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EXTRAIT

Mimicry,

by Dr. F. A. Dixey, F. R. S. (Oxford).

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At the outset of my discourse I should wish to say that I feel highly honoured by the invitation to address so notable a body of scientific men as are gathered together in the First International Congress of Entomology under the guidance of our distinguished President; and to express the hope that this may be the beginning of a long series of Congresses, which in advancing the study of Entomology will confer benefits upon the race, and contribute towards the great object of international amity.

The subject to which I propose to devote this lecture is that of Mimicry; a subject which has formed perhaps the largest part of my studies in Insect Bionomics.

It may, I think, be assumed that all naturalists are acquainted with the main features of what is known as « *Mimicry* ». But it may be doubted whether all naturalists realise how numerous are the facts which can be ranged under this head, or how complicated are the phenomena with which a full consideration of the subject brings us into contact.

We should, I venture to think, be false to all the best traditions of scientific method, if, with this great array of remarkable facts before us, we made no attempt to interpret them. It is hardly necessary for me to point out that while in the region of fact we may reasonably hope to attain a great measure of certainty, our interpretations must be to a large extent provisional. It is true that the day may come when we shall be able to speak positively, and with general agreement, as to the causes and full bionomic significance of these noteworthy resemblances; but the time is not yet,

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and we must be content, for the present, to examine and to test, by every means in our power, those explanations that have from time to time been offered. The fuller our knowledge of the facts to be accounted for, the more nearly true is our interpretation likely to be; and this is the justification for reviewing in some detail any kind of evidence that may have a bearing on the question before us. And I will ask my audience to be good enough to observe that, when I use the term « mimicry », I do so at present, as the lawyers say, « without prejudice ».

Many cases of mimicry between Insects of different orders have long been known. The very remarkable resemblance borne by certain Moths to some of the stinging Hymenoptera long ago attracted the attention of observant naturalists. BOISDUVAL drew attention to the fact that three Butterflies belonging to three different families, namely *Limnas chrysippus*, the female of *Hypolimnas misippus*, and the *trophonius*-form of the female of *Papilio dardanus*, show a close resemblance to each other in outward aspect. Of late years very numerous instances of a similar kind have come to light. Sometimes the observed resemblance occurs between Insects of the same order but of different families, as between the Papilios and Pierines among the Butterflies; e. g., *Papilio nephalion* and *Euterpe rosacea*; sometimes between Insects of different orders. We find, for example, Ants mimicked by *Hemiptera*, *Homoptera* and *Orthoptera*, while other *Hymenoptera* are closely copied by two-winged Flies. It is needless to multiply instances of this sort, for numbers of them must be familiar to all working naturalists. And when the extraordinary prevalence of this phenomenon is once realised, it becomes impossible to dismiss the question as being merely a matter of coincidence. If we had only a few such instances to consider, we might be justified in calling them accidental. But, apart from other reasons, their very number raises the improbability of such an interpretation to so high a pitch as practically to forbid its acceptance.

Let us look at the facts a little more closely. We have seen that some of the nearest resemblances occur between Insects of different orders. We may therefore dismiss at once the idea that the likeness is merely due to affinity. At the same time there is no doubt that the element of affinity does to some extent enter into the question. We shall return to this point later.

A short examination of cases will show us that the mimicry is often confined to the female sex. It is well known that in the instances mentioned just now it is only the *female* of *Hypolimnas*

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misippus that resembles *Limnas chrysippus;* and the same statement applies to *Papilio dardanus*. This latter Butterfly, as is also well known, supplies us with another feature in the case. The female is polymorphic, and each form of the female is a copy of a different Danaine model. I show here a representation of a brood of this *Papilio*, all the specimens being the offspring of a single female. The *trophonius*-form, as we have seen, mimics *Limnas chrysippus*, the *hippocoon*-form resembles *Amauris dominicanus*, and the *cenea*-form is in mimetic relation with *Amauris echeria* and *Amauris albimaculata*. This curious phenomena is by no means an isolated case, as is shown by the next illustration. We have here the male of the African Pierine *Leuceronia argia*, in which sex the species is practically invariable. But the female exists in many different forms, each of which shows a resemblance to a Butterfly of no very close affinity to *Leuceronia*. The mimicked Insects belong to the genera *Belenois*, *Mylothris*, *Phrissura* and *Pinacopteryx*.

There are cases on record in which both male and female of a sexually dimorphic Butterfly are mimetic, but the respective models of the two sexes are different. I do not at the present moment recall any instance of a species where the male is a mimic and the female not.

We have then reached this point : that the female sex is more susceptible to the mimetic influence, whatever it may be, than the male. This is shown by the numerous cases of sexual dimorphism in which the female alone mimics, and also by those examples of polymorphism, confined to the female, in which each separate form assimilates itself to a different model.

We may now pass on to another consideration. In all the instances that I have shown, the forms that so resemble one another are found in the same, or nearly the same, regions and localities. In many cases they are observed to have similar habits. It has often happened that a group of Insects, diverse in affinity but closely allied in aspect, has been taken, not only on the same day and within a limited area, but actually on the same plant. The illustration I now exhibit depicts a wonderful assemblage of Insects, all characterised by the same arrangement of colours, comprising Wasps, Braconids, Moths, a Bug, a two-winged Fly, and Beetles of different families; many members of which assemblage I have myself seen settled on or flying about the same tree at East London in South Africa. And what is perhaps even more remarkable, we find that when geographical races, or represen-

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tative species, inhabit different areas of the same continent, the members of these mimetic groups all change their aspect together, and in the same direction. By the kindness of Professor POULTON, I am enabled to illustrate this statement by a very beautiful series of Butterflies from Central and South America. The assemblage in question contains species of very diverse affinities, including Ithomiines, Heliconiines, Danaines, Nymphalines and the females of certain Pierines, all characterised by a peculiar arrangement of the colours red, yellow and black. While these figures are being shown on the screen, I quote from a former description of my own : « The members of this assemblage as it occurs in the northern part of Central America — Guatemala to Nicaragua — present in common a remarkable streakiness of pattern, a feature that makes them easily recognisable among the corresponding forms from other regions of the same continent. Passing on to Venezuela, we find among the geographical races, or, if we like to call them so, the representative species, that there replace the Central American forms, a tendency to the breaking-up of the streaks, and a slight encroachment of the red ground-colour upon the yellow of the apex. In Trinidad there occurs a general paling of the ground-colour, due to an increase of yellow pigmentation, and running, as before, through the entire group. Next, taking the corresponding Guiana forms, we find a further breaking-up of the streaks into spots, and also a general darkening, especially of the hindwings, which gives a most characteristic aspect to the whole assemblage. In East Brazil we have a modification which somewhat recalls the Trinidad facies, though here the yellow streak on the hindwing is better defined, and a pale spot makes its appearance on the apex, the dark area of which is less broken up. At Ega, on the Upper Amazon, a curious dark chestnut tinge pervades the group, while in Peru a characteristic spottiness takes the place of the streaky pattern we saw elsewhere, and the apex becomes more uniformly dark. Finally, in Ecuador the streaks have all but disappeared, and even the spots have become almost blocked out by a dark infusion which now occupies, not only the apex, but also a large part of the base of the forewing, and the whole, or nearly so, of the hindwing. After a little study of some of the typical members of each of these geographical groups, it becomes easy to pronounce, with a considerable degree of confidence, upon the local habitation of a species that we may never have met with before. »

There are two genera of African Pierines, *Mylothris* and *Phris-*

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sura, not very nearly allied to one another, but exhibiting in many of their species, or geographical races, a curious parallelism. Nearly every form of *Mylothris* has its own copy among the forms of *Phrissura*; and exactly as in the instance of the South American assemblage we have just been examining, the changes observed in passing from one portion of the African continent to another are alike in the corresponding forms of the two genera. Thus, as is shown by these lantern illustrations, *Mylothris narcissus* is associated in East Africa with *Phrissura lasti*, both being Butterflies with lemon-yellow hindwings and black marginal spots. A form of *Mylothris* from Uganda, white with a dark apex to the forewing, a row of dark marginal spots on the hindwing, and a basal patch of bright orange on the forewing, is accompanied by a form of *Phrissura* (*P. sylvia*) showing the same characters of colour and pattern. In the Congo region we find a form of *Mylothris* (*M. asphodelus*) similar to that just mentioned, except that in the basal patch the orange is replaced by lemon-yellow; and from the same region comes *Phrissura perlucens*, in which exactly the same change has taken place. Tropical West Africa has a form of *Mylothris* (*M. bernice*) in which the patch of basal orange takes on a darker tinge and is somewhat modified in shape. In both these respects the *Mylothris* is followed by a form of *Phrissura* found in the same locality. Lastly, there are parallel pairs of the same genera, inhabiting respectively the same localities, which show a curious barring or striping of the marginal area, accompanied in one instance by a brown coloration of the forewing, affecting the representatives of both genera.

These instances — and it would be easy to multiply them — derive their principal interest from the special resemblances, often, to our view, minute, which obtain between pairs or assemblages of different species, and which change in an identical manner when we pass from one locality to another.

Taking a more general view, we cannot avoid noticing that certain distinct systems of colouring are broadly characteristic, though with modifications, of certain definite large areas of the earth's surface. Anyone, for example, seeing a Butterfly with a uniformly dark coloration, the forewing being crossed diagonally by a crimson band (as in the representations here shown of a *Heliconius*, *H. guaricus*, and two Pierines, *Pereute leucodrosime* and *P. charops*) would in nearly every case be right if he pronounced them to be natives of the Neotropical Province, that is to say, of Central or South America. So too, the general aspect of *Mylothris*

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is shared not only (as we have seen) by *Phrissura*, but also by members of several other distinct genera; but all these are African. Another very recognisable type of pattern is common to several species of *Danainæ* and the females of many species of *Nepheronia*; this type is found in the Oriental and Australian Provinces, but nowhere else on the globe. It is quite true that we come upon occasional instances of the occurrence of types resembling some of these local developments of pattern in far-removed regions of the earth's surface; but such case are very rare, and in most instances may in all probability be fairly put down as accidental. There is, for example, a curious little South American Nymphaline, *Cybdelis mnasylus*, which looks very much like a miniature version of the Indian *Hypolimnas bolina*. But the hardiest framer of theories would scarcely venture to suggest any special bionomic significance in a phenomenon of this sort. It may legitimately be set down as a coincidence. The case, however, is widely different when we contrast with sporadic occurrences such as this the enormous number of instances in which the forms that so closely resemble each other inhabit the same localities, the extensive « homœochromatic » combinations all changing together as one passes from one part to another of the same continent; and also when we consider the wide prevalence, throughout a given region, of a characteristic pattern like the dark ground-colour with a crimson band of Central and South America. The facts are undeniable; their interpretation may be in doubt, but to deny that there can be any underlying principle to regulate such phenomena as these would argue a scepticism so extreme as to pass the proper limits of scientific method.

Now let us turn to a fresh series of considerations. We have already noticed the fact of sexual dimorphism in its relation to the phenomena of mimicry. There is another kind of dimorphism, examples of which are not unknown among the Butterflies of temperate regions, though its full development must be sought in the tropics. I refer to the changes which are observed in successive generations of the same Insect in correspondence with the change of season, from hot to cold or from dry to wet. An instance of this seasonal dimorphism probably well known to all is furnished by the European *Araschnia prorsa-levana*, the spring and summer emergences of which Butterfly differ so completely in aspect that it seems at first sight impossible to believe that they can be conspecific. Equally strange instances abound in the tropics, and their number has within recent years been increased by the researches

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in especial of Mr. G. A. K. MARSHALL, who has proved by breeding that some of the forms of the genus *Precis*, most distinct from one another in aspect, are nevertheless related to one another as offspring to parent. One of the most remarkable of these instances, *Precis octavia-natalensis* and *P. sesamus*, is here shown on the screen. It has also been proved by the same indisputable evidence that, in many cases, forms of African *Pierinæ*, notably in the genus *Teracolus*, which had previously been described and named as distinct, were merely seasonal phases of the same species. In very many, probably most, of these examples of seasonal dimorphism as exhibited by tropical Butterflies, the dry season phase is far more closely assimilated in aspect to its inanimate surroundings than is the wet; in a few instances, while the dry season form is well concealed when reposing among dead leaves or on the ground, the wet season form of the same species is comparatively conspicuous, and bears more or less resemblance to another Butterfly of remote affinity. On the other hand there is a case where the model (*Mylothris agathina*) is sexually, not seasonally dimorphic. One of its mimics (*Belenois thysa*) is both seasonally and sexually dimorphic. The male of *Belenois thysa* copies the same sex of the *Mylothris* in both seasons, but much better in the dry season than in the wet; while the female *Belenois* is a close mimic of the female *Mylothris* in the dry season, but frequently departs altogether from its model in the wet.

We have learned then that in seasonal, as in sexual dimorphism, it may happen that one phase of the species may be mimetic and the other not.

Let us now turn to the consideration of the actual nature of the resemblances themselves. The outstanding feature which must strike everyone who gives them his attention is, that they are purely superficial. Take the case of *Limnas chrysippus*, the female of *Hypolimnas misippus*, and the *trophonius*-form of the female of *Papilio dardanus*, three Butterflies which we have already noted as presenting a remarkable and even deceptive likeness in general aspect. One of these Butterflies is a Danaine, another is a Nymphaline, and the third a Papilio. I need hardly remind any of my present audience that each of these groups is characterised by certain features, which are called « structural », belonging especially to the segments and appendages of the legs, and to the number and arrangement of the veins in the wings. But do we find any mutual approach in these structural particulars corresponding to the very striking assimilation in obvious aspect? We do not; and

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the same remark will apply to every one of the cases that we have had under observation. Not only in the instances of resemblance between Insects of different Orders, as between Hymenoptera and Diptera, but also where the affinity is much closer and the divergence in structure is comparatively slight, we never encounter the smallest indication that the process of assimilation involves anything but superficial and easily recognisable features. Less obvious external characters and all the details of internal organisation remain unaffected, except in so far as they may assist the superficial resemblance. If there is any significance at all in the phenomena under discussion, we seem led to the conclusion that they must stand in some relation or other to the faculty of vision.

Akin to the foregoing point is the fact that in the establishment of a mimetic resemblance, the same broad and visible effect is often produced by different means. It has been established, for example, that although certain South American Pierines, as we have seen, are excellent copies of the red, yellow and black Ithomiines and Heliconiines of the same region, the red and yellow pigments of the Pierines are chemically distinct from those of their models. A still more striking illustration of the same principle is due to an interesting investigation by Prof. POULTON. There is a large number of cases in which the resemblance is in great measure dependent on an acquired, or rather secondary, transparence of an originally opaque wing. It might have been expected that this quality of transparence had been in all cases brought about in the same manner, the visual effect being practically identical. But POULTON has shown that « whereas in the Ithomiines the transparence is due to an alteration in *shape* and diminution in *size* of the minute scales which normally clothe the wing, in the Pierines the same effect is produced by a mere diminution in size, the shape remaining unaltered. The Danaines [which enter into this combination] owe their transparence to a reduction in the *number* of the scales, not to any alteration in shape or in size; while in the associated Moths the effect results, not from any change in size, shape or number of the scales, but from the fact that the individual scales themselves become transparent, and are sometimes set up vertically, so as to let the light pass between them » (the Author, in « Nature » for October 31st, 1907, p. 675). Here then we have another proof that the assimilation does not extend further than to easily obvious features.

A further point that soon impresses itself upon the observer of the phenomena of mimicry is this : that the resemblances which

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present themselves to his notice differ widely among themselves in respect of completeness. In some instances the superficial likeness between two Insects is marvellously close, extending to the most minute particulars. This may happen even when the affinity between the two is remote. BATES was so much impressed with the excellence of the resemblance in some cases, that he speaks of « a minute and palpably intentional likeness which is perfectly staggering ». This phrase, especially the use of the word « intentional », is no doubt open to criticism ; but most students, for example, of the neotropical lepidopterous fauna will admit its virtual accuracy. In other cases the resemblance, though sufficiently arresting, is less exact. In a further series of instances a resemblance, while certainly present, may be of so remote a kind that opinions may legitimately differ as to whether it possesses any bionomic significance at all. Between the two extremes every degree of transition is found to exist. I show on the screen specimens of *Heliconius aranea* (underside), *H. leuce*, *H. alithea* (underside) and *H. galanthus* (underside), together with *Perrhybris lorena* ♀ (underside), *Pieris noctipennis* ♀ and *Pieris locusta* ♂ (underside). Here we see examples of resemblance between *Heliconius* and Pierine as to the significance of which I am quite prepared to find that different views might be taken, though I am myself for various reasons inclined to the opinion that the likeness is what BATES would have called « intentional ». Some, again, may be disposed to doubt whether the Danaine here exhibited (*Melinda formosa*) bears more than an accidental resemblance to this *Papilio* (*P. rex*). The individuals before us are, however, both males, and their respective females, though easily recognisable as each belonging to its own male, show a mutual resemblance which is really close. I may mention that both sexes of each species, with other most interesting forms, have been well figured in « Trans. Ent. Soc. Lond., 1906 », pl. XI, and by Mr. ELTRINGHAM in his fine work on African mimicry just published.

In many cases there exists a resemblance, not to any other Insect in particular, but to a group or assemblage in general. In all these instances, it is perhaps superfluous to mention, there is no necessary dependence on affinity. But that, as before suggested, the influence of affinity cannot be entirely ignored, we see from such an example as that of the African *Acræas*, many species of which are superficially so much like one another that it requires a skilled observer to distinguish between them. The same may be said of many of the Eastern *Euplœas*. Contrast this

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with a group of the European *Vanessas*. These are probably as nearly allied to one another as are the *Acræas* and *Euplœas*, but though presenting in common the characteristic *Vanessa* facies, they are distinguishable from one another at a glance. There is therefore in all probability some other factor at work in bringing about the resemblance between the members of these tropical groups besides that of mere affinity.

Certain other points remain to be noticed before we can be quite sure that we are in possession of all the data needful for an explanation. It is no doubt natural to enquire as to the comparative numbers of the various forms concerned. The answer here is perfectly definite; sometimes one of a pair, or several of an assemblage showing a common aspect, is much rarer than the rest; also it often happens that some one form of the combination is much more abundant than any other constituent of the association. But on the other hand there are plenty of cases in which most, if not all, of the mutually resembling forms are common. This fact was a great puzzle to BATES, as it plainly did not fit in very comfortably with his theory. On this point I shall have more to say before concluding.

Once more; we find that these mimetic assemblages or combinations, so to call them, are not sharply marked off from one another, but show frequent passages from one to another by almost imperceptible gradations. Take for instance such a series at that now shown on the screen, which might be considerably extended. The *Papilio* at the top (*P. iphidamas*) and the *Heliconius* at the bottom (*H. venusta*) are each of them members of a large mimetic association. The yellow patch on the forewing is common to both, though its shape and position on the wing show differences; in other respects the patterns exhibit much divergence. But the three intermediate Butterflies (*Euterpe approximata*, *E. bellona*, and *E. nigrina* [underside]), which are all Pierines, show an array of connecting links which enables us to pass by an easy gradation from one extreme of the series to the other. This is only a single example of a state of things, which is constantly to be met with in the lepidopterous fauna of tropical regions.

What then have we learned in the course of this brief survey? The points may be summed up as follows :

1. The cases of resemblance between distinct kinds of Insects are very numerous — too numerous to be accidental.

2. These resemblances are to a very great extent independent of

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affinity. Some of the most striking are those between Insects of different orders.

3. They are peculiarly liable to occur in Insects of the female sex.

4. They are, speaking generally, found only between the inhabitants of the same region.

5. They may affect one phase of a seasonally dimorphic Insect differently from the other.

6. No structure or detail of organisation is involved in these resemblances except in so far as a modification therein may assist in producing a superficial likeness in aspect or behaviour.

7. In the production of these resemblances the same effect is often brought about by different means.

8. Every transition exists between a likeness, which is so remote as to be fairly disputable, and a resemblance, which may even deceive a skilled observer.

9. In some cases there may be great disparity in point of numbers between the forms linked together by community of aspect. In other cases the numbers may be nearly equal.

10. The combinations of two or more forms resembling one another are in many cases not isolated, but are often connected with other combinations by a more or less complete series of gradations.

So far we have been concerned with facts. What is to be said about their explanation? We have already seen that these cases of resemblance are too numerous to be reasonably considered accidental; moreover their evident relation with conditions of sex, locality and visibility seems of itself to forbid such an interpretation.

When we consider the fact of the limitation of a given system of pattern and coloration to a particular area of the earth's surface, and especially when we examine the changes that affect a mimetic assemblage in common as we pass from one portion to another of such an area, as in the series just now exhibited of successive modifications undergone by the same general type of coloration in the passage from Guatemala to Peru, we are tempted to conjecture that geographical conditions may have some bearing on the matter. We may remember that many arctic Animals are white, and that both Birds and Mammals inhabiting desert regions are frequently assimilated in colour to their sandy surroundings. But if we attempt to find in these circumstances an analogy with the phenomena under present discussion, we are at once confronted with difficulties that may well appear insuperable. The prevailing coloration of Animals that live amid snow and sand respectively is with high

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probability attributed, not to the direct influence of their surrounding conditions, but to the advantage they gain from concealment whether from enemies or from prey within their respective environments, their community of coloration being, to use Prof. POULTON's term, syncryptic. But though Mr. ABBOTT H. THAYER, who surveys the subject from the point of view of an artist, maintains that the variegated patterns of the Butterflies in question similarly aid concealment, I do not think that naturalists in general will find his arguments on this head convincing. At any rate his contention does not accord with my own experience in the tropics. But even if his theory be sound with regard to Butterflies, it will not account for the resemblance of a Moth to a Hornet, or of a two-winged Fly to a Carpenter-bee. It will scarcely be denied that both Hornet and Carpenter-bee are even aggressively conspicuous. And what are we to say to the case of a Locustid, which is, so to speak, painted to look like an Ant, or to that of a Membracid, which screens itself beneath a sculptured representation of a similar model? These are not cases of syncryptic modification; nor is it conceivable that the direct influence of external conditions, even if they are similar (which may be doubted), can impose a deceptive picture or piece of sculpture upon the body of an otherwise unaltered Insect. Take again the case of a Butterfly like *Papilio dardanus*, the subject of female polymorphism. Community of external conditions can scarcely be appealed to in order to explain the likeness between each form of the female and a distinct species of Danaine, when the individuals of the same brood of the *Papilio*, all presumably exposed to the influence of identical conditions, have diverged along these three or four different channels. Taking all the facts into consideration, we must, I think, conclude that the influence of a common geographical environment, whether its influence be directly or indirectly exercised, fails to explain the phenomena of mimicry.

A view that has often been put forward, and maintained with great ability, attributes these resemblances to internal causes, which compel various species to pass through similar phases of development. These phases, it is held, must from time to time coincide, and so we may get between distinct forms a correspondence in aspect, which will present the appearance of mimicry. As a rough illustration of this view we may suppose a series of kaleidoscopes, each furnished with a similar set of fragments of glass, and all undergoing rotation together. From time to time it may no doubt happen that the patterns shown by two or more of the instruments

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will practically coincide. But the application of any such principle to the phenomena of Insect mimicry is attended with serious difficulty. The cases to be explained are not scanty in number, but abundant. Then again, many of the resemblances occur, as we have seen, between Insects widely separated in point of affinity. Take the Lycoid assemblage that we have previously mentioned. Is it probable that Beetles, Braconids, Wasps, Bugs, Moths and two-winged Flies should all have been impelled by internal causes to reach the same stage of colour-development at the same epoch of their phylogenetic history? And if this be considered not impossible, why should the various members of this assemblage be all found together in the same place, many of them actually on the same tree? We have already given attention to the fact that the forms resembling each other are as a general rule inhabitants of the same localities. It is not by any means clear how this is to be explained on the theory of internal causes of similar development. It is true that, as we have seen, there are sporadic cases of resemblances that have to all appearance developed independently of one another. But why should they be so few in comparison with the enormous number of instances, which occur under the conditions of a common habitat? There is no apparent reason, under the theory of internal causes, why there should be any connection between the likeness and the locality.

Those of my audience who happen to be acquainted with my writings on this subject, will have anticipated the solution of the problem which I should myself favour. I should find myself in agreement with Mr. THAYER to the extent of believing, with him, that these resemblances are of service to the forms exhibiting them, and that their establishment and survival have taken place under the control of natural selection. But I cannot follow him in the opinion that all the patterns which we have been considering, and which are so widely adopted by Insects of such different affinities, are calculated to render their possessors invisible against their background. On the contrary, and I think the experience of most observers will here bear me out, it appears to me that the Butterflies, which exhibit these brilliant and variegated colours, are for the most part conspicuous on the wing. Moreover, many of them adopt a slow, deliberate mode of flight, which seems to court observation. This is certainly the case with members of the genera *Mylothris* and *Amauris,* and with several of the *Acræas*. We have now a good deal of evidence that some of these forms are unpalatable to certain Birds, and are at any rate not taken by preference.

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Probably no form is absolutely immune; it should always be recognised that these matters are relative. But it seems to be clearly established by observation and experiment that some Birds at all events avoid some of these conspicuously marked Butterflies, and that there are various degrees of preference. Certain observers, it is true, have denied that Butterflies are fed upon by Birds at all, but there exists now a considerable body of evidence to the contrary. This being so, we are led to the conclusion that the brilliant colours of these Insects are, to use Prof. POULTON's term, « aposematic », that is to say that they are warning marks, which signify to insectivorous enemies such as Birds the presence of some quality whether of taste, or of odour, or of toughness, which makes their possessors unsuitable for food. If this conclusion is well grounded, we can find in the theories of BATES and of FRITZ MÜLLER a sufficient explanation of the significance of mimicry. BATES pointed out, just upon fifty years ago, that a palatable Insect might escape attack by sailing under the false colours of an inedible species, and he was followed about twenty years later by FRITZ MÜLLER, who called attention to the fact that if Birds had to pass through an education in order to learn by trial what Insects to capture and what to avoid, the combination of unpalatable Insects into mimetic associations would protect each constituent of such an assemblage from a certain amount of experimental tasting. It has been shown, chiefly by Prof. LLOYD MORGAN, that this education of young Birds in what to eat and what to avoid is a reality and no mere assumption; and the theory of FRITZ MÜLLER may thus be said to rest on a substantial foundation. The first of these theories, that of BATES, is the theory of what may be called true mimicry. That of FRITZ MÜLLER, as has been pointed out by Prof. POULTON, is more correctly designated as *synaposematism,* or the adoption by two or more forms of a common warning pattern.

Opinions may legitimately differ as to the relative importance of these two theories; and until more data are at our disposal, it will be possible to doubt as to which of them is applicable to this or that given instance. But the theories are complementary to one another, and not mutually exclusive. And it is to be observed that both of them, equally with that of THAYER, imply the preservation, by natural selection, of appropriate variations. Let us now see how far these theories are in accordance with the facts with which we started.

1. In the first place, it is obvious that the abundance of cases

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constitutes no objection. If it be granted that the possession of a common pattern is advantageous, there is no reason why its adoption should not be of frequent occurrence.

2. Nor is the fact that the resemblances are largely independent of affinity adverse to the theories of BATES and MÜLLER. Natural selection will work upon any material that comes to hand, quite irrespective of its taxonomic relations.

3. That the female sex should be more liable to enter these associations is also to be expected. It is a matter of common observation that the female of many Birds and other Animals is better protected from attack by coloration and habits than the male; no doubt, as was pointed out by WALLACE, because the life of the female, as guardian of the future brood, is especially valuable to the species. Prof. POULTON has also drawn attention to the fact that the female, being in Butterflies often more subject to individual variation than the male, gives greater scope to the operation of natural selection.

4. The fact that the forms resembling each other are usually found together, finds a ready explanation; inasmuch as it implies that they have been exposed to the attacks of the same enemies. Otherwise, the adoption of a common aspect would carry no benefit.

5. With regard to seasonal dimorphism, it is generally found that the dry-season phases, which occur when Insect-life is scarce and competition among Insect-eaters is keen, are better protected than the wet-season phases of the corresponding species. Hence, we need not be surprised to find that in some cases the wet-season phase is mimetic, while the dry-season phase adopts for its protection what is probably the more efficient method of cryptic coloration. Nor, again, is it surprising that a Butterfly like *Belenois thysa*, which is mimetic in both seasons, becomes much more strongly so in the dry.

6. The fact that the changes from the normal are all in the direction of a resemblance that is merely superficial, is strongly in favour of the theories. For these superficial modifications are plainly an appeal to vision, and it is not easy to conjecture what alien vision can be of importance to these Insects, except the vision of their actual or potential enemies.

7. That the same apparent effect is often brought about by different means is quite characteristic of natural selection; which, as we have already seen, proceeds by adopting any means that offer, irrespective of affinity, homology, or any similar consideration.

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8. The existence of every transition between resemblance which is practically complete and resemblance which is so slight as to be even disputable, is exactly comparable with what may be observed in other modes of protection; as for instance in cryptic assimilation to the ground, leaves, twigs, bark or other indifferent objects. These matters, as has been so often stated, are relative. Probably no means of protection gives absolute security, but different grades exist; as indeed we should expect on any theory of evolution. And it is often observable that where one kind of protection is feeble, it is compensated for by excellence in another method.

9. The fact that forms resembling each other may be severally common, is to some extent an objection to the application to such cases of the theory of BATES, which is usually considered to postulate the comparative scarcity of the mimic. It is, however, no obstacle in the way of synaposematism; for each accession of inedible individuals only tends to increase the common safety.

10. So too, the fact, that the associations are connected with one another by intermediates, is consonant with the theory of natural selection; for these gradational forms may be looked upon in effect as sign-posts showing the course which the evolutionary process has taken. Their survival is quite explicable on the Müllerian theory; for if themselves distasteful, each transitional form would be capable of sharing protection with the nearly resembling forms on each side of it, and thus would be established a chain of mutually protective links, reaching from one inedible assemblage to another.

I am not sanguine enough to suppose that everyone in my audience will agree with the interpretation of these phenomena, which I have ventured to advocate. I must be content with having tried to put the case of those theories, which seem to me to account for the facts better than any others that have yet been developed. And I would urge in conclusion, as I did at the outset, that the data, about which there should be no dispute, are interesting and curious in the highest degree. Any rival explanation, which neither neglects nor distorts the actual facts of the case, will deserve and, I am sure, will receive the closest attention of all scientific naturalists.

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