leaves (as in the observation quoted on p —), they are much less conspicuous and occasionally very difficult to detect. Yet even here their movements sometimes quickly betray them. I have walked round a row of large guava bushes, the ground below thickly littered with fallen leaves, and made a note of the *Charaxes* I have seen feeding amongst them. Immediately going round again, this time „beating“ with my net, I found I had only missed one. And, curiously, it is just at these times, when they are often so conspicuous, that *Charaxes* tend to become completely absorbed and indifferent to danger, although the indifference will disappear and may even give way to the most extraordinary wariness in response to oft-repeated attack.

That birds may learn to frequent fruits for the express purpose of preying on *Charaxes* was shown by my as yet unpublished observations on a Hawk and a Roller, to say nothing of the fact that a search under my orange trees (when the fruit was ripe and *Charaxes* plentiful) always revealed many fragments of battered-off wings and, more than once, a disabled *Charaxes* that some bird had evidently failed to reduce to a condition in which it could be swallowed.

Defences of *Charaxes*.

A. Nauseous qualities.

I have used, I suppose, some hundreds of *Charaxes* of various species in my general preference experiments on numerous birds and one or two mammals, but have failed to obtain any good evidence of nauseous qualities in any butterfly of this genus. It is true that *C. neanthes* Hew. and its white form *zoolina* Westw. have sometimes been treated with what seemed to be marked suspicion, and have even been rejected after acceptance, but I have thought it possible that this was not on their own merits but, rather owing to the rough likeness of the *neanthes* form to *Atella phalantha* Dr. which is slightly distasteful, and of *zoolina* to a Pierine such as *Belenois*, which is rather considerably so. Even the trials resulting in immediate rejection that occur in the experiments I am about to describe were unmistakably trials for „feel“, not for taste. Texture is recognised by a mere perfunctory pressure with the extreme point of the bill such as one learns to distinguish from the method employed when other qualities are being tested.

It is possible, nevertheless, that some of the smaller species may yet be found to supplement their lack of strength by some degree of nauseousness, and the undersides of one or two species of *Charaxes* that I have not had the opportunity of testing, such as *C. epijasius* Reiche, certainly suggest that they could not be worn with impunity unless accompanied by some unpleasantness.

There can be little doubt, however, that the quality in virtue of which *C. ethalion* and *C. etheocles* mimic their larger cousins is not nauseousness.

B. Difficult flight.

The flight of *Charaxes* is undoubtedly difficult. Strength, large inequalities, speed on occasion and strenuousness are more or less characteristic of all the species that are known to me. But, in a genus the members of which become so lazy with security and so ultra-wary and dashing and active with persecution, it is very difficult to draw trustworthy distinctions between the different species. There is something distinctive in the flight of *C. varanes vologeses* Mab., and in general it is true that strength of wing, like „fighting weight“, may be measured in the genus by size of thorax; yet even so small a species as *C. ethalion* possesses, in the appropriate circumstances, a most dashing flight, great dodging power and immense wariness. Of the four commonest large species I can safely say that *C. cithaeron* Fell.

is more dashing and difficult to catch than *C. brutus*, *C. candiope* or *C. pollux* Cr. and this fact is again correlated with its possession of a more muscular thorax; yet its greater scarcity may also contribute to it by increasing its liability to experimental attack.

The larger *Charaxes*, when upon the wing, are difficult for birds to seize successfully, owing to their great strength which enables them to break away if held loosely or merely by one wing, and strength may thus deter many birds from attacking both them and their mimics; but this method of escape comes rather under the heading of „fighting weight“ to be discussed below, than under swift or skilful flight. In the latter qualities alone I do not think that there is really sufficient difference between the powers of the model and the mimic to render the superficial resemblance of selective value.

A further relevant point is the fact that even a large *Charaxes* when attacked by a bird, very commonly abandons flight and dashes to the nearest cover, most usually the ground. It then remains perfectly motionless with closed wings until the danger is past. A large *Charaxes* that I had seen escape in this way from a Drongo remained motionless while the bird vainly searched for it: the butterfly finally permitted me to pick it up by the wings. This habit may contribute to explain the fact that most of the specimens in my eye-spot experiments (Section F, p. 494) had obviously been damaged while at rest.

C. Wariness.

The great wariness of *Charaxes* is best displayed by their frequent indecision before settling down to feed — an indecision that, in *C. brutus* especially, is very commonly accompanied by a great display of the upper side coloration. The behaviour almost suggests that the butterflies are determined to show themselves thoroughly to any lurking enemy, to deter him if disinclined for that particular prey, or, otherwise, to draw any attacks that may be forthcoming while the insect is still alert enough to outwit them. *C. brutus*, when making this display — and, for that matter, at other times — has often reminded me strongly of *Papilio echerioides* Trim., which is quite highly distasteful. *Charaxes cithaeron* sometimes indulges in an intricate display of its own.

A *Charaxes* will often fly straight to the fruit, settle and close its wings; at other times it will display as already described, or it may circle round and round every stem and leaf as though searching for a hidden enemy, or perhaps in the attempt to show itself to one, for there is usually much special display of the upper surface. I have myself

been apparently subjected to exhaustive inspection by individual *Charaxes* that were coming to fruit beside me and at the last moment evidently noticed and suspected me. They would fly round and round, then settle on some leaf facing me, then again fly round me, before perhaps going off altogether. Or they might merely (as *C. candiope* has often done) fly up to some large leaf four or five yards off and there remain facing me, ready to go off at a sudden movement, and apparently waiting for the suspected object to move away.

On finally settling *Charaxes* often remain at first painfully wary, and sometimes (for a time) frequently show their upper surface or even rise and repeat the whole display; but they gradually become absorbed and can then often be captured quite easily, either by a grab or by a cautious movement terminating in a seizure such as I have seen practised by *Mantis* and a wild Bush-shrike. A few alarms, however, make them as wary as ever. Several of the Tabanidae equal *Charaxes* in their indecision before settling and in their absorption afterwards.

Crenis rosa Hew. at fruit is an extreme instance of indecision, probably to be explained as display for the eyes of potential enemies.

As one instance (out of many) of the indifference that overtakes *Charaxes* when finally settled to feed, I may mention that a child two years old captured a feeding *C. candiope* in his hands and brought it to me. As an illustration of their wariness when much subject to attack, I may say that at such times the most carefully guarded approach to, for example, a bunch of split ripe bananas massed with mixed *Charaxes*, will produce, at perhaps six yards distance, a general departure of half the butterflies and at nearer approach the flight of the rest, except perhaps two or three relatively unwary or self-confident individuals that refuse to be disturbed. Yet it is extraordinary how smartly even these remaining individuals will sometimes slip away when the fingers have almost closed on the wings and escape seems impossible. A feature that I have noted a few times is the giving of the alarm by some individual butterfly (it has usually, if not always, been, I think *candiope*) that, having risen with the first batch, wheels round and dashes back headlong into the midst of those that have stayed behind and having thus roused them, itself joins in their retreat. Whether, as is reputed of green Fruit-pigeons, they ever thus dash in and give a false alarm, and then settle down to the repast themselves, I have, I fear, not observed. But I believe such behaviour would be beyond even *C. candiope*!

Variability in wariness, evidently depending much on the extent to which the butterflies have been subjected to attack, is a phenomenon

by no means peculiar to *Charaxes*, although I have witnessed some remarkable extremes of wariness in species of that genus. These differences must sometimes have led two observers, in different localities or at different times, to form quite contradictory opinions (both of course correct) as to the behaviour of the same species, or to make a false comparison between the habits of insects of different species which for some reason happened at the moment to have been subjected to different strains. I have found, I think, that great wariness in a brood is usually correlated with much wing-damage and that both wariness and damage tend to be specially present at times of general scarcity of more eagerly attacked insects, and when the brood itself is a small one; also, in a mimic, when its model is absent. These facts, as I have noticed, hold for *C. ethalion* in relation to *C. cithaeron* at Chirinda, and it is probably this adaptability that enables a mimic sometimes to outrange its model, as in the migration to and establishment in the West Indies of *Hypolimnas misippus* L. In an example of this kind one of two things seems likely to result in order that the species may counteract or retrieve the loss of the leisure that it formerly enjoyed in its feeding and breeding and resting. Either some alteration in its habits must take place, probably through selection, and its coloration persist (as is likely to happen, if the species be but slightly unpleasant, when its appearance is known and variations from it are liable to selective destruction), or the habits may alter less and the colour more, in the direction either of concealment or mimicry of a new model.

D. "Fighting weight" and difficulty of reduction.

When this investigation was suggested I had already been experimenting on the food preferences of birds and had found that the smaller birds, while greatly appreciating the soft parts of the large *Charaxes*, experienced much difficulty in killing them and reducing them to an edible condition and probably (as in the case of my swallows) in dealing internally with the hard chitin of the thorax even after swallowing the butterfly, and that all these things acted as a deterrent to attack.

Dead *Charaxes* of the larger species would sometimes be accepted when live ones were refused, wingless *Charaxes* when winged ones were neglected, and, by less hungry birds again, *Charaxes* with thorax-chitin well broken up or (better) removed, when unbroken wingless individuals were refused.

It seemed to me therefore that it was perhaps their greater „fight-

ing weight" (a term suggested later by Prof. Poulton), and difficulty of reduction in relation to the smaller birds, rather than differences in powers of flight, that would tend to make the larger species of *Charaxes* useful models for mimicry by the smaller.

To test this view further I carried out the special experiments of which I shall here record only a few. They were conducted upon common Bulbuls (*Pycnonotus layardi* Gurn., three individuals), Kirk's Babbler (*Crateropus kirki* Sharpe), and a Forest Bulbul (*Phyllastrephus milanjensis* Shelley). The birds were kept without food for two or three hours previously in order to whet their hunger.

1st Oct. 1919. — *Pycnonotus layardi*, Layard's Bulbul, A. — The bird at once set off in chase of a *Charaxes candiope*, which fluttered violently all over the cage, the Bulbul in hot pursuit. He almost invariably seized it by the hind margin of the wings, which, after the first two or three minutes, resembled the much-chipped wings of so many captured butterflies, but rapidly became more and more ragged. Once the Bulbul seized it by the abdomen but the butterfly even then tore away and was immediately afterwards seized in front by the base of a fore-wing. Struggling and flapping violently, however, it escaped again and the chase recommenced. Once more the Bulbul seized it by the shoulder but was unable to retain his hold. In all, from the commencement, the butterfly must have been seized and, despite the confined space, have escaped, scarcely less than thirty times, whether by the breaking of the wing tissue or by the sheer strength and violence of its struggles. When finally stripped and swallowed the thorax and abdomen were almost reduced to a pulp.

Crateropus kirki: Kirk's Babbler. — I first placed a *Charaxes candiope* in the cage. A great chase at once ensued, the Babbling Thrush following the butterfly with the greatest activity all over the cage. It seized it several times by the wings and each time the butterfly broke away. Finally the bird gave it up as a bad job, and, retiring to one of the perches, ignored it. I removed it and later placed in the cage a *Charaxes brudus* of about equal liveliness which was chased with far more persistence and determination than its predecessor and was seized by some portion of the wing quite a number of times and each time easily broke away. Finally the bird darted out its foot as the butterfly glanced past close to the ground, and, seizing it most skilfully in its claws, pinned it thereby to the ground, at once pulled off its head and lost no time in disabling it further by pecking at the thorax with the greatest vigour. The whole butterfly then received a great pecking, battering and crushing, but the Babbler, though it considerably reduced the size, failed to remove the wings and finally abandoned the insect. I kept the bird for some time without food but, though it renewed the attack on the *Charaxes* more than once, all attempts to eat it were ineffectual.

Pycnonotus layardi: Layard's Bulbul, B. — Allowed food in the cage. I put in a lively male *cithaeron* just caught: the small eyespots in the hindwings had been removed, apparently by a bird. I held it by one costa and the Bulbul at once seized the other and attempted to batter it, but the insect, by dint of violent flapping that nearly blinded the enemy, succeeded in escaping, apparently undamaged. The Bulbul gave chase but I took the *Charaxes* out and again handed it in by one costa, the bird once more taking the other, but the butterfly escaped for the second time as before. The usual chase then ensued, and in the

course of it the greater part of the insect's wings remained behind in the bird's mouth. The latter finally secured it by the very base of a fore-wing, and, holding on tight without attempting to batter or change his hold, he allowed the insect (which was now however comparatively exhausted) to flap its own wing off. The same thing then happened with a hindwing, after which the butterfly was seized by the head and battered and crushed and the remaining hindwing and two-thirds of the other forewing removed. After ten minutes more of attempts to reduce the butterfly, he threw it away, already, it seemed to me, fairly thoroughly crushed and with the stump of wing considerably loosened, and went to his banana. After a short feed, he returned to his perch without another look at the *Charaxes*.

Half-an-hour later (the bird did not appear to have returned to the banana) the butterfly was still lying in the same place uneaten. Removing the banana I picked the insect up and re-offered it, when the bird once more set to work to crush it and batter at the stump, but finally once again abandoned it. I then offered a large specimen of *Neptis agatha* Cr. (a slightly nauseous butterfly) and this was crushed and swallowed, wings and all; then a *Precis artaxia* Hew. with two-thirds of a forewing attached (to correspond in size with the one-third forewing still left on the abandoned *Charaxes*). This, too, was crushed and swallowed. I now placed a fresh *Charaxes brutus* in the cage, but, though the bird looked at it and occasionally leant towards it, he made no attempt to capture it beyond giving a half-hearted peck at the eyespots on the two occasions when the butterfly happened to walk immediately in front of him.

Half-an-hour later the *Charaxes* was still walking about minus eyespots, but otherwise undamaged; but half-an-hour later still I found that the bird, which must have been growing hungrier all the time, had captured and killed it. All four wings were still attached and in sound condition and the bird was holding the butterfly by the head; presumably he had thus seized it while it was at rest. With a great deal of trouble he battered off the wings and broke up the thorax into two or three pieces and ate them, but completely abandoned most of the abdomen with the rest of the thorax to which a hindwing was still attached.

Pycnonotus layardi, A. — I then placed a fine fresh female *Charaxes candiope* in the cage that was now jointly occupied by A and D. Both had been kept without food and the latter was evidently greatly excited, but, being afraid of A, made no attempt to take the butterfly. A at once took it from me by one costa, but the butterfly, by dint of struggling, got free. A chase ensued and the butterfly was once more captured, this time at rest, by both costae, and seemed to be quite at the bird's mercy. On his commencing to batter it, however, one of the wings slipped out and the butterfly at once commenced to struggle and ended by forcing itself free. The bird, after a second chase, again secured it by one costa but the butterfly once more escaped and a very long chase ensued, during which the greater portion of its wings disappeared. I now extricated it and gave it, much enfeebled, to C, also hungry. At first she took little notice of it — the butterfly lay on its side —, but at last went up and seized it by a shoulder. I was interrupted here and left the butterfly fluttering in the bird's beak. On my return, twenty minutes later she had divided it into three parts, namely the abdomen with part of the thorax, and the two front wings (somewhat reduced) each with a piece of thorax at the base. These latter she swallowed, but abandoned the former part to which the base of each hindwing remained attached.

Observation on wild Bulbuls (*P. layardi*). — A wild pair of *P. layardi* that I watched feeding a nestling would have nothing to do with a *C. candiope* laid

down by myself nor with *Charaxes* frequenting ripe peaches a yard away, though they accepted and gave the youngster *Pyrameis cardui* L., *Precis artaxia*, and grasshoppers, including a somewhat unpleasant species. The only time when they seemed even to think of taking the *Charaxes* was when — being evidently hungry, all three of them — they brought the nestling two highly unpleasant grasshoppers. One of them then inspected the *Charaxes* but decided against it; the other actually picked it up, but, after wavering, dropped it and flew off. They also would have nothing to do with the large-winged moth *Nyctipao macrops* L., very common here and very difficult to „reduce“ though apparently in no way unpleasant as food. The *Charaxes* was practically dead and lying on its side (I had pinched the thorax); therefore it was neither the labour of catching nor that of holding, but the difficulty in reducing that probably deterred the birds. The two smaller butterflies were swallowed whole.

Conclusion. — It appeared likely, from such experiments as the above, that if seized, when resting, from in front, i. e. by both forewings, a *Charaxes* may be helpless against a Bulbul that has learnt to batter directly after capture. If seized by one wing only, the chances are (should the wing not break off at once) that it will free itself. Even when killed, the trouble of softening it and removing the strongly attached wings is likely to be more than a bird of this kind will undertake unless distinctly hungry.

Brittle wings, the large size of which also helps to hold attack „at arms' length“, „fighting weight“ and difficulty of reduction when killed were the defences that had been displayed.

My opinion is that, of these three after-capture defences, a *Charaxes* will owe his escape far more frequently to mere unimportant wing-breakage than to the other two: that „fighting-weight“ will doubtless account for numerous escapes and probably be far more highly deterrent to future attacks than will mere wing-breakage, which is common, more or less, to most butterflies; but that to a bird of the Bulbul size the difficulty of removing the wings and of reducing the butterfly generally to an edible condition (that is toughness and size) is probably a much greater deterrent than either. Even my Drongo was often disinclined to tackle a large *Charaxes* and would not do so towards the later stages of repletion.

As for „fighting-weight“ I have seen even wild Bee-eaters experience much difficulty in holding large *Charaxes* and actually, more than once, completely lose their hold. For instance on 31st March, 1911, I released a *Charaxes brutus* in the presence of *M. apiaster*. The butterfly was captured, but the bird had the greatest difficulty in holding it and for several minutes the two swayed about in the air, now up, now down, the *Charaxes* beating vigorously with its free wings and several times evidently nearly slipping from the bird's

grasp. Finally, very high in the air, it actually did so and half-a-dozen birds that had been attracted by the spectacle from considerable distances — none had been in sight at the commencement — dashed for it simultaneously, and after the usual confusion and snapping of bills, one of them seized it and made off, followed closely by two others that were disposed to dispute its possession.

As regards weaker-billed birds than the Bulbuls I doubt greatly whether the matter will often go beyond „fighting-weight“. Not many such birds are likely to be given the chance of discovering that a large *Charaxes* is not only difficult to hold and kill, but also, once killed, to break up and swallow. As to whether mere wing-expanse would deter a moderately hungry Flycatcher (such as *Batis*) or Warbler from attacking, this can best be tested by further experiment on wild birds. I doubt it; for I have seen a wild Warbler, *Apalis thoracicus* Shaw and Nodder, carry out a vigorous and quite unhesitating attack on a *Papilio angolanus* Goeze, which is a fairly large species.

E. Mimicry,

I venture, at the outset, to direct attention to certain evidence provided in the following experiments, evidence bearing upon an aspect of animal psychology of the utmost importance for the evolution of mimicry. It will be seen that, immediately after the persistent refusal of all the possessors of some appearance already associated in the enemy's mind with unwelcome qualities, the bearers of a new appearance will be subjected to special testing. I can best make the point clear by describing a brief experiment on an „enemy“ of a very different kind.

We have at Chirinda two species of Drongo (*Dicrurus afer* Licht. and *ludwigi* Smith), a Flycatcher (*Bradyornis ater* Sundev.) and a Cuckoo-shrike (*Campephaga nigra* Vieill.) that are often very hard to distinguish from one another in the field. They are black above and below, and there is reason to believe that the two last-named birds are mimics of the first two. We have a Tit (*Parus niger* Bonn.) that is also black, entirely so below, but with some conspicuous white markings above. I threw down before my cat which had been nauseated by a Drongo and now disliked that bird intensely, a Drongo, a black Flycatcher, a male Cuckoo-shrike and the Tit, in this order, back downwards. He ignored them all. I then turned each over one by one, first the Drongo then the Flycatcher and the Cuckoo-shrike. He still ignored them. I turned over the Tit, displaying the white markings. At once the cat came forward and tested it. So with the *Charaxes* in these experiments.

The results may be regarded, I think, as a practical demonstration of the process by which enemies contribute to distinctiveness and uniformity within a species, sex or synaposematic group, and bring about conformity to the model's appearance in the mimic. The process may be summarised as the elimination of departures from well-known standards of appearance.

The experiments were conducted at Chirinda in 1911. When the specific name only is quoted, the genus *Charaxes* is to be understood.

March 22. — *Pycnonotus layardi* (Layard's Bulbul), B. Had been feeding. He refused positively to touch a *Charaxes brutus*, a *candiope*, a *cithaeron* ♂, an *ethalion* ♀ or an *ethalion* ♂, all with closed wings; similarly refused *C. achæmenes* Feld.¹⁾ and *saturnus* Butl. both with outspread wings; but readily accepted and ate a *Precis cebrene* Trim.; once more refused to touch a *C. cithaeron* ♂ or an *ethalion* ♀ resembling it (both with upperside displayed) but at once seized on the male of the latter offered in the same way, as also on a *Precis elgiva* Hew.

March 23. — *Pycnonotus layardi*, B. Hungry. Ate two dead *brutus*, both with difficulty and much delay: the second must have taken nearly twenty minutes to reduce. Battered well and ate only the head of a third, but finally abandoned the rest of it and would have nothing to do with it when re-offered (with wings closed). I now offered a *Papilio echerioides* ♂, with upper surface displayed (colour-pattern like *brutus*). It was also refused, as was the *brutus* re-offered, but the bird at once came forward to a *candiope* and tried its thorax in his bill, thereafter refusing to touch it again; once more refused to try the *brutus*; came forward at once and tried a *cithaeron*, underside shown, and, again, upperside; thereafter refused to touch again either it or *guderiana* Dew. underside, but, on my opening the wings of the latter, looked at them closely and attempted to take the butterfly. I rescued it for further experiment. He then once more refused to touch an „upperside“ *Papilio echerioides* (a nauseous species), but at once seized on it when re-offered with closed wings, tasted it thoroughly, rejected it, picked it up and tried it again and threw it away once more. Then again refused the *candiope* but on my stripping off the wings in his presence, crushing the thorax and offering him this and the abdomen separately he ate each with the greatest apparent relish, and after them several small grasshoppers, showing that his refusals were by no means due to repletion.

March 23. — *Pycnonotus layardi*, D. (previously wild). Had been feeding on banana. Ate, after the usual struggle and difficulty, two *candiope* and refused a third; refused to touch a *brutus* (already known to the bird); tried a *cithaeron* ♀ with wings closed, and refused both it and a ♂, a *rosae* Butl. ♀ of *ethalion*, a ♂ of the same species and a *bohemani* Feld. ♂, all with wings closed. Also, with wings open, *cithaeron* ♂ and *ethalion* ♀ *rosae*, and, once more with closed wings, the ♂ of the latter, and, with upper surface displayed, the ♀ again. But on my now re-offering the ♂ with open wings it was at once taken. Re-

1) I have been led to assume — and Mr. Swynnerton has since informed me that the assumption is correct — that when *achæmenes* and *guderiana* are mentioned with no indication of sex, the males are to be understood. The females of both are mimics of *saturnus* (p. 528), while the white-barred male of *achæmenes* enters into the *brutus-Papilio echerioides* association (p. 536). E. B. P.

quiring it for further experiment, I had to rescue it from a battering. The bird then refused (with closed wings) a *pollux*, a *castor* Cr., a *saturnus* and a *brutus*, and, with open wings, the *brutus*, *castor* and *achaemenes* ♂; finally, with closed wings, a *guderiana* ♂. But on my re-offering this last with its upper surface displayed, it was inspected and at once attacked. The wingless body of a *candiope* was then eaten piecemeal from the forceps, and also three or four small grasshoppers.

March 23. — *Pycnonotus layardi* (B. or C.). Hungry, and eagerly accepted a *Charaxes brutus*, but after a struggle with its flutterings, and a prolonged and unsuccessful attempt to remove its wings, abandoned it, having eaten only the head and the fore part of the thorax. He obviously regretted having to leave it for he kept picking it up again and holding it in his bill — once for nearly five minutes, but evidently felt unequal to the further exertion required. He finally abandoned it altogether and persistently refused a second, offered with closed wings, as also, all with closed wings, one example of each of the following species of *Charaxes*: — *saturnus*, *cithaeron*, *castor*, *ethalion* ♀ *rosae*, *pollux*, and *ethalion* ♂; also *saturnus* and an *achaemenes* with open wings; but at once seized on the *achaemenes* when offered with its wings closed; refused to touch *bohemani*, similarly shown, tried its thorax rather doubtfully when re-offered with open wings but was obviously deterred by the „feel“ of it; refused a ♂ *cithaeron* with open wings and after it a ♀ *ethalion*, but, as yesterday, at once seized on the male when offered in the same way with upper surface displayed. I rescued it and gave the bird back the original *brutus* with wings removed and thorax crushed, when it was eaten readily.

23rd March. — *Phyllastrephus milanjensis* (Milanji Green Forest-Bulbul). Ate two *Charaxes brutus*. The second took a very long time and was carried about in the bird's bill for nearly half an hour. He evidently hardly felt equal to completing the diswinging process but finally did so and ate a portion of the body, dropping the rest. He then accepted a *candiope*, but after battering it a little, abandoned it and refused to touch it again, though he readily ate a small grasshopper. He then refused to touch a *brutus*, *saturnus*, *castor* and *pollux* all offered with closed wings; also a *brutus*, *achaemenes* and *castor* offered with upper surface displayed; again refused *castor* underside, and *achaemenes* upper-side, but at once seized on the latter when offered with closed wings and commenced to batter it vigorously. I rescued it with difficulty, and after conveying it (as usual) out of sight, offered it again with upper surface exposed, when it was persistently refused. Directly, however, I re-offered it with closed wings it was once more snatched at. The bird then proceeded to refuse to touch *cithaeron* (previously experienced), *bohemani* ♂ and *ethalion* ♂ and ♀, all offered with closed wings, but at once snatched away the latter's male when I offered it showing its black upper surface, and once more commenced to batter. I removed it and, again after momentary concealment, re-offered its underside. It was refused without tasting. But, upperside showing, it was once more snatched away and battered. The bird then tried the thorax of a *cithaeron* ♂ and drew back and refused to touch again either it or *ethalion* ♀ *swynnertoni* Poul., offered in the same way, but once more snatched at the latter's male (upperside). Finally he refused to touch a *guderiana* with closed wings but, after a little hesitation, attacked it when offered with the upperside displayed; then ate readily, piecemeal from the forceps, a wingless and crushed *brutus*.

The „success“ of these and other similar experiments was striking. It might have been expected that mimicry would be most useful in the

field, but that when the butterflies were thus offered in succession at close quarters the smaller ones would have been taken regardless of their coloration — for it was impossible that the bird should not have noted the difference in size. The results strongly suggested that the birds did not associate their trouble with its real cause — the size — but with the „kind“, and considered that a small specimen of the same „kind“ would probably give them the same sort of trouble as a large one. The behaviour was apparently similar to that of Prof. Moebius's pike, quoted by Darwin²⁾!

It is possible that had large and small been offered side by side the Bulbul would have discriminated. Birds are certainly expert at selecting the largest insect they can tackle when hungry enough and given a choice. At the same time I have had other instances of the same queer apparent confusion of ideas as occurred in the last experiment. Thus one of my Drongos used to treat an *Acraea* like a hive-bee, rubbing the „sting“ end well against the perch before swallowing it, although the deterrent in each is so different and situated chiefly in the thorax of the *Acraea*. And in cases of „unpalatability“ it is not unusual for a smaller or a larger mimic to be refused immediately after a very different-sized model (e. g. *Acraea encedon* L. or *Mimacraea marshalli* Trim. after the larger model *Danaida chrysippus* L., large *Pseudacraea trimenii* Butl. after a smallish specimen of the model *A. zetes acara* Hew.). This is intelligible, since the birds must be accustomed to finding individuals of various sizes within a single species, all of them protected by one kind of deterrent quality; and one can understand how the experience might be applied to examples in which the deterrent quality depended on size.

To refer further to the fact that birds tend to take the largest of two insects, both acceptable, that are offered side by side, it is possible that the smaller species of *Charaxes* may obtain protection against those enemies that can easily deal with the larger species by the probability that, when they are found feeding with the latter, these would usually be selected.

Resemblances between *Charaxes* in the field.

Both sexes of *Charaxes cithaeron* are resembled in the field by our two commonest female forms of *ethalion* (*rosae* like the ♀, and *swynnertoni* like the ♂) although when all are out together *cithaeron* is usually less abundant than its mimics. It is abundant enough, however, at times.

²⁾ „Descent of Man“, 2nd Ed., p. 115.

Although the blue is of a different shade, the likeness, except in size, is quite convincing. I have several times taken model and mimic feeding at the same single fruit, and have numbers of times seen them feeding within a few yards of each other. The males of *ethalion* are always a good deal more plentiful than the females although these are sometimes very abundant; but the species (at Chirinda) is frequently absent or nearly so for many months together, so that *cithaeron* would be more continuously known to birds. The wariness of *ethalion* is sometimes extraordinary; at other times relatively slight. I have seen males continue to feed after I had clapped the net down over them. Its degree of wariness seems to depend both on its own numbers (suggesting that it may itself possess some power of deterring enemies) and, greatly, on the presence or absence of its model. *C. violetta* Gr.-Sm., intermediate in „fighting weight“ and toughness between *cithaeron* and *ethalion*, in both sexes much resembles the former, and *C. etesipe* Godt. ♂ of which I have taken only, I think, three specimens, bears also, with its broadened hindwing band, quite a good resemblance to the male of *cithaeron*. *C. ethalion* ♀ *rosae*, when on the wing, is often very like the larger specimens of *Neptis agatha* and, when they have occurred abundantly together, I have often caught myself looking hard at both of these before deciding on the species before me. Naturally there is no question of mimicry, but the resemblance possibly often protects the *Charaxes* from attack; for *Neptis* is somewhat distasteful to birds.

Charaxes cithaeron, *bohemani*, *violetta* and *ethalion* — to mention only the members of this group that occur at Chirinda — have much the same underside. The similarity no doubt originates in affinity, but it is not complete in detail, even in the large members of the group; while the *ethalion* mimetic females, at Chirinda and elsewhere, have each a somewhat different underside, in apparent correspondence with the differences between the undersides of their respective models. Thus the white bar of the forewing that *cithaeron* ♀ displays so prominently when feeding with closed wings is also shown by the *rosae* ♀ of *ethalion* similarly engaged, and shown in the same way — by holding the forewings specially far forward. The *swynnertoni* ♀ like its model, *cithaeron* ♂, does not possess this white bar. The third, the *ethalion* ♀ of *ethalion*, with its diagonal white bar as seen from below, is with *achaemenes* ♂, at a little distance or under certain light conditions, roughly reminiscent of *brutus*, the resemblance being more convincing on the upper surface. Furthermore, curiously and unexpectedly, those members of the *ethalion* ♀ form which have the fore-

wing spots tinged with orange arc, when seen imperfectly on the wing, often reminiscent of *azota* Hew. The detailed appearance is of course that of its probable true upperside model, *ameliae* Doumet, not found at Chirinda. It is possible that such partial resemblances to locally existing butterflies (often very deceptive in the field), help this form to hold its own in the absence of the proper model.

There are numerous other field resemblances in the genus *Charaxes*, due to affinity, chance or mimicry, that I have not space to discuss here, but most of which, in the light of the experiments I have just quoted, would seem to be of use. An interesting case of perhaps a chance resemblance is that of the uppersides of *brutus* and *Papilio echerioides* ♂. The latter is rather highly distasteful to birds and has in my experiments led to refusals of the *Charaxes* when offered afterwards, while birds, deterred by the strength of the *Charaxes*, have refused, on sight, the *Papilio*.

F. "Eye-markings".

I have many times observed that an „eyespot“ is specially attractive to a captive bird and has drawn its attack, and I have seen my tame but unconfined Ground Hornbills peck the anal angle eyespots out of the wings of *Charaxes* butterflies feeding at fallen fruit. Often an astonishing proportion of these butterflies exhibit typical birdbill marks in this part of the hindwing.

In October, 1909, I took advantage of the fact that great numbers of *Charaxes* were daily frequenting the bunches of bananas hanging in my verandah, to carry out a special experiment with marked individuals. The results confirmed the opinion that „eyespots“ and other conspicuous markings on the wings may draw attack, and therefore, when situated well away from a vital part, may be advantageous for purposes of misdirection.

Conspicuous „eyes“ or lines of bright yellow or vermilion oil-paint were painted on to the butterflies' undersides in the positions shown in the diagrams of Plate 14, each insect also receiving a number. In all fifty-one butterflies were used, selected from the *Charaxes* frequenting my verandah. The bunches of bananas were inspected several times daily, returning individuals made a note of and any fresh damage they had sustained recorded on a diagram. Some of these injuries are shown on Plate 14, the number given being that which was attached to the butterfly, and two of them (Nos. 13 and 32) show examples of the beautiful imprints of birds' bills, without fracture

of the wing, that appeared on some of the specimens, — in No. 32 crossing the wet paint.

1. *Did the „eyes“ draw attack?* — Out of a total of forty-seven injuries to the wings (this excludes such as had been inflicted before the first capture) thirty-six implicated „eyespot“, natural or artificial, or else were touching them, while most of the remaining eleven were of the kind that is illustrated by Plate 14, No. 39 — conceivably attempts to reach an „eyespot“ placed at a distance from the wing margin.

2. *Were the insects flying or at rest when attacked?* — My notes show that twenty-five of the injuries involved both of a pair of wings, twenty-two being unilateral. But nearly all of these twenty-two were at or just beside an under surface „eyespot“. This seems to suggest that, even with ample allowance for coincidence, many of these, too, may have been inflicted when the insect was at rest; for the wings (particularly the hindwings) are not always quite closed. Hence the experiments favour the view that the insects were at rest when the great majority of the injuries were inflicted.

3. *Were the attacks chiefly delivered during feeding or during prolonged rest?* — If the latter we might expect to see more injuries after the enforced rest of wet weather; but the few experiments which it was hoped might indicate the answer to this question were conducted with a small number of butterflies and gave indecisive results.

My present opinion (which of course may not be borne out by further experiment) is that, apart from wet weather, *Charaxes* are likely to suffer more attacks from birds while feeding than during prolonged rest; this for two reasons: (1) that I have often found them to be both unwary and conspicuous — sometimes extremely conspicuous — when feeding at wild fruits, the excreta of wild or other animals, or meat, and I cannot believe that they are ever thus distantly conspicuous when roosting amongst foliage, though even then they may well attract the attention of such 'searchers' (mostly smallish birds) as may pass close to them; and (2) that they seem to rise early and roost late, leaving but little time in the day for „resting“ attacks except during temporary rest when they are usually still quite wary.

4. *Survival value of slight differences in power of flight.* — This part of the experiment was undertaken at Dr. Marshall's suggestion (and in relation to the suggested view that *C. ethalion* and *ethocles* mimicked the large species in virtue of the latter's hypothetically stronger flight) to test the possible survival value of slight differences in power of flight. The tip of one forewing was snipped off in a

number of the individuals used (in *brutus* between the highest and second white spots. It seemed to me, as the result of a preliminary trial, that anything more than this handicapped the *Charaxes* too much (at all events till it adapted itself) in view of the object of the experiment— the testing of „slight differences“. Fifteen of the fifty-one butterflies used were not seen again after their first release: only five of these fifteen had been mutilated. Of the remaining thirty-six two remained under observation for one day only (one mutilated, one not), eight for two days (four mutilated, four not), eight for three days (three mutilated, five not), one (mutilated) for six days, two for seven days (one mutilated, one not), one for eleven days (not mutilated), one for twelve days (mutilated), two for thirteen days (not mutilated), one for fourteen days (not mutilated), one for fifteen days (mutilated), one for seventeen days (not mutilated), one for nineteen days (mutilated), two for twenty days (one mutilated, one not), one for twenty-one days (mutilated), and one for thirty-four days (mutilated and originally damaged in addition — No. 34, plate 14).

When a butterfly disappeared it did not of course necessarily follow that it was dead. On the other hand I ought, perhaps, to have seen it again some time or other either at the verandah bananas or at those on the outskirts of the forest close by. At any rate, assuming, purely for the sake of argument, that when an insect ceased completely to return it was dead, the above figures do not show that the unmaimed individuals had any advantage over the maimed. In other words the experiment tends (on the above assumption) to support one of two views (1) that such slight difference in flight power as was produced by the mutilation inflicted does not necessarily possess survival value, or (2) that the captures (if any) were not made during flight. That the latter conclusion is likely to be the correct one was indicated rather strongly by the examination of the wing-damage. This, in turn, may suggest that the flight of *Charaxes* is deterrent to attack on the wing, but not that the flight of the larger species is more deterrent than that of the smaller.

To return to the wing-damage once more, the unmaimed *Charaxes*, added up, are equivalent to 123 *Charaxes* for one day: they suffered twelve unilateral injuries, in all = 9.75 %. The aggregate of the mutilated *Charaxes* is equivalent to 160 for one day and these suffered ten unilateral injuries or only 6.25 %. The total injuries (twenty-six for unmaimed, twenty-one for mutilated) would give a very similar result — and so would support the conclusion already suggested by the „defaulters“.

5. *Basal versus marginal eyespots and absence of these markings.*

— A comparison of the diagrams (Plate 14) is suggestive. Each is sufficiently typical of others not figured. It is true that the evidence afforded by the „life“ of the butterflies hardly bears out the suggestion that the incidence of the damage conveys. The fourteen with basal markings lasted on an average seven days; the twenty-nine marked near the outer margins averaged six; and the eight not marked at all (except for a relatively dull number in the centre of a hind wing) averaged only 1.75! Three of the latter did not return at all, two stayed one day each, a third only two and another only three. The „marginals“ included eight non-returners and the „basals“ only two. The average of the latter was also greatly improved by the inclusion of four individuals that lasted thirteen, twenty-one, twenty and fourteen days respectively, the first three without an injury. In the case of the second and third I have noted that the yellow paint became greatly dulled towards the end of their respective periods. Were it permissible to draw any conclusions from these figures one might suppose that the brilliant eyes with which I had endowed the fourteen and the twenty-nine respectively had greatly helped to protect them, either by misdirecting attack, or, through their vivid colours, by warning some birds off.

6. *A further complicating factor.* — It is possible that unusual wariness may have had a great deal to do with the escape of the first three of the four individuals last referred to. I have repeatedly, and in several different species, noted a tendency on the part of a whole brood to vary together in this respect. But I have also observed considerable individual variation — the „unwarics“ being probably those that had not yet suffered much attack — and variability in this respect must always vitiate so small an experiment unless specially looked for and recorded in every case. The two insects that I do happen to have recorded as noticeably possessing wariness in a special degree each remained under observation for quite a long time, though one of them did not acquire his full wariness until he had already sustained two wing-injuries.

7. *Long survival after serious damage.* — No. 16 (illustrated) was an interesting case. It not only sustained the damage shown on its wings, but lost three out of its four functional legs; yet it kept coming back for some days and exhibited considerable activity, hooking itself on and hanging by its one surviving leg, when it wished to settle. No. 34 had suffered marked injury to a forewing before first capture and had its tip amputated by myself. Yet, with two further

small injuries, it remained under observation in the verandah and at the bananas on the outskirts of the forest, for no less than thirty-four days — the longest of all. It was probably a matter of wariness.

8. *Direction.* — I released some of the first few butterflies not at the verandah but at various points between this and the Zona River (in the Chirinda Forest), intending to follow this up by releasing others with varnished or amputated antennae at the same points. But I soon desisted when I realized that I could not well combine it with the rest of the experiment, and that great numbers would have to be used in any case. I found the insects capable of finding their way back from 300 yards inside the forest (i. e. about 800 from the verandah) — though carried thither in dark receptacles continually twirled! — two even arriving back in the verandah before myself.

9. *Conclusion.* — I felt I could legitimately deduce only two things from the experiment:

(1) That the majority of the attacks were made on the butterflies when settled;

(2) That the majority of those „settled“ attacks were, probably, guided by the „eyespot“ and other painted markings. There seemed to be an indication also that these markings did confer some protection on the individuals to which they were applied.

Why do eyespots continue to draw attacks? — That a bird should be deceived at first by the apparent solidity of eyespots is quite intelligible, as is the probability that, with an insect so difficult to seize and hold as a butterfly, he will try everything that seems to offer a chance of success. That he should go on making the mistake indefinitely is more difficult to understand. Yet my hornbills continued, at any rate occasionally, to make it.

It is probable, however, that our lifelong experience of pictures and with the evidence that solidity can be counterfeited, may have made it impossible for us to realise fully how very different must be the mental attitude of a bird. It is even possible that individual birds may go on constantly repeating the mistake, puzzled no doubt, yet so convinced by the eyespots' „obvious“ solidity that (as Dr. Eltringham has suggested to me), they conclude each time that they must have made a bad shot. Variety in the nature and position of eyespots must make for additional misplaced trial. So must the dry season's relative rest to the enemy's memory. Yet the essential view is, I think, that while a bird will tend to go on making these mistakes through actual misapprehension, to at any rate a greater extent than is quite intelligible to ourselves, he does learn what eyespots are; but that,

having learnt, he will, with that impulsiveness in relation to a suddenly seen object that I have so very frequently noted in insectivorous birds, both captive and wild, — an impulsiveness that must be very necessary to an animal gaining its livelihood by sheer quick decision — continue to make many mistaken attacks on the eyespots of otherwise imperfectly distinguished insects. I have had instances in my experiments in which a bird has been about to attack the eyespots on impulse, but has seen his mistake in time and quickly transferred his attack to a more vital quarter.

Eyespot movements. — Relatively easy to understand is the capacity of an eyespot to draw attacks repeatedly where it is accompanied by appropriate movements. Both to my various captive birds and to a wild Bush-shrike (*Dryoscopus guttatus* Hartl.) on which I experimented much in the field, movement has nearly always proved an excitant and has given rise to an impulse to attack. Movement of the eyespots and „hind-antennae“ is well illustrated in *Charaxes*. On the least alarm — as when a person passes a few yards away — a *Charaxes* that has till then been peacefully pushing its proboscis up and down in the fruit will, if a wary individual, pull it half out and remain stockstill, at the same time commencing to rub its hindwings vigorously up and down alternately, or sometimes together. This of course imparts the lively motion to the false eyes and false antennae of the hindwing anal angle underside that is so well known in Lycaenidae, and it has the additional effect of alternately concealing and exposing the conspicuous anal angle spots of the forewing. *Cithaeron* sometimes quite suddenly shoots up a forewing and thus exposes over the edge of the hindwing an „eye“ that almost startles one by the suddenness of its appearance and might well lead to an attack „on impulse“. In both *brutus* and *cithaeron* this „eye“ is sometimes kept exposed while the butterfly either goes on feeding or moves its hindwings. In other cases the hindwings are held slightly open, with, once more, the effect of exposing the forewing underside marking.

Hence, probably, the comparative frequency of injuries at the junction of the fore and hindwings. The impression, it always seems to me, is much more striking than one would gather from an examination of the „eye“ in a captured or set butterfly, and it is possible that the separate parts of the wing are liable to impulsive attack as the result of suddenly catching the eye by movement, just as I have often noticed the whole butterfly to be. The forewing „eye“ in *Charaxes* and the movements that reveal and re-conceal it are probably, as Prof. Poulton has suggested for the similarly used „eyes“ of Satyrines, for the

purpose of drawing attack, if there is to be any, at a moment when the butterfly is prepared for it⁴). It is more conspicuous than are the always exposed anal-angle „eyes“ of the hindwing. It of course can afford to be.

Bearing of the above conclusions on the upperside mimicry in Charaxes. — It does not follow, from the fact that most of the attacks in these experiments were probably made on resting butterflies, that it is only during flight that these large *Charaxes* display the qualities or the appearance which will serve to deter attack on their mimics. These butterflies, when feeding, are continually opening and shutting their wings, slightly or more widely, in clambering over the fruits, in trying to dislodge each other, in display and in coming to and fro. They always show the upper surface when attacked; and while being battered, if they are successfully seized, the bird has ample time to study it, for the battering may last half an hour. No bird can attack a *Charaxes* at rest without learning its upper as well as its under surface and associating these with the butterfly's defences. Thus the mimic will tend to be preserved from attack whether resting, feeding or flying — whether its upper surface is displayed or its under.

G. Procryptic undersides and habits.

Although the upper surface of the wings is displayed on the many occasions of different kinds that I have described on p. 480 of the section entitled „Special Exposure to Danger when Feeding“ (and of course always in flight), the normal feeding-attitude of *Charaxes*, at any rate if the fruit is large or on the ground, and the foothold therefore good, is with closed wings. During temporary rest the wings are not always closed and a *Charaxes* may be very conspicuous as it remains perched head downwards on some prominent leaf in the sun with the wings somewhat open, thoroughly alert. Yet even here it will commonly close the wings, heliotrope, and become thereby, for as long as it chooses to remain so, relatively or even completely inconspicuous⁵).

There are few of our butterflies that do not on occasion heliotrope. Even *Acraea* and *Amawris* sometimes do it — and all species of *Charaxes* with which I am well acquainted in the field are adepts at it. Its value, I should judge from much observation, lies not merely in the

⁴) Trans. Ent. Soc. Lond., 1902, p. 441.

⁵) Compare Dr. G. B. Longstaff's notes on heliotropism in „Butterfly-hunting in Many Lands“, Lond., 1912, index: also in Trans. Ent. Soc. Lond., 1905, pp. 67 and 136; 1906, pp. 97—106; 1908, pp. 643—655; and Proc. Ent. Soc. Lond., 1905, p. XXVIII; 1906, pp. XXVI—XXIX. — E. B. P.

reduction to a minimum of the shadow cast by the butterfly on its surroundings (the usual explanation), though this is no doubt valuable, but in the breaking up and obscuring of the colour of the wings by means of the grey (or sometimes earth- or leaf-reflecting) shadows of the nervures on the wing-membrane itself. The concealing effect of this in relation to surroundings of any kind is wonderful. You see a brilliantly sun-lit butterfly or, from the other side, its conspicuously dark silhouette. Suddenly it adjusts its position, often merely leaning over to the requisite degree if side on to the sun, or turning slightly if more or less head to or away from it, and the conspicuous object of a moment ago has become dulled on both surfaces into complete inconspicuousness. A *Charaxes* feeding on fallen fruit on open ground, or resting on open ground or on leaves, often heliotropes, especially on being approached. And a butterfly heliotroping in full sunlight is far less conspicuous than one settled in a large shadow. Primarily or incidentally the habit leads to a result which may be advantageous — the shading of the butterfly's body, or (when, as often, it is away from the sun) its head.

There is also a more thorough form of temporary rest, which partakes of the character of long rest in that the *Charaxes* then takes some slight pains to choose harmonious surroundings, leaves or twig-masses of its own colour or, e. g., the underside of a twig. I have seen only a very few probably definite instances of all night rest, but they were of this kind, and in some of them the *Charaxes* had matched its own coloration exceedingly well. A *C. nichetes leoninus* Butl. was exceptionally good and even *brutus* resting amongst the smaller white twigs of an *Aberia macrocalyx* Oliver was very well concealed. Finally, when a *Charaxes* is driven to ground by pursuit it is, like various other butterflies, sometimes quite quick to select and make for material harmonizing with its own colour if it be available.

I add a few illustrations from one of my notebooks.

„September 10, 1913. — *C. neanthes* feeding at a fallen orange was not heliotroping perfectly. On my making a slash towards it the butterfly heliotroped by a quick little movement. I approached quite close and clapped my foot on the ground sharply eighteen inches away. It only flew at the third stamp, probably trusting longer to coloration than the average *Charaxes* would have done. It flew into a Loquat tree and settled under a branch which bore quite a marked reflection from the bricky earth, and in consequence was by no means different from the *neanthes*. Nor were the under surfaces of the surrounding leaves — again owing to the reflection.“

„September 11, 1913. — A *C. brutus* was resting on a twig

amongst leaves, itself, like the leaves, sharply broken up by strongly contrasted light and shade. A male sunbird (*Cinnyris venustus niasae* Rehw.) came and settled right beside it with a long, thin, green larva (probably a Geometer) in its bill. The *Charaxes* at once darted down, to the bird's obvious surprise — for it had evidently not seen it —, and settled on a lower twig, wings downward and also heliotroping — quite well disguised even from myself, and, from the bird, by the twig as well.“

„September 14, 1913. — *C. cithaeron*, settled in Loquat foliage and heliotroping, was quite inconspicuous. Even the white patch looked simply like a leaf with its sheen cut through by the vein-valleys.“ Actually, when feeding — and so likely to be seen in any case because of its movements — the female *cithaeron* is often rather specially given away by the white patch which tends to be conspicuous both by reflected and transmitted light through the butterfly's habit of holding its forewings very strongly forward.

„*C. brutus* was settling under branches as thick as one's finger, quite well hidden in the midst of strongly sunlit foliage, itself in shadow and its white underside bar merely suggesting a shiny leaf-surface.

„*C. varanes vologeses*, a very leaf-like individual (captured later), on my striking and missing it, at once flew to a Loquat branch and settled with its body and legs adpressed to it (as they all do), wings down — a marvellous likeness to a withered leaf hanging on the branch, and slight sunlight striking only the part forward of the ‚midrib‘ made the effect still more realistic.“

Accurate choice of surface for all-night rest, which I have also seen illustrated in *C. candiope*, and its definite employment sometimes during temporary rest — the wonderfully disguising effect of heliotropism — heliotroping suddenly on alarm — the effectiveness, even without very accurate choice of surface to rest on, of a definitely leaf-like underside — the concealing effect of strongly contrasted light and shade, whether it breaks up the animal's pattern or not — and the usefulness both of sky reflections and of earth reflections — are some of the main points illustrated by the notes on the habits of the genus from which I have given these quotations.

The general undersurface of the *cithaeron*-coloured group is conspicuous enough during feeding but it is undoubtedly one that is likely to harmonize with its surroundings when at rest and this applies particularly to the underside of *ethalion*, with a somewhat browner tendency than that of its models. Even the red and silver underside

of the *brutus* type can, as I have seen, be fairly easily matched with suitable surroundings, and, as Prof. Poulton has suggested to me, the same may probably be said of the conspicuous-seeming underside of *etesipe*; but neither any of these nor at any rate *cithaeron*, are, to my mind, comparable in the matter of their opportunities for concealment with *C. nichetes leoninus* or the two species about to be mentioned.

Charaxes candiope candiope Godt. This, with *brutus natalensis* Stgr., is by far the most abundant species at Chirinda. Its underside is capable of being matched very fairly closely amongst dry leaves, most closely amongst those of its food-plant, *Croton sylvaticus* Hochst., and I have seen it actually taking advantage of this fact.

Charaxes varanes vologeses Mab. This species strikes one in the field, as it is regarded in the cabinet, as rather a thing apart. It has a highly, though variable, procryptic leaf-like underside, and makes, I should say, more ready and direct use of it than any of its congeners at Chirinda. Its eyespot (of a kind to be sufficiently conspicuous during feeding, yet part of the procryptic scheme in suitable surroundings⁶) is placed on the outer angle of the hindwing instead of, as in all the other species, at the anal angle of that wing or of the forewing. Its body has always in the field given me the impression of being somewhat lighter and weaker relatively to wing-expanse than are the bodies of our other large *Charaxes* and it is this wing-expanse⁷) which is perhaps the main protection of the species. Of tough wing-attachment, so troublesome to a small-billed bird, it probably also possesses quite a share. It is, in my experience, relatively timid (possibly because relatively scarce) and less readily becomes absorbed in its repast than the other large *Charaxes*, but frequently makes from its food quite quietly to the nearest cover at a very slight hint of danger and remains away sometimes for a considerable time. Its high-bounding and wide-lunging more prolonged flight is often rather reminiscent of that of *Salamis anacardii*.

⁶) Col. R. S. Wilson also wrote 7th February 1920, of *varanes* and its favourite tree in the Nuba Mountains Province, *Albizzia amara* Boirin: „*C. varanes* when hanging downwards from a twig with closed wings is extraordinarily like a partially broken and dry seed-pod (which is then reddish brown) both in colour and pattern, the small circular markings on the underside of the butterfly looking like the seeds which show through the constricted parts of the pod where they lie.“ (Proc. Ent. Soc. Lond., 1920, p. XXIV). — E. B. P.

⁷) How useful wing-expanse may be for keeping attackers „at wing's lengths“ may be inferred from an examination of the much bitten into specimens, that one so constantly takes, of *Salamis anacardii*.

Summary and Conclusions.

1. Although *Mantidae* doubtless dispose of many individuals even of the largest species (vide observation on p. 480), birds are the most important enemies of *Charaxes* and almost the only enemies, probably, to which the selection of the defences of these butterflies is due in much of East and South-east Africa.

2. *Charaxes* are especially exposed to attack during feeding, when their constant movements make them conspicuous and they tend in addition to become unwary.

3. There may be a suspicion that some of the smaller species, as *C. neanthes* and its white form *zoolina*, possess slightly nauseous properties, but experiment with some hundreds of individuals of different species negatives this view for the genus generally and especially the larger species.

4. The flight of *Charaxes* shows strength, large inequalities, speed and strenuousness, and is certainly a fine protection, but no observations were obtained in support of the view that the larger species are so conspicuously better protected by flight than e. g. *C. ethalion*, as to be made greatly worth mimicking thereby, and the former in any case dash to the ground or other cover when pressed by a bird.

5. The wariness of *Charaxes* when much subjected to attack is very great indeed. When there is little attack it is slight. *C. ethalion* is fully as wary under the former conditions as are the larger species it resembles.

6. The larger species are very hard to seize and in special experiments in cages have escaped from birds of the Bulbul size as many as thirty times on end, owing to their great strength and the fact that they can by means of it break their wings against the pressure of the bird's bill, and also, owing to the great *expanse* of brittle wing that interposes distance between the body of the butterfly and a short-billed attacking bird.

When definitely seized they are not easy to kill owing to the force of their struggles. When killed they are very difficult for a small bird to reduce to an edible condition, owing to their size and the relative toughness of their chitin and especially the strong attachment of the wings which the smaller birds cannot swallow. They possess effective enemies amongst the larger or stronger-billed birds, but in all the above points they are far better protected than the small species of the genus, including *C. ethalion*, from the great bulk of the insect-eating birds of a given locality, and it is probably

especially in virtue of these differences that they are advantageous models for mimicry.

7. The value of resemblances in the genus *Charaxes*, including that of the females of *C. ethalion* to some of the larger species, was tested on birds that tended to be deterred from attack by the strength of the latter. It was found to be very great. The mimicking females were refused though their non-mimicking males were freely accepted; and these refusals, due to appearance alone at such close quarters that the difference in size should have been noticed, suggested a mistaken reasoning on the part of the birds equivalent to that of Prof. Möbius's pike (p. 492). The results suggested also that resemblance generally in the genus, whatever its origin, may be of the greatest use from the point of view of synposematism. Underside resemblances were as useful as upperside.

8. An experiment was carried out in which 51 *Charaxes*, regularly frequenting a certain spot, were used, many being painted on the undersides with brilliant eye-markings, and the effect as regards the position of subsequent bill-marks on the wings, noted daily. It was concluded (1) that the majority of the attacks were on the butterflies when they were settled and (2) that the majority of these „settled“ attacks were, probably, guided — or mis-guided — by the „eyespots“ and other painted markings. It seemed also, from a comparison of the apparent periods of survival, that these markings did, probably, confer some degree of protection. One butterfly continued to return for 34 days.

9. The fact that the attacks which reached the wings were made mostly on butterflies showing the under surface is completely compatible with the fact that the resemblance exists on the upper surface as well as the lower. The wings are always opened on attack and during battering and the appearance of both sides is thus learned — to the advantage of the mimic, no matter which surface it may be displaying.

10. The possession, in varying degrees of excellence, of a procryptic element in the underside colouring and a choice of surface to match it for all-night rest and even sometimes during temporary rest; heliotroping — sometimes suddenly, on alarm; the sudden interposing of a twig or branch by the butterfly between itself and enemy; twisting and doubling on attack by a bird, dropping to the ground and remaining there quietly with wings closed till the danger passed, are amongst the other defences of the genus that were noted.

11. The value of heliotropism from the view-point of coloration lies

not merely in the elimination of the shadow cast by the butterfly but in the breaking-up and obscuring of the colour of the wings by means of the grey (or sometimes earth- or leaf-reflecting) shadows of the nervures on the wing-membrane itself.

Explanation of Plate.

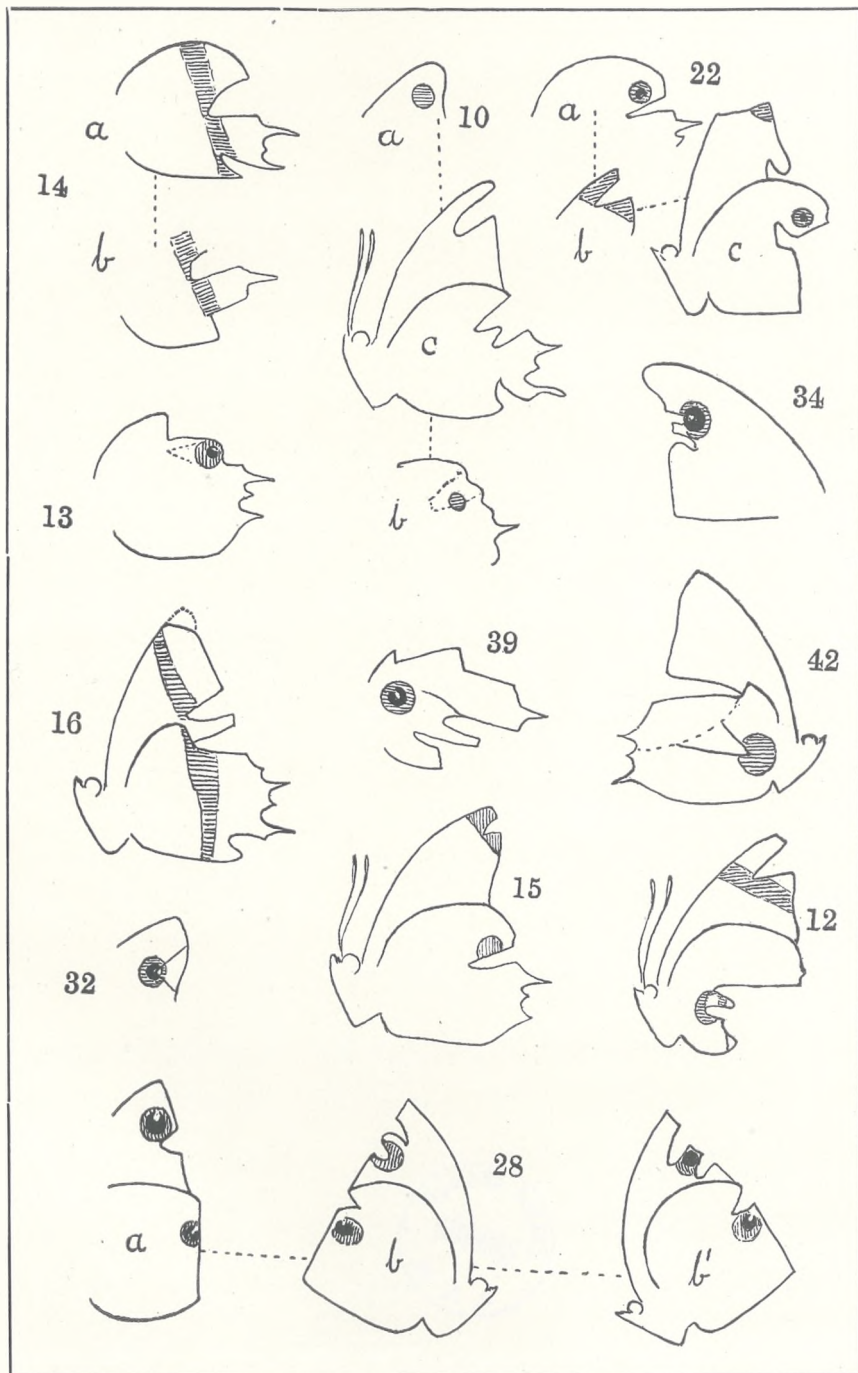
Evidence, in „birds' bill marks“ of the effect of conspicuous markings (represented on the plate by shading: horizontal = red, vertical = yellow) experimentally painted on the under surface of the wings of large *Charaxes*. The numbers are those that were actually painted on the butterflies, with the exception of 10, the actual number of this specimen being lost. The letters and dotted lines connecting some of the figures indicate the appearance of the same wings at different periods of the experiment.

Figs. 12, 14 and 16 represent apparent attempts to seize a conspicuous red line.

Figs. 13, 34, 10, 22, 32, 15 and 28 all show obvious attacks on marginal eye-spots and markings, two of them (13 and 32) being in part imprinted on the wet paint. 28 b¹ is the reverse of 28 b.

Figs. 39, 42 and 12 (hindwing) appear to be attempts to reach an eye-spot placed far from the margin.





Stygmerton: An investigation into the defences of butterflies of the genus *Charaxes*



