

MIMICRY, NATURAL SELECTION, AND ACRAEA JOHNSTONI.

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A mimic is one who consciously assumes for his own purposes, the attributes, material or non-material, characteristic of another individual; mimicry is a deliberate act, and one not part of the normal life of the mimicking individual. Yet students of insects nowadays use the term for certain insects which resemble others: how can this be used for creatures which can have no consciousness as we know it, and which cannot assume and discard characters at will?

The term "mimicry" with reference to insects, is made more unsatisfactory by loose usage. In olden days, the resemblance of a caterpillar to a stick, or of a beetle to bark, was commonly recognised as a wonderful example of "protective mimicry" designed by the Creator to enable an animal to escape its enemies. But this teleological explanation omitted to consider the other side of the question—namely, the welfare of these enemies which were equally the work, and presumably the care, of the Creator! But let us put aside these out-of-date ideas, and come to the modern usage of the word mimicry. The resemblances just mentioned are nowadays called "Protective Resemblance": a technical term has been devised for them, derived from the Greek, and laying emphasis on the concealment afforded: these are known as Cryptic Colouration. The term Mimicry, as used for the past seventy years, however, implies something far removed from concealment, and is used of one conspicuous insect resembling closely, in superficial characters only, another of a very different group. This phenomenon, like Cryptic Colouration, is also more conveniently and accurately described by a term of Greek derivation which will be explained later.

Before considering Mimicry, however, and in order that it may be seen in its proper perspective, and thus put in its niche in one general scheme explained as a whole only by Darwin's great principle of Natural Selection, it is best to begin with the simplest examples of Protective Colouration. Professor Poulton of Oxford was the first to devise a classification of all the kinds of colouration of animals founded on the principle of Natural Selection, and no other classification has since been devised which embraces the phenomena as a whole. Attempts are made from time to time to explain this or that example by other means; but this always results in that particular example having to be pigeon-holed, as it were, in a compartment of its own. The best explanation of any one phenomenon is that which brings it into line with the others, and enlarges our views, rather than narrowing them.

The value of the study of mimicry is that it is only explained by the theory which has thrown so much light on the processes by which we ourselves have evolved; any work which makes the complicated phenomenon of mimicry intelligible thus throws light on our own development. Students of butterflies and other insects need not be, as they popularly are, regarded either as children or feeble-minded old men!

When the colours of insects are considered it is quite obvious from the beginning that any observant person would divide the insects as seen under natural conditions, into two main groups: those easily seen, and those found only with difficulty, although they may be very abundant, as grasshoppers. Let us take the second group first: the insects composing it are said to be Cryptic, or Concealed. They may resemble only in a general way the broad features of their environment, such as a grasshopper among grass, or on soil. Each individual is protected by its colouration over quite a large area of its environment, and so long as it keeps still, cannot be easily seen. Since this colouration is for the protection of the insect, it is known as Pro-cryptic colouration, or as an example of Procrypsis. Procryptic insects are certainly abundant, yet in collections made casually by curiosity hunters, the opposite would appear to be the case. The reason is partly the extreme perfection of the resemblance which renders the insect hard to discover, but there is another reason, which especially applies to active creatures such as butterflies and moths. Cryptic insects hide themselves because they are highly appreciated as food by other creatures: this has been proved by experiments conducted with birds, monkeys, and other animals. But if discovered or alarmed, two courses are open: either to seek safety in flight, or to remain immobile and trust to the excellence of the device until the bitter end. Butterflies usually adopt the former course, also many moths, while others, particularly those that resemble a dead stick or rolled-up dead leaf, choose the latter. Consequently, when alarmed, cryptic insects are often very difficult to catch, and hence are less common in collections than the more easily caught conspicuous creatures of which more will be said later.

Many cryptic insects are highly specialised and resemble some very characteristic object easily recognised by an insectivorous enemy as of no food value. A seed, a thorn, a dead leaf or a bit of stick, a pebble, the excrement of a caterpillar or bird, would be of no interest to an animal which would pass by such objects, or anything that resembles them. Except in times of great scarcity of food, such as the northern winter, or the African dry season, any insect resembling these things might escape. In hard times, however, a hungry creature would have to examine everything more closely, and the least perfect examples of pro-crypsis would be the first to be suspected: thus the standard is kept up. A soft-bodied insect does not

bear much handling and examination: even if ultimately discarded, it may have been so injured that reproduction is impossible, and it is of no more use to its species. It is best for an insect to avoid all contact with an enemy.

These detailed resemblances to some small part of the environment are examples of Special Pro-crypsis. A few cases are known where the colouration is anti-cryptic, that is, of use for aggression against some other insect. There are preying mantis which simulate flowers so that they attract to themselves the butterflies, bees, etc., upon which they prey. Anti-crypsis is much less common than pro-crypsis: the vast majority of cryptically coloured insects have this colouration as a means of avoiding enemies, by resembling an object of no value to them as food.

The butterflies whose wings in the position of rest so marvellously resemble a dead leaf, have a very particular interest, for the explanation of their resemblance by the Darwinian principle of Natural Selection. The time when most dead leaves are about is the time of greatest scarcity of insect life, so that insectivorous creatures have to search more keenly for food. Now, if every individual butterfly of a kind that resembles a dead leaf were of *exactly* the same appearance, an enemy hunting among dead leaves might be struck by the curious and unusual fact that a number of them were exactly alike and would be tempted to try one. This having been found to be an edible insect, the animal or bird would be invited to try what the other similarly leaf-like objects tasted like, and eventually it might actually be dangerous to resemble a dead leaf. In nature, no two dead leaves are exactly alike, so that insects which resemble dead leaves must also be variable, and this is what we actually do find. "Leaf-butterflies" vary enormously, not only in the lightness or darkness of their colouring, but in the details of the markings which resemble tears or fungus marks, or even the moulds themselves.

It is difficult to frame any explanation of these facts other than Darwin's. How absurd would it be to suggest that the resemblance is due to similar conditions: that a Membracid bug looks like a thorn, a caterpillar like a bird-dropping, a grasshopper like a pebble, a butterfly like a dead leaf, because similar conditions have acted on them both similarly! Yet the analogous explanation is held by some to apply to cases of true mimicry which will be discussed presently, while a satisfactory explanation applicable to both classes of cases is provided by Natural Selection.

No other explanation renders the fact intelligible that when a dead leaf is the object resembled, no two specimens of the insect are quite alike: we shall see later that when another type of object is resembled, it is to the advantage of the insect resembling the object that all specimens should be as much alike as possible: Natural Selection is again the only satisfactory explanation.

We may take it as proved that a protectively coloured, or, to use the more accurate phrase, a cryptic insect overcomes the danger of its edibility by a likeness to its surroundings, general or special, which makes it appear to be of no food value to an insectivorous animal.

How then can we account for the numerous insects which, as it were, flaunt their glaring colours in front of one's eyes, and can easily be captured in the fingers? This group forms the opposite class to the cryptic insects: experiment has shown that they are distasteful and ignored *when other food is scarce*. These last words are purposely italicised because this point is of extreme importance and often forgotten. Edibility or inedibility are entirely relative affairs: no person readily eats old boots or leather belts, yet this is done under certain circumstances. I have never forgotten seeing, once, in mid-winter in England, a wren which was hunting for food among dead leaves in a wood, pull out and eat a large, black, evil-smelling beetle of the species commonly known as "Devil's Coach Horse," which possesses all the attributes of the type of insects now considered. These conspicuous insects may be said to give warning of their possession of a distasteful quality, or of a sting, poisoned spines, etc., and hence the technical term Aposematic (signing away from) has been devised for this group. Aposematic colouration is the exact opposite of pro-cryptic: the latter conceals that its owner is edible, while the former advertises its inedibility. Aposematic colouration, be it noted, depends for its efficiency upon the abundance of pro-cryptic insects. If there were never any other meat for us to eat than leather belts or old boots, we should learn to eat them without a qualm, though we should learn to distinguish some as specially nasty and possibly develop a liking for others. Similarly, if the only prey for insectivorous creatures were conspicuous insects, their colouration would merely help to destroy them. But if, for example, a monkey has had a good meal of grasshoppers, as I have often seen them doing, he will be loath to eat, though he may catch and examine, a gaudy, but evil-smelling beetle on a flower-head.

Hence it is to the advantage of an insect which will not be eaten to advertise as plainly as possible the fact that it is not nice, or is actually harmful, and thus we find, in practice, that such species are bold in demeanour, and often sleep freely exposed so as to give an enemy as good a chance of recognition as possible.

Recognition, however, implies previous experience: an enemy must taste in order to see how good, or otherwise, the food is which is so readily offered. It has been already pointed out that "experimental tasting" may mean death to an insect just as much as being eaten: it is better not to be interfered with. But if it must undergo rough handling, it is better to be tough and resistant, and this is what we find in nature. A typically aposematic insect has its con-

spicuous colouration correlated with a surprising degree of resistance to injury. The bright red *Acraea* butterflies, characteristic of Africa, have such pliable wings that they can be bent double without breaking, and it is difficult to kill them by a pinch which at once destroys the life of a butterfly of the "Meadow Brown" type. They are also very resistant to the poison of a "killing bottle." Only such an insect can afford to offer itself to undergo rough handling by an inexperienced enemy desirous of investigating its food value: the more conspicuous and simply coloured it is the more readily will another individual be recognised as of the same type of colouration and therefore probably possessed of the same distasteful quality and not worth catching when other and better food is abundant.

Let us pursue our former simile a little further. A castaway who had had perforce to eat his boots, and had had horrid pains in consequence, would not be tempted, in the saloon of the ship that rescued him, by a pie made in the guise of a boot by an ingenuous chef, if there were an obvious plenty of roast beef available.

Natural Selection can be seen thus to furnish an explanation of Aposematic as well as pro-cryptic colouration: I know of no other theory that will do so. Very interesting is the consideration of those kinds of butterflies which appear in two quite different phases according to the season. Specimens taken in the wet season may be quite conspicuously coloured, while others, in the dry season, are well concealed. Eggs laid by one form produce the other. A particularly good example is *Charaxes zoolina*. This butterfly, when insect life is abundant in the wet season, is greenish-white; in the dry season it is brown and marvellously resembles dead leaves, as I have frequently witnessed. How can this be explained? It is dangerous for the *Charaxes* to be conspicuous when insects are scarce; it does not matter so much when food for birds is abundant. The argument is sometimes adduced that greater humidity may be the cause of darker colours: it is a general rule that animals in large forests, where humidity is usually greater, are of darker tints. But in the case of *Charaxes* the reverse is the case: it is the dry season form which is darker.

We have now seen that Darwin's principle of Natural Selection affords a good explanation of pro-cryptic and Aposematic colouration, and of the decreased conspicuousness of dry season butterflies. Now let me go a step further and consider the phenomena to which the term mimicry is now applied.

The first discoverer of mimicry, H. W. Bates, about seventy years ago, noted that among the conspicuous abundant butterflies on the Amazons, there were some that were anatomically quite distinct from the majority, only resembling them in general appearance of colour and pattern. Further investigation showed that the individuals of this minority belonged to a group from the usual type of coloura-

tion of which they had departed in an extraordinary degree, the departure producing a likeness to the colouration of the majority. The latter he termed models, the former, mimics.

The models belonged to groups having all the characters of aposematic species: the mimics belonged to groups not specially protected by unpleasant taste or odour, often of shy habits and pro-cryptic colouring. The interpretation of these phenomena which best fits the facts is that the edible mimic lives on the unsavoury reputation of the model. A well-fed enemy would be likely not to give a second thought to a passing insect whose appearance reminded him of a previous unpleasant experience.

I would here redirect attention to what was said about the necessity of variation among insects relying for defence upon likeness to dead leaves. If, of a given type of colouration, an enemy tasted a number and found that quite a considerable portion were worth eating, it might be worth his while to catch and taste every one that he saw, with disastrous results to the mimic whose tissues are less resistant than those of the model. So that it is found, as a fact, that species of an edible group which have departed from the general appearance of that group and mimic another are always rarer, sometimes very greatly rarer, than their models. Bates estimated in one case the proportion of mimic to model as 1:100.

The mimic thus lives on the unsavoury reputation of its model. The simile previously used can be again referred to. The chef of the rescue ship, knowing that a starving castaway was going to make havoc among his works of art, could protect his most cherished pie by making it look like a boot.

The colouration now being considered, conveying a false warning of inedibility, is known as Pseud-aposomatic: it is what is nowadays meant by mimicry, though this is a bad term, as explained in the opening paragraphs.

Note that the means by which a pseud-aposomatic insect escapes the undesirable attentions of an enemy are precisely comparable to the means of defence of a pro-cryptic species. Both escape by resembling an object of the immediate environment which would be disregarded by an enemy in search of palatable food: in the latter case because it resembles a thorn, in the former because it resembles some definitely disagreeable insect.

Few would now doubt the interpretation of the latter case as largely due to natural selection, yet some who accept the principle of evolution as a whole by Natural Selection, advance theories to explain mimicry which neither accord with the known facts nor explain so large a body of analogous phenomena as does selection. It is difficult to understand why in one case Natural Selection is accepted as an explanation but rejected in the other because the

object which is protectively resembled happens to be another insect instead of an object belonging to the vegetable kingdom!

There is still one more class of colouration to be considered, and this was discovered by Fritz Muller some time after Bates' discovery. He pointed out that among the great assemblage of similarly coloured insects to which Bates had drawn attention, there were represented several families, each of which could justly lay claim to being typically aposematic, and had not the characteristics of a hardly-pressed rare group protecting itself by a resemblance to a better-protected group. In other words, there are a number of insects which are now known as syn-aposomatic, characterised by showing, in common, warning colouration.

But each subdivision of the whole group is well able to look after itself. Here again a ready explanation can be found along the same lines as before. Suppose there are 1,000 examples of a species with aposematic colouring type A, and 1,000 of an equally distasteful species with quite different aposeme type B. An enemy before it learns that either A or B are distasteful will have tasted, and perhaps destroyed, say 100 of each. But if there appeared one day a variation of B which, to even a slight degree resembled A it might remind the enemy, sufficiently, of A to be left alone when normal B was being tasted and harassed. Hence B¹ would be more likely to survive and leave offspring than B, and out of its offspring a certain number will resemble it or even show the variation in an enhanced degree. Hence there might be developed a type B¹, which would be so like A in superficial characters that it could be mistaken for A. Then there would be, instead of 1,000 A and 1,000 B, 2,000 of A plus B¹, and the loss of 100 would fall on both combined, so that the loss of B¹ would be only half of what B had lost, and the species has gained to that extent by the change, in superficial characters only, for the true characters of the B type would not have been affected, from appearance B to appearance B¹. A plus B¹ is what is termed a syn-aposomatic combination.

The example given is one ideally simple. Mathematicians have amused themselves by calculating what will happen to both A and B if one is more numerous than the other, but for the present purpose there is no need to complicate matters. But one further complication is of considerable interest, and the detailed study of it was first made by Dr. F. A. Dixey of Oxford. Just as B gains by approaching A, so will A gain by approaching B.

1,000 A and 1,000 B may develop into 2,000 A plus B¹, but A itself may be altered towards B so that the end result may be 2,000 A¹ plus B¹ whose pattern may be distinctly different from either of its parent patterns A or B, but yet can be traced into either: it is, as it were, a compromise between typical A and typical B. Each has

given up certain of its familiar characters that make it different from the other.

This rather complex situation has been termed by Dixey "Disposematic approach," and falls into line with all the other phenomena we have been considering.

It will, of course, be obvious that for the production of all these resemblances, *variability* is of the first importance. A curiously warped argument is sometimes put forward that because Natural Selection does not explain *why* variations occur, therefore it does not explain the production of mimicry and other protective resemblances. Supposing that many people lost their lives in a train because another train ran off the rails and crashed into them. The explanation of their death is that it was due to the other train running off the rails: no one would argue that that was no explanation of the cause of death because it did not say why the other train ran off the rails. The problem of why and how variations occur is for the geneticist, and while there are indications that the second question may in time be answered, the first will probably remain unsolved much longer. The Selectionist, however, is mainly concerned with what happens to these variations when they have been produced, and thus offer material for selection to work upon. We cannot now consider the causes of variation at any length, nor attempt to explain why one species, such as, for example, the Painted Lady butterfly is so remarkably stable, although it occurs almost all over the world, while another species such as *Papilio dardanus* is so unstable that it is difficult to match two specimens of the female.

It is noteworthy that female insects are generally more variable than the male. Cases of polymorphism without mimicry are known; such would obviously be the first step, but unless one of the forms resembles a known aposematic model the phenomenon cannot of course go further. Mimicry among butterflies is thus often confined to the female sex: cases are extremely rare in which a male is mimetic and a female not so.

It must not be thought that mimicry is confined to butterflies: there is a remarkable tendency for critics of the subject to confine their remarks to butterflies only, and hence narrow the field, and draw conclusions which cannot be upheld when mimicry is considered among all kinds of creatures, many of which are not insects, but spiders or crustacea. For example, there is a statement by Professor MacBride in 1925: "Eimer has shown that the changes in colouration which the mimic is supposed to have undergone in order to increase its resemblance to the model are of a kind which supervene independently in all families of butterflies and moths as a reaction to climatic conditions."

Even if butterflies only are considered, it is evident that this statement is based on insufficient knowledge of the facts: for

example the changes in appearance of certain species of Acraeinae butterflies which occur right across the equatorial belt of rain forest from W. Africa into Uganda. One species, *Planema consanguinea*, as it passes from west to east, becomes much paler, both sexes being equally affected. Another, but closely related *Planema epaea*, becomes darker in both sexes as it is traced from west to east. Another species, *Acraea alciope*, however, responds in a third way, the male remaining unaltered, while the female becomes lighter. This is surely a strange jumble of contradictory effects of climate acting upon three different members of one sub-family!

The attempt to explain similarity between mimic and model as due to environmental influences fails even more when the great group of Lycid beetles and their host of mimics among different orders of insects are considered.

Lycid beetles are sluggish, flat, conspicuous red-brown and black insects found freely exposed on flower heads or tall grass stems. They fulfil all the canons of an aposematic insect and have been proved to be highly distasteful to birds and monkeys. Their larvae are carnivorous, feeding freely in the open. These beetles are mimicked, wherever they occur in the tropics, by an astonishing assemblage of insects living as larvae under conditions of great diversity. There are Lycid beetles whose grubs feed inside dead wood for years; others feed on leaves; there are Lycoid wasps whose grubs feed in holes in the ground on other insects brought them by their parents; then there are Lycoid moths with caterpillars feeding on leaves; Lycoid flies whose grubs are carnivorous and live probably in mud; Lycoid bugs some of which feed on plant juices while others feed on the juices of other insects.

How could the similar *adult* colouration possibly be due to the operation of such diverse environmental conditions, and such diverse food supply, upon the immature stages of a host of unrelated insects?

Those who strain at the gnat of Natural Selection must swallow the outsized camel of the influence of environment.

Much more stress should be laid upon the importance of the "inherent" powers of variation of the organism. Certain species seem to vary very little, although found in very diverse environmental conditions; for instance, the Painted Lady butterfly, well known in England, and found all over Africa and in many other parts of the world in the same guise. At present there is no explanation of this: the fact just *is*. On the other hand, in quite a small area, with comparatively uniform environment, such a butterfly as *Pseudacraea eurytus* in Uganda has an astonishing number of forms grading one into the other. Again, this can only be stated as a fact, not explained. Once variations appear, Natural Selection has something to work upon, and certain individuals have more chance of surviving to reproduce their like than others have.

I now come to the last section of my paper, to which the first part has been the somewhat lengthy introduction: we shall now consider some points in the geographical distribution of a common East African Acraeine butterfly, *Acraea johnstoni*. The importance of the study of the geographical distribution of forms of a polymorphic species is great: it will be remembered that this subject was one of the several that so deeply impressed Darwin on his voyage round the world. In geographical races we have species in the making. The great collections of Lord Rothschild at Tring, and at the University Museum of Oxford, have long been the centres of especial study of butterflies from this point of view, and the point which is now to be considered could only have been made by the use of large collections. This exemplifies the usefulness of butterflies for this sort of study: they can readily be collected, stored and examined in large numbers; and in the hands of Professor Poulton at Oxford and Dr. Karl Jordan at Tring have yielded overwhelming evidence of the truth of the theory of evolution by Natural Selection.

Acraea johnstoni is a medium-sized, not very attractive butterfly with many forms which are united by transitions from one to the other. The ground colour varies from black to brown; there are four large whitish spots on the fore-wing and a light central area on the hind-wing.

The species is typically East African and is found abundantly in Kenya and Usambara in Tanganyika Territory; it extends westwards into the Eastern Province of Uganda, and is abundant in the neighbourhood of Mt. Elgon. It does not seem to occur in the Entebbe area north of Lake Victoria and is not found again westwards until we come to Ankole when it occurs sparsely. It is, however, not uncommon along the Uganda - Tanganyika - Congo border from Ruwenzori to the north end of Tanganyika, and is found on the west side of Lake Kivu in the Congo. Its north and south range is much more extensive on the eastern side: it extends up to the S.E. corner of the Sudan (Didinga and Imatong mountains) and southwards beyond the south end of L. Nyasa where it is abundant, and of a characteristic *facies* with the white spots much enlarged.

Its extreme southern limit appears to be in the neighbourhood of Masetter on the border of S. Rhodesia and Portuguese E. Africa. It is abundant at Mombasa and occurs at Lindi.

Wherever it occurs it appears in several forms, in both sexes, with one exception. A form with the spots in the fore-wing pale yellow is always male: it appears to be what the geneticists term a "sex-limited" form. The commonest form is *confusa*, black or deep brownish-black, with the spots on the fore-wing white; this probably enters into syn-aposomatic combination with species of *Amauris*, viz. *echeria*, *albimaculata* and possibly *psytalea* and *egialea*.

The form to which attention is here specially directed is a very interesting one; the brown tint has acquired a peculiar purplish hue on the inner half of the fore-wing. The spots have become so greatly enlarged that they form an irregular band across the wing, which is orange in colour. These two main characteristics of this form, which is known as *butleri*, produce a mimetic (syn-aposematic, not pseud-aposematic) likeness to a larger butterfly of the same sub-family but a different genus, namely, *Planema quadricolor*. This butterfly is found more particularly on the mountains and highlands of Eastern Equatorial Africa: it is abundant on Ruwenzori, Elgon, Kilimanjaro and on high ground in the neighbourhood of these mountains. Specimens from Ruwenzori are like those on Elgon; it is not found in between the areas. The specimens on Kenya show, however, a difference in reduction of the orange band, and similarly on Kilimanjaro. At Itumba, in Tanganyika Territory, however, the band is even broader. We are now in a position to appreciate an interesting fact in the distribution of the form *butleri* of the *Acraea*: it only occurs on the western fringe of the area inhabited by the species, but in this area it is the only form to be found. This area is, roughly, the western rift valley neighbourhood, from Ruwenzori to the north end of L. Tanganyika. This fact may be repeated: where *butleri* occurs, there are no other forms of *Acraea johnstoni*, and it is not found among the many other forms outside the western rift valley area.

In order to verify this, I have examined, or obtained notes upon over 1,300 specimens of this species of *Acraea* in the National Collection, and the Museums of Oxford, Tring and Witley. Dr. van Someren very kindly sent me notes of his specimens in the Nairobi Museum, and I am also indebted to Capt. Stoneham for notes on his specimens at Kitale. Among these 1,300 specimens were 64 of the form *butleri*, none of which occurred outside the narrow limits previously mentioned. Now if this fact be compared with what was said about the range of *Planema quadricolor* we see that while on Ruwenzori and in the Kivu area the *Planema* occurs with *butleri*, for which it is the model, and there is no other form of the *Acraea*, precisely the reverse is the case on Elgon where the *Planema* occurs with abundant *Acraea* of several forms except the *butleri* form.

If the environmental influences have, on Ruwenzori, made the *Acraea* like the *Planema*, how is it that on Elgon where the *Planema* occurs and presumably shows the effect of the environment, the *Acraea* is so singularly stubborn and occurs in many forms none of which resemble the *Planema*? Similarly, on Kenya and Kilimanjaro. It is not that the *Acraea* does not vary: it is extremely variable wherever it occurs.

It appears to me that the theory of environmental influences utterly fails here, but that if one lays more stress on the importance

of the appearance of a certain variation the phenomena become more understandable. It is at least legitimate to suppose that the eastern and western *Acraea* populations, separated by 200-300 miles, differ in the direction in which they vary. At some time or other the western population has produced a variation with the spots enlarged and a definite purplish tint on the brown of the fore-wing: this has been sufficiently like the *Planema* to give Natural Selection something to work upon, with the result that the mimetic form *butleri* has been produced.

Support is given to this by the fact that the only specimens of the *Acraea* that show the early steps in the production of *butleri* from *confusa* occur in the western area in the neighbourhood of Kivu, where *confusa* just meets *butleri*. But it seems that the eastern *Acraea* population has not varied in this direction, so that although the same *Planema* occurs there, no resemblance to it on the part of the *Acraea* has been possible.

The problem would be made intensely interesting if some naturalist would breed the form *butleri* and find out whether it can produce other forms or whether it is so fixed a variety that it will always breed true to its parental form. Dr. van Someren and Canon St. A. Rogers have bred very interesting polymorphic families in Kenya, but the species has not been bred in its western area.

So much for an explanation of the curious facts which is given from the standpoint of the consideration of the variability of the species and the forms that may or may not have been produced.

We may now consider another point of view, the environmental influence of other species of butterflies with which *A. johnstoni* is associated. It is possible, for instance, that the *Planema* on Elgon and other eastern mountains which serve as a model on Ruwenzori, is not so good a model owing to the predominant influence of some other conspicuous and well-known distasteful species? I have previously mentioned that the form *confusa* of the *Acraea* is sufficiently like certain species of *Amauris* to be syn-apsematic with them. This type of white-spotted *Amauris* with a large pale area on the hind-wing is extremely abundant in East Africa and extends as far south as Nyasaland and S. Rhodesia; it is particularly striking in the more eastern and southern parts of its distribution. Now it is an interesting fact that it is in these areas that the *confusa* form of the *Acraea* has larger spots and a more purely white area on the hind-wing. Specimens from Mt. Elgon have these pale markings smaller and darker, and here the white-marked *Amauris* are not so predominant as they are further east and south. One of the species concerned, *A. psyttalea*, shows a very interesting transition as we trace it across Uganda from east to west. Around Entebbe it shows considerable variation in the amount of white on the black wings, but as we trace it westwards to the Congo we find that it becomes darker and darker,

and may have the hindwings almost entirely dark. It has apparently been influenced by the typical dark species of *Amauris* of the Congo (*hecate*, *tartarea*, etc.) with which it is now in syn-aposomatic association: while in East and South Africa it is in association with the whiter *albimaculata*. The same change is shown by a larger species (*niavius*) which becomes darker as it is followed from east to west.

Thus it is possible that the predominant white-marked *Amauris* of the Eastern area provide a better model for *Acraea johnstoni* than *Planema quadricolor* owing to the abundance of individuals of several species occurring in the East. But these fade away in importance on the West so that the appearance of a variety of the *Acraea* on Ruwenzori with some degree of resemblance to the *Planema* might well have resulted in the species as a whole resembling the *Planema* which in that area has a bigger relative effect than when it is, as it were, overshadowed by the white-marked *Amauris*.