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A NEW THEORY OF MIMICRY IN INSECTS.

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Introduction.

The phenomenon of the resemblance of an animal either to the background on which it is normally found or to some other animal has been a source of great interest to naturalists of all times. In this address I shall call this phenomenon "mimetic resemblance," in spite of the fact that the term "mimicry" is commonly now used in a more restricted sense, for the restriction of the latter term appears to have left the major problem without a suitable name. Considerable controversy has raged round this problem, particularly with regard to the evolution and significance of mimetic resemblance, and the controversy has by no means diminished with the passing of the years. On the one hand there are many biologists who have studied large numbers of cases of mimetic resemblance and have been impressed by the beautiful and often very complex adaptation exhibited. The perfection of this adaptation has convinced them that it must be of fundamental importance to the animals exhibiting it, and they have therefore put forward theories as to the evolution and significance of mimetic re-

semblance which are dependent on the primary hypothesis that it is of vital importance to the possessors. When one applies these theories to the known facts of mimetic resemblance, however, it is found that in many ways they are inadequate. Probably the most important objection to the theories put forward is that in many cases there is considerable evidence indicating that mimetic resemblance does not give the possessors any advantage over non-mimetic animals.

In order to deal with this objection it has been suggested that the factors operating against mimetic animals are more effective than those operating against non-mimetic animals, but there is absolutely no evidence that this is so. There is also a considerable number of other important objections to the theories commonly put forward with which I cannot deal at present, though many of them will be dealt with later. The unsatisfactory nature of these theories has caused many other biologists not only to dispute the theories, but often to doubt the actual existence of mimetic resemblance, apparently on the general principle that a phenomenon which cannot be explained satisfactorily therefore cannot exist. This is obviously illogical, but it will be found that practically the whole of the arguments directed against mimicry are actually only arguments against the truth of the current theories as to the evolution and significance of mimicry. In this, as in all other scientific problems, it is important that a sharp distinction should be drawn between fact and theory.

It is the purpose of this address first to examine the evidence for the actual existence of mimetic resemblance and then to consider in what manner it may have been evolved. It will be shown that a simple mechanism exists by means of which mimetic resemblance may have been evolved which does not entail any necessity for the vital importance to the species either of the perfected resemblance or of the various steps which must have preceded this in the evolution of many mimetic species. Unlike the theories already mentioned, the theory concerning this mechanism appears to be in entire agreement with the known facts, which it explains without the assistance of any supplementary hypotheses. Whether this theory is to be considered as giving the true explanation of the evolution of mimetic resemblance will depend on the manner in which it explains, or fails to explain, such new facts as come to light, for direct proof appears to be out of the question, but it at least forms a more satisfactory working hypothesis than previous theories.

As far as possible I shall illustrate my remarks with examples of Australian mimetic insects, for we have in this country large numbers of such insects, few of which have yet been described. It will be possible to illustrate most types of mimetic resemblance in this manner but, when dealing with the objections to mimicry which are commonly put forward, it will be necessary to deal with certain exotic forms, as these are specifically involved in some of the objections.

Before going any further I must define what I mean by the term "mimetic resemblance." Using the term in the broad sense I have adopted it may be defined as the phenomenon of resemblance in an animal produced as a response to the appearance of another animal, or of some object in its natural environment. It is the problem of resemblance, resemblance itself being the end product of some process and not simply the incidental attribute of some other factor. Similarity of appearance and not of structure is its characteristic, and the appearance of the mimic is essentially a response to the appearance of the model which it resembles, and would not have been produced, or at least preserved, if the model had not existed. It is most important that this necessary dependence of the appearance of the mimic on that of the model should be borne

in mind in order to exclude other types of similarity which are due to other causes. Thus similarity in fundamental structure due to close relationship often causes resemblance, and unrelated animals which inhabit a common environment often exhibit similar modifications in structure which cause them to appear very much alike. In such cases similarity in structure is produced in two or more animals by some common cause and, appearance being simply an attribute of this structure, resemblance must be considered fortuitous. As mimetic resemblance is purely a phenomenon of appearance, it is obvious that such cases do not come within the scope of the subject under consideration.

It is probable that some biologists will take exception to the definition of mimetic resemblance given, on the grounds that I imply one type of explanation, to the exclusion of others. I contend that this implication is a necessary part of the definition in order to confine attention to a single homogeneous problem. If it should be proved that resemblance is never produced, as such, but is always the accidental result of the independent production of structures which have either a fundamental or superficial similarity, my view is that it would be proved that the phenomenon of mimetic resemblance does not exist, rather than that a different type of explanation is the true one. The supposed phenomenon of mimetic resemblance would be proved to be only a part of the phenomenon of convergence.

It has been the practice in recent years to confine the use of the term "mimicry" to one portion only of the subject under consideration, that is, to the mimetic resemblance of one animal to another, and I have but little doubt that I shall be severely criticised by many interested in this subject for using the term in a much broader sense than is usual, in spite of the fact that I have modified it slightly. Unfortunately there appeared to be no other course open to me, for the restriction of the term "mimicry" to only one portion of the subject which it originally designated has left the major problem without a suitable name. Also "mimicry," involving as it does the idea of imitation, appears to be the only really suitable term for the problem I have defined, and I therefore feel justified in using this term in its original sense, even at the risk of adding a little further confusion to that which already exists owing to its use in a number of different senses by different authors. The only other term which appears to me to be in any way suitable is "adaptive resemblance," but I do not consider this to be as suitable as "mimetic resemblance." The problem is sometimes considered under such headings as "animal colouration" and "adaptive colouration," but it is evident that these do not adequately cover the problem under consideration.

It is evident that some term is now required for the phenomenon of the mimetic resemblance of one animal to another, as I no longer use "mimicry" in this sense. The alternative term proposed by Poulton, "pseudosematic colouration," does not appear to me to be completely satisfactory as it is unwieldy and directs attention to only one portion of the subject, viz., colouration. I shall, therefore, use "deceptive resemblance," as this term is descriptive of the two outstanding features of mimetic resemblance of one animal to another. The other major division of mimetic resemblance, that is, the resemblance of an animal to some portion of its normal background, is commonly referred to either as "protective resemblance" or "cryptic colouration." The former term is particularly unsatisfactory as it is not descriptive, but indicates one possible explanation of this type of resemblance. Also, according to the theory usually put forward as to the significance of mimetic resemblance, this term applies

equally well to all cases of deceptive resemblance. It will be shown later that "protection" has probably but a very minor significance in all kinds of mimetic resemblance but, whether this be so or not, it is desirable that a term used to define a phenomenon should describe it rather than indicate a particular explanation. I shall therefore use "cryptic resemblance," which simply describes the phenomenon and does not confine attention to colouration only.

Now that I have defined what I mean by mimetic resemblance, a few examples of different types of similarity will illustrate more clearly the limitations of this term. It is so obvious that resemblance due to close relationship cannot be considered as a problem of appearance, that illustrations are scarcely necessary; but I might give the resemblance of the fox to the wolf as an example. There never has been any suspicion that the considerable similarity of these two animals is due to mimetic resemblance. The resemblance is evidently due to the fact that both have arisen from a common ancestor, comparatively recently, and that each still retains the general structure of that common ancestor and only differs in minor characters from the other. The appearance of each is simply an expression of this fundamental similarity in structure, and resemblance has not been produced, but remains. The problem is rather to explain the differences which have arisen between the fox and the wolf, than the general resemblance which persists.

The similarity in appearance of animals, which are only very distantly related, due to similar adaptation to a common environment, may not at first sight appear so obviously to be unrelated to mimetic resemblance; but it can easily be shown that resemblance is fortuitous and, in itself, of no significance to the animals bearing it. Thus several very distinct types of beetles which bore in wood in their adult state are extremely similar superficially. These are the Bostrichidae, the furniture beetles and their allies belonging to the Ptinidae and the ambrosia beetles belonging to the Scolytidae. In each case the beetle is cylindrical in form, the sides being parallel, the ends appearing to be truncated, and the cross-section is almost circular. Also the mouthparts are borne on the periphery, the thorax being hood-like, causing the head to occupy a ventral rather than an anterior position. This form is excellently adapted to the environment of the insect. A cylindrical form is most suitable for an insect which has to move about in a tubular gallery, the truncated ends enable it to push the debris, produced while burrowing, out of the hole, or to pack it into the portion of the gallery it no longer occupies, as is the common habit. The situation of the mouthparts on the periphery of the insect enables it to bore a hole large enough for its body to pass through.

In the same manner many insects which live under water have a considerable general resemblance owing to similar adaptations to the aquatic environment. The Dytiscidae, Gyrinidae and Hydrophilidae amongst the Coleoptera, and the Notonectidae, Corixidae, Belostomatidae and Naucoridae amongst the Hemiptera have much in common in appearance. The parts of the body are beautifully coadapted so as to give simple contours to the insect, consisting of gentle and continuous curves, which enables the insects to slip easily through the water, and the legs are modified to form oar-like structures for the purpose of swimming, these often being built on exactly the same mechanical and structural plan in widely distinct forms, for example, in the Dytiscidae and Notonectidae.

Similar functional requirements also often give rise to similar structure in dissimilar animals, though it is impossible to draw a sharp distinction between

the results of functional requirements and environment. Thus the Mantidae and Mantispidae, belonging respectively to the widely separated orders Orthoptera and Neuroptera, have a very considerable superficial resemblance (Pl. iii., figs. 9 and 10). The insects belonging to both families are predaceous, and the striking similarity is due to similar adaptations to the predaceous habit. The front legs are highly modified to form efficient grasping structures which are built on exactly the same plan in each case, and the front coxae and prothorax, normally very short structures in insects, are greatly elongated to give the insects a longer reach. In a similar manner oar-like hind legs are built on exactly the same plan and have been evolved quite independently by a series of distinct types of aquatic insects and, though this can be considered as an adaptation to a common environment, as I have already shown, it can also be considered as due to similar functional requirements.

It is evident, therefore, that similarity in appearance is often due to structural similarity, this, in its turn, being produced in some manner as a response to the similar requirements of the insects; or, in other words, it is the result of similar environmental or functional influences. The structure in each form is produced without reference to other forms which happen to have a similar structure. The fact of resemblance is quite fortuitous and without significance to the animal bearing it, and it therefore cannot be considered as mimetic resemblance. In such cases the similarity is referred to as convergence.

It sometimes happens that two or more insects resemble one another owing to the fact that they have all developed a mimetic resemblance to the same type of background. For example, certain longicorn beetles and weevils which live on tree-trunks have a considerable general resemblance to one another, and each species is inconspicuous in its normal habitat. It is evident that the resemblance between such beetles is fortuitous, similarity in appearance being due to the fact that each species has responded to the same environmental influence, viz., the appearance of the tree-trunks on which the insects live. This is referred to as syncryptic resemblance and is not mimetic.

When one considers the vast number of different species of insects and the comparatively homogeneous nature of the class, it would appear highly probable that purely accidental similarity must sometimes occur. That such cases exist there can be very little doubt, but they are difficult to recognise as it is necessary first to prove that the similarity has not been produced as the result of some common cause. For this reason it is difficult to give examples from the Insecta, but the type of similarity under consideration is such as exists between certain flowers and sea-anemones, or between the stalked green eggs of the green-lacewing, *Chrysopa*, and the sporangia of certain mosses, as a species of which they were originally described! It should be noticed that the chances of such an apparent mimic resembling its apparent model in more than one conspicuous character, and differing widely from its close relatives in these same characters, is extremely improbable; and that therefore cases of such apparent mimicry would be extremely unconvincing except, possibly, in a museum collection. It is possible that a certain number of the cases of mimicry which have been described should be placed in this category; but, for reasons I shall give later, I do not think they are many.

There is at least one other possible type of similarity in addition to mimetic resemblance. When two groups of insects are fairly closely related it is probable that the genetical constitutions of the individuals will be very similar, for they have all been derived from that of the common ancestor. With similar genetical constitutions it seems probable that the potencies should be similar, so

that mutations of the same, or very similar, type might be expected to occur quite independently in the two groups. In this manner species might be modified, or new species arise, in exactly the same manner and quite independently in the two groups; the resultant resemblance being the expression of some underlying genetical similarity. This is not the same as similarity due simply to close relationship, as in this case it is due to something new which has appeared independently in each group, and not to the inheritance by each of the structure of the common ancestor. In such cases the resemblance might be very great and even extend to more than one character, but it should be noticed that this is not necessarily independent of a mimetic explanation. If a new mutant receives any advantage from its resemblance to some other form, this advantage will be an important factor in its preservation. Therefore, though resemblance takes no part in the production of such a mimetic form, it may play an all-important part in its preservation. On the other hand, it must be admitted that, even though it be proved that such a mimetic form receives some advantage from its apparent model, a mimetic explanation to account for its production or preservation is not warranted, as it is superfluous, unless there be evidence to show that the mimetic form would not have been preserved in the absence of the model.

In his classical work, "Mimicry in Butterflies," Punnett has shown that there is strong evidence for believing that many of the striking resemblances between somewhat distantly related butterflies are due to the similar genetical constitutions of the groups to which the mimics and models belong, and that therefore there is a possibility that such resemblances are not truly mimetic. It is evident, however, that all supposed cases of mimetic resemblance cannot be considered to be explicable in this manner; for, in the first place, reasonably close relationship is necessary and, secondly, mimics resulting from similar mutations must have a similar structural basis for the colour, form, etc., which produce the resemblance. When, for example, colour markings on the mimic produce a resemblance to the form of the model, or the corresponding colour markings which appear so similar in the two insects are found to occupy different morphological positions, it is evident that the resemblance cannot be due to similar mutations, that there is no actual underlying similarity and that therefore there is nothing but appearance in common between the two insects.

I have now outlined the various types of resemblance which may exist between animals for which a mimetic explanation is superfluous. It remains to show what evidence there is for the existence of true mimetic resemblance, and to describe the main types of mimetic resemblance which will be illustrated as far as possible with examples of Australian mimetic insects. After this I shall describe the probable method of evolution of mimetic resemblance.

The Existence of Mimetic Resemblance.

At the outset it is necessary to point out that we are faced with two distinct questions:—

1. Has mimetic resemblance been evolved?
2. How has mimetic resemblance been evolved?

The problem is essentially a branch of the larger problem of evolution, and it presents the same difficulties. I think it can safely be said that at the present time all biologists believe in the fact of evolution, but there is by no means general agreement as to the process of evolution, and there is still considerable controversy between biologists with regard to the latter problem. This con-

trovery about the process of evolution appears to be taken by the general public as evidence that biologists disagree amongst themselves about evolution, and that therefore evolution is but an unproven theory which need not be taken seriously. A similar confusion between the mechanism and fact of mimetic resemblance by many biologists appears to be the cause of much of the criticism directed against the subject. This criticism is directed almost wholly against the theories commonly put forward as to the manner of evolution of mimetic resemblance, yet the conclusion often drawn is not simply that the evolutionary explanation is inadequate, but that mimetic resemblance does not exist and that some other type of explanation will have to be found to account for the undoubted fact of resemblance. The attitude adopted on this question, as on so many others, is that the fact does not exist because the critic is unable to conceive of a mechanism to account for it. Criticism of mimetic resemblance has been to a very large extent criticism of the theory that mimetic resemblance has arisen by the natural selection of small favourable variations, the cumulative result of which has been the production of a mimetic from a non-mimetic form, and that comparative freedom from attack by the natural enemies which exercise selection is essential to the success of the species. This, obviously, is not a criticism of mimetic resemblance itself, but of one theory of evolution which is still held to be true by many biologists, but is disputed by others. To dispute the fact of mimetic resemblance, because those who write on the subject account for it by a theory of evolution which is at variance with one's own ideas, is indefensible.

It appears to me highly improbable that a direct proof of the fact of mimetic resemblance will ever be possible. It is required to prove that the appearance of a certain animal has been produced as a response to that of some other animal or of some object in its natural environment. To demonstrate this directly it would be necessary to produce a mimic artificially, by breeding under experimental conditions in such a manner that the production of the appearance of this new mimic could only be interpreted as a response, however indirect, to the appearance of the model. For many and obvious reasons such an experiment appears to be quite out of the question.

Alternatively it would be necessary to observe the complete process of the production of a mimic under natural conditions. A singularly complete series of observations would be required in order to prove, not only that a mimetic can be produced from a non-mimetic form, but that the resemblance produced was due to the influence of the appearance of the model alone. This would not only entail a most laborious and lengthy piece of research, but also amazingly good fortune. Mimetic forms are far from common when one considers the enormous numbers of species of animals, and at any given time the number of mimetic forms which are being produced must be remarkably small. In fact it would appear probable that such cases would only be found at intervals of long periods of time, unless the process of production of mimics is extremely slow, in which case observations extending over many human lifetimes would be required. We should be unduly optimistic, therefore, if we expected to obtain evidence with regard to mimetic resemblance in this manner.

In this connection it will be instructive to examine the phenomenon of the appearance of melanic forms of various moths near industrial centres, as it has often been considered that this provides an example of observation of a mimetic form such as I have stated to be desirable for proving the fact of mimetic resemblance. During recent years many records have been made of the appearance of black or very dark forms of a number of different species of moths,

mostly belonging to the Geometrites; and these have practically all appeared near industrial centres, in England, on the continent of Europe and in the United States of America. A series of observations extending over a number of years has demonstrated the gradual displacement of the typical by the melanic form in several different cases; and it is known that in certain districts near industrial areas only the melanic form of a particular moth now occurs, while records show that in the same districts some years ago only the typical form of the moth was known.

For example, 25 years ago only the typical form of *Boarmia repandata* occurred on the Tyneside, while every specimen captured now is black. The case of *Amphidasys betularia*, the "peppered moth," is perhaps better known. The melanic form of this insect, var. *doubledayaria*, is recorded as far back as 1850, but it was then considered to be a great rarity. For many years now it has been the dominant form in many industrial districts, and in some areas it has completely displaced the typical form. This has happened in various parts of England, on the continent of Europe and in the United States of America, and everything indicates that the melanic form has been evolved independently in many different species of moths, and new cases are constantly coming to light.

To many it has seemed obvious that the appearance of black forms of many different moths in association with industrial areas is to be explained as a response of the insects to the altered appearance of their surroundings, due to the deposition of quantities of soot. It has been suggested that the black forms would be less conspicuous on the blackened trees than the typical forms, and that therefore the black forms would be selected by the action of their natural enemies. At first sight this appears to be a very reasonable explanation, but further examination of the problem brings to light important objections. In the first place, my experience, which is by no means inconsiderable, of the appearance of vegetation near industrial centres is that it is by no means black. Trees and shrubs if touched will dirty the hands, but, except for a somewhat lessened luxuriance, they differ but little from trees and shrubs which have received no deposit of soot; so that a black form of a moth would have little, if any, greater advantage than the normal form near an industrial centre than in any other region.

A still more important objection is afforded by the experimental work of Heslop Harrison. He has shown that the melanic forms are produced, not as a response to the blackness of the surroundings, but by the action of metallic salts contained in the sooty deposit on the leaves of the food-plant. He has taken a number of species of moths from areas in which the melanic forms are unknown and, by feeding the larvae of these on food-plant which contained small quantities of certain metallic salts, he has produced melanic forms in considerable numbers. In many of the experiments the cut ends of the food-plant were simply immersed in dilute solutions of metallic salts so that the melanic forms were produced without the influence of any blackness in the surroundings. Further than this Heslop Harrison has proved that the melanic pattern is heritable, and, in fact, behaves like a normal Mendelian character. Once the melanic pattern has been produced under the influence of metallic salts it is inherited from generation to generation in a normal manner, even though the larvae are fed on normal untreated food-plant.

Heslop Harrison's work throws light on a very important factor in evolution. It has demonstrated that the environment may influence the production as well as the selection and preservation of mutations, and one of the most im-

portant evolutionary problems with which we are faced is the nature of the causes which determine the appearance of mutations.

It is evident from what has been said that any attempt to observe the production of a mimetic form in the field is fraught with grave difficulties. Not only is it probable that a suitable opportunity for such observation will seldom be offered, but the greatest care must be taken in the interpretation of such observed facts as appear to have a bearing on the subject. It is particularly important that the mind should not be concentrated wholly on mimetic resemblance, as it must be realised that the true explanation of the observed facts may have no connection with this subject, as in the case of the melanic forms of the moths I have referred to.

In order that the account I have given of the production of melanic forms in moths may not cause confusion at a later stage in this address, I must point out that these melanic forms appear to have completely displaced the typical forms in certain districts entirely without the aid of natural selection. The chemical stimulus has acted on all the individuals in a particular district, causing the independent production of a large number of similar, or probably identical, mutations. The whole of the insects in the community, acted upon by the same new environmental factor, have been modified in appearance in the same manner; and but few of the black individuals are the descendants of the first insect which produced the black mutation. It appears highly probable that most of the mutations which have taken part in the production of the appearance of truly mimetic insects were not of this type. In general mutations seem to be rare and sporadic in their appearance, and it is probable that most cases of mimetic resemblance have been built up or preserved by the selection of such apparently chance mutations as had a special survival value. If this be the case, it follows that all the surviving individuals of a mimetic species must be the descendants of the first insect, or possibly small number of insects, in which the mimetic mutation appeared. It is difficult to conceive how an adaptive character such as mimetic resemblance could have arisen without the action of natural selection. If an environmental influence caused the simultaneous production of the same mutation in all the individuals of a species, there is no reason why the new character should be adaptive and the chances are greatly against this. On the other hand, in order to be selected directly, a character must be adaptive. Natural selection, therefore, is an adequate mechanism for the preservation of adaptive characters, such as mimetic resemblance; while an environmental factor which causes the production of a particular mutation throughout a species is not likely to produce an adaptive character. It must be born in mind as a possibility, however, that some of the apparent examples of mimetic resemblance have been produced as a direct response to some environmental factor. Such resemblance, of course, would actually be fortuitous.

As there appears to be but little hope that the direct proof of the existence of mimetic resemblance will ever be possible, it is desirable that the available evidence should be examined to see whether this supports the contention that it does exist, or not. As cryptic and deceptive resemblance afford somewhat different lines of evidence, it will be necessary to deal with the evidence separately under these headings.

(a) *Cryptic Resemblance.*

Cryptic resemblance is an exceedingly common phenomenon amongst animals and particularly in insects. Insects are to be found in practically every conceivable situation on land, and in most situations some species have such an ap-

pearance that they are difficult to see when on their normal background. Though the Insecta forms a very homogeneous class in many respects, there is a surprisingly great diversity of colouration, form and habit within it. Also the variation in the appearance of the backgrounds on which insects are found is almost infinite. It is evident from these considerations that the probability of any particular insect resembling its normal background purely by chance is extremely remote; and that, therefore, if cryptic resemblance is always due to the accidental association of an insect with a background of suitable appearance, the number of species exhibiting cryptic resemblance should be extremely small. This follows purely from a consideration of probabilities. In actual fact, a very large percentage of insects exhibits cryptic resemblance, so it seems necessary to consider, either that the appearance of cryptic insects is in some manner produced as a response to that of their respective backgrounds, or that there is some mechanism which causes insects to become associated with backgrounds which have a suitable appearance to afford concealment.

When a careful examination is made of even a few species exhibiting cryptic resemblance another important point becomes evident. Concealment in many instances, probably in most, is due not to a single factor but to several. Colouration, form and attitude commonly take part in the production of cryptic resemblance; and each of these factors may be easily divisible into several minor factors which can only be considered to have been produced independently of one another. If there be but a very remote possibility that an insect may accidentally have a general resemblance to the normal background on which it is found, it is obvious that the possibility of accidental resemblance in several independent characters must be extremely remote. The fact that cryptic resemblances commonly consist of several independent characters is additional proof that cryptic resemblance cannot normally be fortuitous.

A further argument against the possibility of cryptic resemblance being fortuitous is that many different mechanisms appear in different insects, each of which causes concealment of the bearers. It would appear, therefore, that concealment is an end attained by the utilisation of any suitable kind of mechanism, and the obvious inference is that cryptic resemblance has been evolved on account of the concealment which it affords.

The foregoing considerations indicate clearly that cryptic resemblance in general cannot be fortuitous, though these do not preclude the possibility that in a few instances the resemblance may actually be due to the accidental association of an insect with a suitable background. As resemblance is produced in many different ways, but is always associated with some particular object in the insect's normal environment, it appears evident that the resemblance must have been produced either directly or indirectly by the action of some environmental factor. It might be considered that general environmental influences, such as temperature, humidity or food material, might bring about the observed result. A detailed examination of the occurrence of cryptic species, however, will immediately demonstrate that this cannot be so in most cases. Many cryptic insects, some of which are closely related, may be found in the same environment. All are inconspicuous on their normal backgrounds, and all are subjected to the same general environmental influences, but they do not resemble one another. The same influences, particularly when operating on closely related species, would be expected to produce the same kind of result in each insect, but they do not. The appearance of each cryptic insect is associated with that of its normal background and not with general environmental conditions. It is evident, therefore, that the factor responsible for the production and preser-

vation of cryptic resemblance cannot be a general environmental factor, but must be one the action of which is in some way determined by the nature of the association of an insect with its background. There is nothing in common between the various cryptic insects except the resemblance of each to its normal background. It appears necessary to consider, therefore, that the manner of operation of the determining factor on each insect should be influenced in some manner by the nature of the resemblance of the insect to its normal background; and to do this it must be capable of being affected by appearance. The factor must have two properties; it must be able to see and it must operate on insects in such a manner that resemblance, when it appears, will tend to be preserved. Only the natural enemies of insects fulfil these two conditions, so it appears evident that cryptic resemblance must have been produced by the discriminative action of natural enemies.

It will be noticed that not only sight, but also discrimination on account of appearance, is necessary in order that cryptic resemblance may be selected. By no means all the enemies of insects are capable of such discrimination. Many parasitic insects, for example, appear to use sight but little when hunting for their hosts; so that, though they are amongst the most important enemies of insects, they cannot take part in the preservation of cryptic resemblance. Higher animals, such as birds, lizards and insectivorous mammals, would appear to be the most probable agents of selection. Another important point is that only those enemies which attack the stage of the insect which exhibits resemblance can bring about the selection; so that, though the severest attack may be delivered against a non-cryptic stage of the insect, the only possible agents for the selection of resemblance are the enemies of the cryptic stage, which may otherwise be comparatively unimportant.

There is a very simple mechanism by means of which discriminating natural enemies may bring about the selection of cryptic resemblance. All that is necessary is that an insect which is more perfectly concealed than most of the individuals of the same species should be less easily found, so that its chance of survival is greater than normal. This greater chance of survival would cause individuals with a more perfect resemblance to tend to increase in numbers and gradually to displace normal individuals with a poorer chance of survival. Actual experiments* have proved that birds do more frequently pass over cryptic insects on a suitable background than when they are on an unsuitable background. It is evident, therefore, that the action of some discriminating enemies at least is modified by the appearance of their prey, in such a manner as to tend to preserve those individuals which are more perfectly concealed than is normal. Provided suitable variations appear, this is all that is necessary to cause the gradual building up of more and more perfect resemblance. I must leave the more detailed consideration of the manner of action of natural selec-

*"Cesnola's Experiments with Mantis.—To test the selective value of color markings, Cesnola fixed specimens of the brown and green *Mantis religiosa* on plants, some of which were against harmonious, others against disharmonious backgrounds. The result was that most of those which were inconspicuous because of a harmonious background escaped, while most of the others were eaten up by birds.

"Poulton's and Sanders' experiments with butterfly pupae. Numerous pupae of various colours were placed under conditions favouring protective coloration and others under opposite conditions. The conclusion was that protective coloration is a real survival factor, and one that operates so as to give the protective coloured individual a decided advantage in the struggle for existence."

H. H. Newman, "Evolution, Genetics, and Eugenics," p. 257.

tion in the preservation of resemblance to a later stage of this address; but I must point out that the existence of such an adequate mechanism for the production and preservation of cryptic resemblance is an added argument in favour of the hypothesis that cryptic resemblance is truly mimetic.

Some cryptic insects are predaceous and it is possible that in some such species the resemblance may have given the possessors a special survival value by enabling them to approach their prey more successfully without being observed. This would permit of the natural selection of cryptic resemblance in such cases, but it is probable that in most, if not all, such insects, concealment from their natural enemies would be a more potent factor in selection than concealment from their prey.

I have pointed out that the natural selection of cryptic resemblance is dependent on the appearance of suitable variations. To some it may appear that natural selection is therefore of but minor importance, and that the major problem is to determine what factors cause the appearance of suitable variations. Undoubtedly this is a most important problem, but its solution is not as essential to a proper understanding of the subject under consideration as would appear at first sight. Everything indicates that the suitable variations are produced entirely without reference to any possible resemblance, and that they are not produced as a response to the appearance of the normal background of the insect in which they appear. Only such variations as happen to be suitable are selected; others, having no special survival value, are not preserved. The factor which causes the appearance of a suitable variation has therefore no direct connection with the production of cryptic resemblance; while natural selection operating through the medium of discriminating agents appears to be the only possible factor which can directly produce true mimetic resemblance. Appearance can only be produced as a response to appearance by some agency which can see and discriminate, and only natural selection appears to be able to employ such an agent. Natural selection is generally considered to be at least one of the most potent factors in the evolution of all kinds of organisms and their adaptations, yet no more is known of the actual cause of the variations which are considered to have been selected in these than of the variations which are selected in the production of mimetic resemblance. Natural selection explains the evolution of mimetic resemblance as adequately as that of any other adaptation.

Before describing a number of examples of cryptic resemblance, in order to illustrate the foregoing considerations, I must mention the criticism often made that, though very inconspicuous when on the correct background, cryptic insects are commonly found in other positions. For example such remarks as this are often made: "Stick-insects would be very inconspicuous if only they would live amongst sticks." It is obvious that the casual observer in the bush, who is not specially looking for such insects, will only see insects with an effective cryptic resemblance when the background does not harmonise with their appearance, that is, when they are not in their natural environment. As the insects are only to be seen easily when in an unsuitable position, a very false impression is apt to be created.

A very large percentage of the specimens of cryptic insects which are taken are found resting on an unsuitable type of background, causing them to be conspicuous; and it is somewhat difficult to prove, even by careful observation in the field, that normally the insects occupy a suitable environment in which they are inconspicuous. That this is so, however, is strongly indicated by such observations as the following. I have sometimes spent as much as half an hour un-

successfully searching for certain green long-horned grasshoppers, which I have known to be present close to me, as I could hear them chirping all around at some little distance. I have also spent practically a whole day collecting insects in a certain small area without seeing a single mantis, and yet at night, by lantern light, mantids were observed in large numbers in the same area, as they have the habit of climbing to the top of grasses and other plants at night, in which position they are naturally very conspicuous. Sometimes, having the good fortune to have distinguished an insect on a suitable background, I have described the insect and indicated its position to within a few inches to a friend, and even then it has taken him a matter of minutes to find it. In the same manner on a number of occasions I have had the greatest difficulty in distinguishing an insect the general position of which had been indicated to me by a fellow entomologist. Also the fact that "rare" species of insects, seldom seen under natural conditions, may be quite common amongst the debris deposited by flood-waters, indicates that the keenest eyed entomologist fails to perceive many insects in their natural environment.

If a long series of insects exhibiting cryptic resemblance be examined, it will be found that concealment is brought about in two quite distinct manners. Some forms closely resemble a definite object which occurs in their normal environment, such for example as a stick or a leaf; and the resemblance is often surprisingly perfect, minute details of the model appearing to be copied with marvellous accuracy. This is termed special cryptic resemblance.

The majority of insects exhibiting cryptic resemblance, however, do not definitely resemble any particular object in their natural environment. The general appearance of these insects is such that it closely conforms with that of each insect's normal background, and when such an insect is removed from its natural environment there is nothing in its appearance to suggest clearly what it resembles. This type of resemblance may be termed general cryptic resemblance.

Many insects exhibiting general cryptic resemblance often appear to be most conspicuously coloured when removed from their natural environment, contrasting colours being distributed over the body in bold stripes or blotches; yet in their natural habitat many of these forms are amazingly difficult to see. The principle of "camouflage" is here in evidence, a principle with which most people are now familiar, owing to its extensive employment recently in war. In order to conceal a gun or other military object it was not given a uniform coat of colour of exactly the same shade as its surroundings, but large irregular blotches or stripes of a number of strikingly contrasting colours were painted on it. From a comparatively short distance the form of a gun so painted was no longer obvious. The attention of the observer was distracted from the shape of the gun, and what appeared to be a number of quite independent and irregular small objects was all that was seen. The outstanding effect of camouflage is to prevent the eye from seeing the light and shade on the object it is desired to conceal, as the visual perception of the solidity of an object depends entirely on the arrangement of light and shadow on it. For the production of the most effective kind of camouflage it is necessary not only to paint a number of irregular patches of contrasting colours on the object, but also to make these approximate to the average shape of the various objects forming the background; and the total effect of the contrasting colours, that is the colour of the whole as it would be seen from a distance too great for the perception of the individual patches, should approximate closely to the average colour of the background.

It might be inferred from the description I have given of the two main types of cryptic resemblance that it would always be easy to distinguish one

from the other. In practice, however, this is not the case. There is a very large number of intermediate forms; and, in fact, these intermediate forms predominate. It is not often that an insect looks like some definite object in its background, but frequently the colour markings or form of the insect appear to be an almost perfect copy of a portion of some object on which it commonly rests, for example, the bark of a tree or the surface of a rock. There is every transition between this type of resemblance and true "camouflage," in which bold markings simply serve to obscure the true form of the insect.

Really good examples of special cryptic resemblance do not appear to be common in Australia. Probably the best known examples of this type of mimetic resemblance are *Phyllium* and *Kallima*, both insects belonging to the Indo-Malayan region. Close relatives of these insects occur in the northern parts of Australia, but they do not exhibit as perfect mimetic resemblance as the Indo-Malayan species.

Phyllium is one of the "leaf-insect" type of phasmid. In colour and form the resemblance to a leaf is very perfect. The insect is bright leaf-green; it closely resembles a broad leaf in shape; and, perhaps the most remarkable resemblance of all, the venation of the front wings has been fundamentally altered so that it looks like the normal venation of a leaf. The front wings cover practically the whole dorsal surface of the insect, so that the resemblance to a leaf is principally due to these.

Kallima resembles a dead leaf and the resemblance is perhaps even more perfect than that of *Phyllium*. In shape the resting insect is almost exactly like a leaf and the venation of a leaf is beautifully indicated by a series of colour markings, which are quite independent of the true venation of the wings. In addition to this there is a number of circular marks which have a considerable resemblance to mould spots on a leaf and in the centre of some of these is an apparent hole, consisting of a piece of clear membrane free from scales. Of a comparatively long series of specimens of a Javan species, *K. paralecta*, which I possess, no two are of exactly the same colour, the ground colouration being of many shades of brown, and in each specimen the resemblance to a leaf can only be described as amazing. The singular perfection of the resemblance in this insect has for long attracted a great deal of attention to it; and, strangely enough, it has been claimed by some writers on this subject that the perfection of this resemblance is strong evidence that a mimetic explanation is inadequate to account for it. The resemblance is so perfect and detailed, they say, that it is impossible to conceive how such perfection could have been produced by natural selection and that therefore some other process must be the true cause. It is generally suggested that some form of orthogenesis has probably produced the resemblance. I shall deal with this problem in more detail later.

Perhaps the best common example of special cryptic resemblance to be found near Sydney is *Acrophylla chronus* Gray (Pl. ix.), though many other less common phasmids are equally good and some may well prove to be even better. This insect is almost exactly like a long leafless twig. The thoracic and abdominal segments are elongate and of almost uniform diameter and the whole insect is dull brown in colour. The legs are very long, and the front legs are often held straight out in front of the insect, the pair being closely applied together to form a thin prolongation of the body; and there is a special excavation near the base of each leg to accommodate the head when they are held in this position. At the posterior extremity are two structures, the cerci, which look like small curled portions of dead and dry leaves. The perfection of the concealment afforded by this form and colouration will be appreciated by referring

to the photograph of this insect (Pl. ix.), which, like all similar photographs illustrating this address, was taken of the insect in its natural environment, just as it was found and without interfering with it in any way. In one respect, however, it must be admitted that the concealment is not perfect and, had it not been for this curious defect, I should certainly not have seen the specimen I have photographed. I have noticed, not only in this species, but also in a number of other species of phasmids, that when disturbed they will often commence a curious movement consisting of a slow jerky swaying of the body from side to side. The movement is so unusual as to attract attention immediately. However, I do not believe that it is an invariable response to the approach of a possible enemy. I have taken specimens of phasmids which did not behave in this manner, and the almost invariably accidental manner in which I first observed such specimens leads me to believe that I must frequently pass by specimens which are fully exposed.

Many other orthopterous insects show special cryptic resemblance, but this is usually less perfect than amongst the phasmids. Many long-horned grasshoppers not only have a green colour which almost perfectly matches the leaves amongst which they live, but the shape of the exposed wings is very leaf-like and the venation has often a strong resemblance to that of a leaf. The wings meet over the back of the insect at such an acute angle that the insect appears to be not only flat but excessively thin, which adds further to its leaf-like appearance. A photograph of such a long-horned grasshopper, *Caedicia olivacea* Brunn., is shown on Pl. viii., fig. 2. It will be observed that the legs are stretched out behind the insect and are not greatly flexed. This appears to be the normal position of rest and renders the insect distinctly less conspicuous than when the legs are flexed ready for jumping, which position is commonly assumed when the insect is disturbed. The insect photographed was not in its normal environment, but on a rose tree in a garden. Its colouration and form render it much less conspicuous when living, as it normally does, amongst leaves of *Angophora* and *Eucalyptus*. I have already mentioned how very effective is the concealment of these insects and the difficulty I have experienced in finding them, even when I have known that numbers were present in a comparatively small area.

The larvae of geometrid moths have for long attracted attention owing to the almost perfect resemblance to dead twigs which many species show. The long cylindrical form and the position of the legs and prolegs at the extremities of the body appear to be normal for this group of insects; and these characters probably form the basis on which the mimetic resemblance has been developed, and were probably not themselves developed to take part in the production of resemblance. This is indicated by the fact that throughout this group of moths these larval characters are practically uniform, in spite of the fact that in many species the larvae do not exhibit cryptic resemblance; and, in some which do, the resemblance is quite independent of this peculiar form. In many species, however, the resemblance of the larvae to dead twigs is very remarkable, this resemblance being brought about by the colouration, the habit of the larva of clinging to a twig by the prolegs only and holding out its body stiffly at an acute angle to the twig on which it is resting, by its immobility in this position, and, in many species, by the development on the body of small outgrowths which closely resemble irregularities which occur on the type of twig on which it is normally to be found.

I have already pointed out that an intermediate type of resemblance between special and general cryptic resemblance is very common. Examples are extremely numerous and I can select only a few for purposes of illustration.

An excellent example is afforded by the common *Cryptolechia raphidias* Turn (Pl. xiv., fig. 1). This small oecophorid moth has the habit of resting on the bark of the stringy-bark gum and, as will be seen from the photograph, it is extremely inconspicuous in such a position. The front wings, which cover the body when at rest, bear a number of irregular markings varying from dark brown to dirty white, and these markings correspond closely to the appearance of the surface of the bark of the stringy-bark gum. The markings also have the effect of distracting the attention from the general form of the insect.

In the same manner the irregular brown lines and other markings on a general whitish background cause *Ectropis desumpta* Walk. (fam. Boarmiidae, Pl. xiii., fig. 1) to appear very much like the lichens which cover the trees in the brush country in which this species is found. It will be seen that the insect I have photographed is resting with the right wings covering a piece of lichen, while the left wings overlie bare bark. The former are difficult to see, while the latter are quite conspicuous. This illustrates the fact that a cryptically coloured insect is inconspicuous only on its correct background and that it will not invariably settle on a suitable background. There is, in fact, very little evidence that such insects ever select suitable backgrounds. Their colouration has been evolved to be in conformity with the normal background, or some common background, and the selection of a suitable resting place is evidently by means of other characters than suitable appearance. For example, some moths only settle on the surface of rocks, others on particular kinds of tree-trunks, but the appearance of the surface of these objects is by no means always in conformity with that of the insect, though commonly it is.

In *Syncora silicaria* Gn. (fam. Boarmiidae, Pl. xiii., fig. 2) colouration and attitude appear to be definitely correlated in the production of cryptic resemblance. It will be noticed that, in the photograph, the insect is orientated on the tree-trunk in a somewhat unusual manner. Instead of the body being more or less vertical with the head uppermost, as is usually the case when a moth settles, it is horizontal, and it will also be noticed that the bold striped markings render the insect very inconspicuous when settled in this position. If it settled with the head uppermost the markings would be at right angles to the principal markings of the tree, the edges of the flakes of bark, and it will readily be understood that it would be most conspicuous in such a position. Another point of interest is that when an attempt was made to place this insect in a box it was only detached from the bark with difficulty. Instead of flying away the moment an attempt was made to touch it, it remained completely immobile. It was possible to lift up the wings, and even the thorax, without disturbing the insect, which immediately resumed its normal position when released. This habit of immobility appears to be characteristic of a large number of cryptic insects, and it is easy to appreciate its importance in connection with concealment. I have noticed this habit in a considerable number of insects exhibiting cryptic resemblance, and it seems probable from my general observations that it is very common, if not the rule, in such insects, and that it is seldom, if ever, found in other types. In order to prove this interesting and important point, however, it would be necessary to make a statistical record of careful observations on a large number of cryptic and other insects. Though this habit has often been claimed to indicate intelligence in an insect, or other animal exhibiting it, it is almost certainly a tropistic response to a particular set of conditions. There is little question that the insect remains immobile, not because it knows that it is concealed, but because the nervous system is so constituted that under the influence of certain stimuli it responds by retaining the insect in a state of

immobility. This is indicated by the common observation that a cryptic insect remains equally immobile whether the background on which it is resting affords it concealment or renders it conspicuous. On the other hand it is unreasonable to believe, as some apparently do, that a mimetic explanation is disproved because such habits as this can be interpreted as purely tropistic responses. It may be admitted that the insect remains immobile because it cannot do otherwise under the prevailing conditions, on account of the construction of its nervous system, but this does not account for the production of such a habit. It is probable that habits are evolved and submitted to selection in the same manner as structure. In all probability it is actually special structure of the nervous system which is inherited, the habit being an expression of this structure. It is probable, therefore, that habits, such as immobility, have been evolved in mimetic forms as a definite portion of the whole mimetic facies; the preservation of such habits being due to factors similar to those which have caused the preservation of adaptive structure, and that they are dependent on structure just as is appearance. The tropistic theory deals only with the nature, and to some extent the mechanism, of response in an organism with a given nervous constitution, and does not even attempt to deal with the manner in which this nervous constitution came into being. This theory, therefore, does not account for the presence of a particular habit, but describes its nature and manner of operation.

Another Sydney moth which shows this intermediate type of colouration well is a species of *Scoparia* (fam. Pyraustidae) which is very common in Hawkesbury sandstone country in September and October. It is to be found on lichen covered rocks. The marbled wings, of various shades of brown and dull white, approximate to the appearance of the lichen very closely, and I have several times found a moth only after examining a small piece of lichen for the space of a minute or more. The marbling of the wing cannot be considered as a copy of the background, but the small areas of varying colours into which the wing is divided give the illusion of a number of small separate things, like the small expansions of the lichen, and the form of the moth is thus overlooked.

A large number of different species of Australian moths are known to show this type of resemblance, in spite of the fact that the majority of moths are collected after they have been disturbed or when out of their normal environment. There is, however, no point in multiplying the number of examples for the purposes of this address.

Many other types of insects besides moths exhibit resemblance of this nature. For example, a number of longicorn beetles belonging to the Lamiinae are coloured with varying shades of grey and brown, in such a manner as to be extremely inconspicuous on bark; and such forms of these as have come under my notice have the habit of holding the antennae straight out in front of the head, and closely applying them to the bark of the tree. This not only conceals what would otherwise be conspicuous structures, but causes the contours of the beetle to pass almost imperceptibly into those of the tree-trunk or branch.

Cryptic resemblance of this type is also well developed in the Neuroptera. Examples are particularly common in the families Myrmeleontidae, Osmylidae, Hemerobiidae and Psychopsidae. It has not been my good fortune to see specimens of the last family settled in their natural environment; but, from descriptions I have heard, it would seem that they are amongst the most perfect examples of cryptic resemblance. The resemblance of neuropterous insects to their background is considerably assisted by the normal transparent nature of the wings. Blotches of pigment, usually brown or black, commonly exist on the wings, and bring about concealment in the manner I have already described; but

the general colour of the background showing through the transparent parts of the wing causes the insects to be equally inconspicuous on a large variety of backgrounds. The expansive and membranous wings are usually held closely applied to the surface on which the insect is at rest, so that there is no perceptible change in the general contours of the surface. This is well shown in the photograph of *Formicaleo brevisculus* Gerst. (Pl. viii., fig. 1) in which it will be seen that the faintly mottled wings are practically wrapped round the small twig on which the insect is resting, and that all parts of the body are closely applied to it. Thus the head, antennae, and legs, as well as the wings, appear to be continuous with the contours of the twig. An exactly similar habit of *Archichauliodes guttiferus* Walk. (fam. Corydalidae) causes this large and common insect to be seldom seen. On a flat rock surface the wings and the rest of the body are held flat against the surface, while on a twig of a bush at the edge of a stream the insect will often wrap its wings completely round it so that it is equally inconspicuous in either position. Perlids, which closely resemble corydalids in many respects, have in general the same habits as *A. guttiferus* and are equally inconspicuous.

Even a brief survey, such as the present, of the general type of cryptic resemblance would be incomplete without mention of orthopterous forms, as it is particularly well developed in this order. It appears to me, in fact, to be the normal system of colouration in this order, but a few examples will suffice.

Goniaea australasiae Leach is a common grasshopper to be found on the ground amongst dead gum leaves. It is usually pale brown in colour, but there is a considerable variety of shades of brown in different individuals. The variations in colour appear to have approximately the same range as those of dead gum leaves, and the insects are very inconspicuous in their natural environment. Were it not for a special modification in structure, however, the robust nature of these insects would render them conspicuous amongst such thin flat objects as gum leaves. The large prothorax bears a prominent laterally compressed ridge along the mid-dorsal line, and, in the adult insects, this ridge is practically continuous with that formed over the body by the closed tegmina. In the larvae, the prothoracic ridge is continuous with a similar ridge which extends along the mid-dorsal region of all the abdominal segments. This thin edge formed along the whole length of the insect gives a very deceptive appearance of thinness and flatness, except when viewed from immediately above.

In the Mantidae, cryptic resemblance, so characteristic of the family, is almost entirely of the general type. The dull brown and grey and often grotesquely formed Perlamantinae are most inconspicuous on the ground amongst dead leaves and sticks, in which situation they are normally found. The common *Orthodera ministralis* Fabr. is almost uniformly green in colour, and harmonises with the leaves amongst which it lives; and the various shades of green and brown of *Tenodera australasiae* Leach (Pl. ii., fig. 23) cause it to be almost completely concealed. The narrow white line running along the anterior edge of each tegmen tends to break up the apparent mass of the insect, and this effect is heightened by the bold longitudinal green and brown markings. The inconspicuous nature of this insect is well shown in the coloured photograph, but to appreciate this fully it is necessary to imagine its appearance when viewed from a short distance amongst large quantities of vegetation. The insect would probably be even less conspicuous amongst plants with larger leaves, but I can vouch for the fact that it was inconspicuous in the extreme in the position in which it was photographed. I stood within a yard of it for at least five minutes before

seeing it, and it was only owing to the fact that the insect I was trying to photograph flew close to it that I saw it eventually.

I might remark that the cryptic colouration exhibited by predaceous insects, such as mantids, is often referred to as aggressive resemblance. It is considered that the inconspicuous nature of these insects enables them to approach their prey without disturbing it, as well as concealing them from their natural enemies. Cases are known to exist in other countries of mantids which closely resemble flowers, and it is claimed that insects are attracted to these apparent flowers and so fall an easy prey to the mantids. I know of no such case amongst Australian insects.

I have already indicated that every gradation is to be found between the two extreme forms of cryptic resemblance, viz., special cryptic resemblance and camouflage. In many of the cases I have cited in connection with general cryptic resemblance the principle of camouflage is evident; for example, in *Tenodera australasiae* and *Syneora silicaria*. A few examples of insects in which it is developed in almost its pure form will, however, be of interest.

The hawk-moth larva shown in Pl. xii., fig. 1, illustrates the principle very well. The ground colour of the dorsal region is dark green and of the ventral region pale green and at regular intervals along the sides of the body are bold triangular areas bordered by bright blue lines. When the insect is taken from its natural environment it appears to have the most conspicuous type of colouration imaginable, but these large and robust larvae are amazingly difficult to find in bushes in which they are known to be living. Imagine the insect amongst a mass of foliage, instead of being picked out on a single twig as it is in the photograph, and I think it will be realised that it would be far from conspicuous. The bold markings distract the attention from the mass of the insect, which appears to be broken up into a number of disconnected small objects, closely corresponding to the light and shade on the leaves.

In the species of *Betira* (fam. Acridiidae, Pl. xii., fig. 2) photographed, it will be seen that the mass is very effectively broken by a bold longitudinal white line. This insect lives in clumps of wiry grass, and its form and habits are closely correlated with this environment. The whole body is elongate and very narrow, tapering gradually towards the posterior end and more rapidly anteriorly, the head being conical in form, with the antennae arising from the extreme tip. At rest, the antennae are commonly closely applied to one another, appearing to be a narrow continuation of the body; the legs are closely applied to the sides of the body, with the femora and tibiae parallel to it; and the body is held firmly against the grass on which the insect is resting. Smaller species, and possibly the larvae of this species, are uniformly green, or sometimes brown, and such small individuals are of approximately the same thickness as the blades of grass on which they settle. The characteristic form and attitude which I have described causes these small individuals to be very inconspicuous. Were it not for the bold longitudinal white stripe, larger individuals such as the one I have photographed would, however, be conspicuous, in spite of their form and attitude, as they are so much thicker than a blade of grass. The white line completely destroys all appearance of bulk and renders the insect very inconspicuous. It is worthy of note that the white line is not morphologically a longitudinal line but continues from the head across the thorax and then along the femur. Owing to the resting attitude of this insect, a simple and continuous longitudinal line is produced; and the perfect continuity of this line on such a heterogeneous basis is strong presumptive evidence that continuity and straightness have definitely

been produced as such. This in its turn indicates that a mimetic explanation is required to account for the production of the appearance of this insect.

In *Urnisa erythrocnemis* St. (Pl. xi.), a common grasshopper in sandy areas, concealment is also effected by means of a number of bold markings which destroy all appearance of continuity in the form of the insect. In this insect there is a number of irregular black marks on a general pale grey background. The insect is usually to be found fully exposed on the surface of sand; and commonly scattered over this are innumerable small objects, mostly black or dark brown, such as bits of stick and charcoal, which give the surface of the sand a mottled appearance. On this *U. erythrocnemis* is surprisingly difficult to see, unless it moves. Attention is only directed to the dark markings of the insect, which appear to be isolated and irregular small objects similar to hundreds of other small objects on the surrounding sand. The adult grasshoppers illustrate very clearly the efficiency of the camouflage system of colouration, as the one part of the insect not so coloured, the tegmen, is the only part which is in any way conspicuous. The infinite variety of small objects on the sand, however, distracts attention even from these tegmina, though the complete visible form of a uniformly coloured insect would doubtless be conspicuous on account of its special and characteristic symmetry.

In some insects what is essentially a camouflage system of concealment is in evidence which does not depend on a bold pattern of contrasting colours. In such forms irregular expansions and spines conceal the true bulky form of the insect, and special habits and attitudes often assist in the perfection of the cryptic resemblance. *Ertatosoma tiaratum* Mael. (fam. Phasmatidae, Pl. x.), forms a good example. In this insect certain segments of the legs, and some of the posterior abdominal segments, are drawn out into leaf-like expansions, and irregular short spines are to be found on many parts of the body. Also the abdomen is normally curled upwards, so that the end of it lies practically over the thorax. This habit appears to be well developed in all but the full-grown and egg-laden females, in which the body is so large that such flexion would be impossible. It will be seen from the photographs (Pl. x.) that this structure and habit do not cause the insect to resemble a leaf, or any definite object in its background, but they do render it very inconspicuous. The eye does not perceive the large robust insect, but a group of apparently independent irregular flattened objects which do not attract attention. In taking the photograph shown in Pl. x., fig. 2, I, with some difficulty, persuaded the insect to uncoil the body; and it will be appreciated by comparing this photograph with the other shown in fig. 1 how important is the habit of curling the abdomen in rendering the insect inconspicuous.

I have shown that in a suitable environment many insects are very efficiently concealed by their colouration, form and habits. It is important to know to what extent such insects are confined to a suitable environment. Casual observation gives a very definite impression that cryptic insects are almost completely confined to a particular environment, in which suitable backgrounds are common, though they are by no means always to be found on such backgrounds. It appears doubtful if insects ever select a place to settle on account of the concealment it may afford, but if suitable backgrounds are common in the type of environment to which a particular species is confined, it follows that a considerable proportion of the individuals will be found in concealment on such backgrounds. If cryptic resemblance is to give a special survival value to the possessors, it is not necessary that each individual of a species should always be found on a suitable background. It is sufficient that they should often occupy such a posi-

tion. Lack of recognition of this point has led to much irrelevant criticism of the theory of mimetic resemblance.

Casual observations, and impressions created by such observations, are unsatisfactory. It is eminently desirable that statistical observations should be carried out in various areas to show to what extent the colouration, form, etc., of insects are correlated with the environment. For convenience, areas of very distinctive types should be chosen, and closely related insects should be collected in two or more such areas. This will bring out most clearly the correlation in appearance, if any, between the insects and the backgrounds existing in their respective environments. I regret to say that I have so far carried out only one such observation, but it is instructive. Two small areas were chosen and, with the aid of several friends, all grasshoppers were collected first in one area and then in the other, about a quarter of an hour being spent in each. One area consisted of practically bare sand, scattered over the surface of which were numbers of small objects, mostly tiny bits of twigs and charcoal. The other area was under trees, the sandy soil being covered completely by dead leaves, twigs and branches. The grasshopper population of each area was very distinctive. In the former area practically all the grasshoppers obtained were *Urnisa erythrocnemis* (Pl. xi.), which I have already shown to be very inconspicuous in just such areas. In the second area the predominant grasshopper was *Goniaca australasiae*, already referred to as being very like a gun-leaf, and *Coryphistes ruficola* Burm. was common, this insect having a close resemblance to a dead stick. Correlation between the appearance of the grasshoppers and that of objects in their normal environment was therefore shown very clearly.

So far I have dealt only with a constant type of cryptic colouration, but in some species the colouration is variable, either in different individuals of the same species, or in the same individual at different times of its life-cycle, or in the same individual, according to its environment and irrespective of the period of its life-cycle.

Individual variation in colouration is very common amongst insects, and may be due to different environmental conditions operating on different individuals, such as temperature, humidity, light, etc., to hereditary factors, or possibly to some innate tendency to variation within the species. It often happens that each of the various forms of a species is of such a nature that it would be inconspicuous in one or other of the types of environment the species is known to inhabit. It is often claimed that dark forms are predominant in an unusually dark-coloured environment, and light forms in a light environment; and, from superficial observations I have made in the bush, I am inclined to believe that there is some direct relationship between the colour of a variable cryptic insect and its environment. Again, however, careful statistical observations are required, as general impressions may be misleading and most certainly cannot be considered as evidence.

Good examples of this type of variable colouration are to be found amongst the short-horned grasshoppers. Thus *Goniaca australasiae* is as variable in colour as are the dead leaves amongst which it lives and *Cirphula pyrrhocnemis* Stal. varies from pale grey, through all shades of brown to almost pure black, each of these shades of colour rendering the insect inconspicuous in parts of its natural environment. From casual observation there appears to be a tendency for the black form to be more numerous in bush through which a fire has recently passed, and in which, therefore, charcoal is a conspicuous part of the environment. This, and other species of grasshoppers with a similar range of

variation, form very suitable subjects for statistical observation, and it is important that such observation should be made.

Variation in appearance at different periods of the life-cycle is well marked in many species, and a number of such cases have been described. A good illustration is afforded in the larva of *Papilio aegeus* Dou. The young larva has a curious series of black and white markings which, together with its form, give the insect a considerable resemblance to a bird dropping. When the larva increases in size, the colour is completely changed to a bright green with a few vague markings, which causes it to be very inconspicuous on its food-plant. Such variation in colour has evidently an hereditary basis, but it is possible that in other cases the change may be due to a change in the environment. It is possible, for example, that the younger stages of the variably coloured grasshoppers I have already mentioned may vary in colour if they move, say, from a dark to a light environment, the variation being due to a direct effect of the environment. Very interesting, and extremely useful, breeding experiments might be carried out in order to determine if this is really the case.

Some animals have the power of changing their colour, according to the nature of the environment. The chameleon has achieved a quite undeserved reputation in this connection, as many other animals, particularly other lizards and also many fish, have the power of changing their colour much more rapidly, and have a greater range of colour than the chameleon. This type of variable colouration is not common amongst insects though, as I shall show, it is known to occur in some species. The change in colour is brought about by means of chromatophores which lie just under the skin of the animal. These chromatophores are branched and contractile cells, which contain pigment; and there may be several systems of chromatophores, each containing a different coloured pigment. The colour of the animal depends on the degree of expansion of the chromatophores. When these are expanded their pigment determines the colour of the animal, and when they contract the pigment is localised in a number of tiny spots which have little effect on the general colouration. The expansion and contraction appear to be controlled by the nervous system, and this receives the requisite stimulus from the colour of the surroundings, through the medium of the eyes.

It is sometimes said that a mimetic explanation is unnecessary to account for the resemblance to their background of animals which possess a chromatophore apparatus; as it is claimed that a tropistic response of the animal, by means of this apparatus, adequately accounts for the resemblance, and that a mimetic explanation is therefore superfluous. Again there is confusion between a mechanism within the individual and the mechanism of the evolution of the species. It is possible to account for the resemblance of an animal to its surroundings as a tropistic response, provided the animal has already the requisite structure with which to respond; but the tropistic theory does not attempt to explain how that structure was evolved. As this appears to be a clear case of the evolution of appearance, as such, some form of mimetic explanation appears to be necessary. If the colouration of the animal and the manner of operation of the chromatophore apparatus have not been evolved definitely in connection with the animal's environment, it is impossible to explain why the tropistic response under a given stimulus is always such as will cause the animal to resemble its surroundings. There is not merely a variation of response to different stimuli, but the variation is always of an adaptive nature, which strongly suggests the operation of natural selection.

An excellent example of an insect exhibiting this type of variable coloura-

tion came under my notice recently. This is the larva of *Nacaduba biocellata* Felder, a common blue butterfly which ranges over practically the whole of Australia. The larvae feed on the flowers of the wattle (*Acacia* spp.) and vary according to the colour of the flowers. Dr. Waterhouse informs me that the colour exactly corresponds to the colour of the flower on which the larva is feeding, whether this is a deep orange-red or lemon-yellow or green, when the flower is still in bud. I collected a considerable number of lemon-yellow larvae from similarly coloured wattle flowers by shaking these and picking up the larvae from the ground. In spite of the fact that the larvae were very common, prolonged search over the flowers failed to reveal a single specimen in its natural position. The larvae were placed in two white lined glass-topped boxes and one of these was placed in the dark and the other kept exposed to light. When I examined these later I found that all the larvae had changed colour. Those left exposed to light were almost transparent and of a pale cream colour, apparently the nearest possible approach to white. Of the larvae kept in darkness, most had changed to pale green, but two were a deep orange red, and one, which had been slightly injured near the middle, was green on one side of the injury and orange-red on the other. Though I unfortunately had no opportunity of examining these insects under the microscope, there can be but little doubt that the variable colour mechanism of this insect is in the nature of a system of chromatophores. Dr. Waterhouse informs me that there are several other species of lycaenids in which the larvae have a similar power of changing their colour.

In all the examples of cryptic colouration I have already mentioned, the concealment of the insect depends on its close similarity in appearance to its surroundings. In some insects another principle is employed, though it is commonly found in combination with normal cryptic colouration. The insects are so coloured that they may be extremely conspicuous at one moment and almost completely concealed the next. This is sometimes referred to as confusing colouration. I will take as an example the common *Castulo catocalina* Walk. (fam. Aretiidae). This moth has chocolate-brown fore-wings vaguely mottled with cream and white, and when settled on a sandstone boulder it is very inconspicuous. The hind-wings are bright yellow with an irregular black border and are only exposed when the insect is flying. When flying the insect appears to be bright yellow, and as soon as it settles on a rock it almost completely disappears. I think it will readily be understood that such a sudden complete change in appearance would cause an insect to disappear more completely than if the insect were brown both while flying and when settled, the perfection of the cryptic colouration being the same in each case. It is worthy of note that, unlike most cryptically coloured insects, this species takes to the wing readily on being approached, when it flies for a short distance and then resettles. The same system of colouration is found in many butterflies, the upper surfaces of the wings of these being brilliantly coloured and the under sides, the only portions exposed when the insects are at rest, are cryptically coloured. The common yellow-winged grasshopper, *Gastrimargus musicus* Fabr., also exhibits this type of colouration. The exposed portions when at rest, the head, thorax, tegmina and legs, are coloured with green and brown, forming a fairly efficient type of cryptic colouration, while the large fan-shaped hind-wings are bright lemon-yellow with a border of black. This insect also takes to flight easily when disturbed, flying a short distance and then settling again. It has been suggested that this system of colouration has a protective value of another kind. The sudden appearance of a brilliantly coloured insect close to the observer, in a position which a moment before appeared to be completely devoid of insect life,

is apt to startle him and enable the insect to reach a safe distance before pursuit commences, when, almost simultaneously, the insect disappears again. This startling effect is heightened in the case of *G. musicus* by a loud clicking noise emitted by the flying insect. The explanations given seem plausible, and even probable, but careful observation in the field is required in order to prove their truth.

Similar explanations may be applicable to a somewhat different type of confusing colouration which is only too well known to those who collect Diptera in this country. A confusing effect is produced quite independently of any normal cryptic colouration. Some species of bombyliids, and also of a number of other dipterous families, possess a brilliantly shining pubescence which, viewed from one angle, is most conspicuous, but is almost invisible from another. Take, for example, *Systoechus vetustus* Walk., a large and very common bombyliid in the Sydney district. The insect is completely covered by a long and dense pubescence, the hairs forming which slope backwards over the body. When flying in bright sunlight, the insect viewed from in front appears like a small ball of silvery light, but when it turns away from the observer it often seems to disappear suddenly in mid-air. The pubescence no longer shines, owing to the different angle it presents to the light, and disappearance is due to something in the nature of dazzle, combined with the fact that, when following an object with the eye, one does not expect it suddenly to change completely in appearance. Two views of a specimen of this species are shown on Pl. iii. In fig. 17 the insect is facing the observer, and the brilliant lustre of the pubescence will be noticed; while in fig. 18 it will be observed that the insect when viewed from behind is very inconspicuous against a dark background. No great stretch of the imagination is required in order to conceive that the natural enemies of such an insect might sometimes be deceived in the same manner as a human observer. It is suggestive that in this, and many other insects, the position in which the insect is least visible is that in which it is flying away from the observer.

Deceptive Resemblance.

I will now deal with the second main division of mimetic resemblance, deceptive resemblance or "mimicry," using the term in the restricted sense in which it is commonly now employed; but it will be necessary first to outline the theory of sematic or warning colouration, as this is very closely bound up in the subject under consideration.

Many insects have a very conspicuous form of colouration; so conspicuous that it gives the observer the impression that it must have been evolved in order to draw attention to the insects bearing it. It has been shown that, in a large number of such insects, conspicuous colouration is associated with some distasteful characteristic of the insect, such as the possession of a sting or an unpleasant taste. It is claimed that the colouration advertises the fact that the insect which bears it is unpleasant to eat; and that predaceous enemies, having, when young, experienced some unpleasant surprises which were associated with a particular form of conspicuous colouration, avoid insects so coloured. The advantage of this to the possessors of warning colouration is obvious, but it must be noticed that even according to this theory, the protection is not absolute. It is necessary to the theory that warningly coloured insects should sometimes be attacked, so that observations of attack on warningly coloured insects by no means disprove the theory. Still, it is most important that the theory should be based on ascertained facts, and not on general impressions and plausible

theories, as, unfortunately, there has been a tendency to do. It is important that as many observations as possible should be carried out in the field, though it is an unfortunate fact that opportunities for such observation are seldom presented. Much useful information should also be obtained from carefully controlled experiments made by feeding warningly coloured insects, and others, to birds, lizards, etc., in captivity. These experiments must be carried out with the greatest care as, when dealing with animals in captivity, it is difficult to avoid introducing abnormal conditions which may vitally affect the value of the experiments. Many such experiments have already been carried out by a number of competent observers, notably Marshall in South Africa, but the results of these have not been very conclusive, and puzzlingly conflicting results have not been infrequent. In general, however, they do demonstrate that warningly coloured insects are often distasteful to some animals; and the failure to give complete and convincing support to the theory of warning colouration may be due to the difficulties encountered when dealing with animals in captivity, such as varying degrees of starvation and satiety of the predators, or the use of the wrong type of predator. The last difficulty should be clearly appreciated. It is probable that different animals have different likes and dislikes so that, for example, an insect which is very distasteful to a bird may not be unpalatable to a wasp. On this theory it is only necessary that a warningly coloured insect should receive some protection on account of the association of its colour with some distasteful quality; complete immunity from attack by all kinds of enemy is not essential. I hope that in the near future careful experiments will be carried out in Australia on this subject, as we have many beautiful examples of warning colouration in insects which are easily obtained and with which it should be easy to experiment. It is most important that much more work of this type should be carried out than has already been recorded. The whole theory of deceptive resemblance appears to be dependent on the truth or otherwise of the theory of warning colouration.

Before giving examples of Australian insects which exhibit deceptive resemblance, I must point out that two main types of mimic are recognised. Sometimes it appears that a non-distasteful insect mimics a distasteful and warningly coloured model, and, by advertising distasteful qualities which it does not possess, it receives a protection from attack created by the model which is distasteful. Obviously, if protection is to be received in such a case, the mimic must be much less numerous than the model, as otherwise the colouration would not be associated with distastefulness by the enemy. This is known as Batesian mimicry, as the theory is to be attributed largely to the important work carried out by Bates on this subject. In the other type of deceptive resemblance both mimic and model are distasteful, and the terms mimic and model often appear to be interchangeable. If each distasteful species developed a separate type of warning colouration, each species would lose a large number of individuals in the process of educating its enemies and bringing about a recognition of its distasteful qualities. On the other hand, if a large number of species adopt the same system of warning colouration, each species would only lose a comparatively small number of individuals in this process of education, as the total number which must necessarily be destroyed in this process would be spread more or less evenly over all the species; whereas, in the previous case, a similar number of each species would be destroyed. This is known as Müllerian mimicry, after Fritz Müller, another of the early workers who have contributed so largely to our knowledge of this subject.

It has been found that no sharp line of demarcation can be drawn between

Batesian and Müllerian mimicry. It is probable that no insect is wholly distasteful to all kinds of predaceous animals, and every intergrade appears to exist between the most distasteful species and those which are palatable to all predators. Batesian and Müllerian mimicry are therefore to be considered as the extreme types of deceptive resemblance, and not as two separate phenomena. As will be shown later, it is probable that exactly the same processes have been involved in the evolution of each of these types.

In view of the complete lack of experimental evidence as to the unpalatability or otherwise of Australian mimetic insects, it will be impossible to divide them into the categories I have described; though it is possible to indicate, from various general considerations, to which category many mimics probably belong, with, I think, a fair degree of accuracy.

From an examination of the coloured photographs with which I am illustrating this address, it will be seen that there are many examples of remarkable resemblance between totally unrelated forms, often belonging to widely distinct orders of insects. It will be noticed that this resemblance is due to colouration, form and size, while some of the other photographs show that habit and attitude are also often involved in the resemblance. The latter characters also occur in many other mimetic forms, which I have not had an opportunity of photographing when alive, but I shall be able to give descriptions of some of these. Unfortunately there are a number of the mimetic forms I have figured with which I am not familiar in their natural environment, but I have every reason to suppose that, when observed in their natural state, many will show mimetic habits as equally perfect as those of the insects I am about to describe. Again I must stress the importance of making observations on the living insect in its natural environment. That insects might come to resemble one another in, say, colour, it is not difficult to believe; but, when resemblance involves such fundamentally dissimilar characters as colouration, form and habit, and when, further, it is found that close resemblance in one such character is commonly associated with resemblance in the other types of character, accidental resemblance appears to be quite inadequate as an explanation. As habit and attitude, which play such an important part in producing resemblance in many forms, are only to be observed when an insect is in its natural environment, it is important that research on this subject should be carried out as far as possible in the field.

If a long series of mimetic forms be examined, it will be found that these can be classified in various manners. One convenient method is to divide them into specific and group mimics: that is, those which have a single model and those which have a general resemblance to a group of closely related insects, but do not resemble any single species in particular. There is, however, no sharp dividing line between these two groups. For example, in a series of similar mimetic forms which have a general resemblance to wasps, some species may have a fairly close resemblance to one type, or even species, of wasp, while others resemble a different type, but a definite specific model cannot be found for any one of the mimics.

In this country specific mimics appear to be very rare and the best examples I can give are the species of *Systropus* figured (Bombyliidae, Pl. ii., fig. 5) and *Sceliphron laetum* Sm. (Sphecidae, Pl. ii., fig. 6), and *Chrysopogon crabroniformis* Roder (Asilidae, Pl. ii., fig. 3) and *Abispa ephippium* Fabr. (Eumenidae, Pl. ii., fig. 2). The resemblance in detail between mimic and model in these two cases is very remarkable, but it is possible that neither mimic exhibits a truly specific resemblance. In addition to resembling *S. laetum*, the species of *Systropus* mentioned bears a considerable resemblance to certain species of *Am-*

mophila; and *C. crabroniformis* resembles *Abispa splendidum* just as closely as *A. ephippium*. These two extremely similar species of *Abispa* are considerably different in appearance from any other species of eumenid, principally on account of their large size; and it is natural, therefore, that if these act as models for a mimetic insect the latter should resemble them specifically. On the other hand, when a long series of related species are similar in appearance and size and act as models, one would expect mimetic insects to approximate to the general colouration, form etc., of this series, rather than to that of individual species of the series. This is found to be so, for example, in the long series of mimics of *Odynerus* and related genera. This consideration would seem to account for the fact that specific mimetic resemblance is so common amongst butterfly mimics. Differences in appearance between closely related species of butterflies are often so great that a general resemblance to a group of butterflies would be of little use to a mimic; in fact it is difficult to conceive a general resemblance possible in many cases, so greatly does the colouration of related forms differ. It is a curious fact that those groups of butterflies which serve as models are precisely those in which specific differences in colouration are most marked; while groups with a fairly uniform system of colouration, such as the Lycaenidae, Pieridae, Hesperidae and Satyrinae, seldom or never serve as models. Excellent examples of such specific mimics amongst butterflies in other countries are well known and are to be found described and illustrated in most articles dealing with mimicry. When one considers the dominant position butterfly mimics have assumed in almost all discussions and considerations of mimicry in the past, it seems strange that such mimics should be almost completely absent from Australia, but such is the case. The only possible example I know of is the well known case of the female *Hyppolimnas missippus* Linne., which is said to mimic *Danaida chrysippus* Linne., but, compared with other species of mimetic insects with which I am familiar, the resemblance in the field is not convincing. Colouration is certainly very similar, but the habits of the two butterflies are so very distinctive that they can be distinguished at a glance, even at a great distance.

Practically all the mimetic insects which have come under my notice are group mimics. To show clearly the perfection of these mimics it would be necessary to illustrate in each case the whole group of insects which serves as a model; but limitations imposed by space and expense forbid this. In the plates illustrating this portion of the present paper, therefore, I have selected from the groups of models representative species which illustrate the general colouration, shape, etc., of the models. It will be noticed that the mimics do not resemble such isolated models in detail; nor should they be expected to do so, though the resemblance is often very remarkable. Such selection of models might be considered to be open to criticism, as it is necessary that model and mimic should occur in exactly the same situation and at the same time; and I have to admit that not only were most of the specimens of models and mimics illustrated not taken together, but that in some cases I have not observed either model or mimic in the field. I can safely claim, however, that the majority, at least, of the models and their respective mimics illustrated do occur together. The models are almost all insects with a very extensive geographical and seasonal distribution and certainly occur in the localities in which the mimics were taken. Also, I have observed that the majority of the models and mimics illustrated are to be found together in exactly the same situation, and there can be but little doubt but that the other forms, which are nearly all closely related to the forms I have observed, will also be found together. I therefore consider that the selection of models I have mentioned is justified.

If an examination be made of the occurrence of mimetic forms in the various orders it will be found that this is by no means haphazard. In some orders mimetic forms are comparatively numerous, in others they are very rare or completely absent. Also, within a particular order it will be found that mimetic species are often confined to a few small groups, such as sub-families or genera, in which they are common, or may even be the rule; while completely absent from, or rare in, all the remaining groups of the order. Two types of such mimetic groups can be distinguished; those in which all the species resemble models belonging to a single group of closely related species, and those in which different species resemble very distinct types of unrelated models. The former type is much the commoner, but the occurrence of the latter is very significant and gives rise to important considerations which will be dealt with later. A further examination of the cases in which the species belonging to one group of insects resemble models belonging to a single group will show that these can again be divided into two categories. In the one the models and mimics belong to the same order and therefore have a general similarity in fundamental structure on which the mimetic resemblance can be superimposed. In the other the mimics and models belong to different orders and therefore differ considerably in fundamental structure, so that the resemblance is of a more superficial nature, though not necessarily less perfect, than in the previous case. This type of mimetic resemblance is naturally the rarer of the two under consideration but it is the most significant, as such mimics show most clearly that there is nothing but appearance in common between mimic and model; and therefore the clearest evidence for the fact of mimetic resemblance is to be expected from the examination of mimics of this type.

Though most mimics belong to a comparatively few definite groups, there are a few which are to be found scattered apparently at random through the remaining groups of insects. Many of these are very perfect, and their very marked dissimilarity from their close relatives gives very convincing evidence in favour of the fact of mimetic resemblance.

I find it convenient to classify the examples of Australian mimetic insects I am about to describe in the manner I have just indicated, as the manner of occurrence of mimetic forms in the Insecta has an important bearing, both on the evolution and significance of mimetic resemblance.

When examining these examples of mimetic insects two main considerations should be borne in mind. First the evidence for the fact of mimetic resemblance. In particular it should be noticed that in most mimics resemblance is due to two or more characters which are evidently independent of one another, and the resemblance is often of a very complex nature. When one considers the great variety of structure and appearance existing within the Insecta, it is evident that the chance of any two unrelated insects accidentally resembling one another even in a single conspicuous character is very remote; while the chance of resemblance in two or more independent characters is so remote that very few insects should possess such resemblance. Actually it is found that in most insects which show distinct resemblance in one character there are other independent characters which also take part in the resemblance. This being so it can only be concluded that resemblance has definitely been produced as such; for, if resemblance were purely accidental, the vast majority of mimics should show resemblance in one character only. The second important consideration to be borne in mind is that, though the best cases for demonstrating the fact of mimetic resemblance are those in which the mimic differs greatly from its close allies and resembles a totally unrelated form, it is not to be expected that even

the majority of mimics will be of this type. When a mimetic form arises, it is natural that it should resemble a suitable model which in appearance or fundamental structure differs as little as possible from that typical of the group to which the mimic belongs. This involves a minimum amount of change in the production of a mimic and, evolution being simpler, mimics of this type are more likely to be produced, and would be expected to be commoner, than those in which a more complex change is involved. This is found to be the case, and the above consideration appears to me to account, in an adequate manner, for the fact that the non-mimetic relatives of many mimetic forms often exhibit certain of the characters which take part in the mimetic resemblance of the latter. These characters, by themselves, do not produce a convincing resemblance to the model of the mimetic form and it is probable that they have been produced quite without reference to the appearance of the model and that, therefore, such slight resemblance as they produce by themselves is purely fortuitous. It seems reasonable to suppose that this primary fortuitous resemblance permits the commencement of natural selection, so that on this basis a truly mimetic resemblance can be built up. The change involved in the production of such mimetic resemblance is sometimes very slight, such as a simple change in colour, but it is usually fairly complex; though the fortuitous characters I have mentioned, such, for example, as the form of the insect, may still play an important part in the production of resemblance.

Before natural selection can commence to operate in the production of a mimetic form it is necessary that the incipient mimic should first bear a sufficient resemblance to a suitable model to be mistaken for it occasionally, and this primary resemblance must necessarily be fortuitous. It is not surprising, therefore, that most mimics resemble models belonging to their own order, or to an order in which the general appearance does not differ greatly from that typical of the order to which the mimic belongs. Thus normally beetles mimic beetles, wasps mimic other wasps, and flies mimic other flies or wasps, the last two types of insects having a certain superficial similarity. The exceptional forms, in which this does not apply, are most easily recognisable as true mimics but, if it be considered that these forms demonstrate that mimetic resemblance does exist, there is no reason why the less highly specialised form of resemblance I have mentioned should not also be considered as true mimetic resemblance.

An excellent example of a complex group of mimetic insects within one order is afforded by the red and black beetles illustrated in Pl. i., figs. 56-68 and 73-95. These beetles constitute one of the most conspicuous groups of flower-visiting insects in this country. The lampyrids, belonging to *Metriorrhynchus* and related genera, are extremely common; while the similar insects belonging to other families are very much less numerous than the lampyrids, which must therefore be considered to form the model group. It will be seen that these models have a very simple type of colouration and, though there is considerable variation within certain well-defined limits, the appearance of all these insects is very similar. They are rather broader than many other lampyrids, the elytra have a characteristic series of longitudinal ridges and the surface has a dull, almost velvety, appearance. The colour varies from pure red on the elytra and black on the rest of the insect, through forms with varying degrees of the displacement of the red from the central portions of the elytra by black, and sometimes with red borders to the thorax, to pure black forms. Pure black species are rare, however; the darker forms usually having conspicuous red borders and tips to the elytra. The mimics, belonging to the families Cerambycidae, Curculionidae, Buprestidae, Cantharidae and Oedemeridae, have exactly the same

type of colouration, with a similar range from red to black in each family; their size is within the rather considerable range of that of the models; the shape is very similar and, in the majority of cases, the surface has a dull, velvety appearance and the elytra have longitudinal ridges similar to those characteristics of *Metriorrhynchus*. In most of these characters the mimics differ considerably from their close relatives.

A system of colouration in which all parts of the body are black except the elytra, which are bright red, can only be considered as very simple; and it is reasonable to suppose that the genetical basis for such a system of colouration should also be very simple. Red and black pigments are very common amongst insects, and, given the similar structural basis afforded by the common structure of all beetles, it seems probable that such a simple distribution of common pigments might occur independently in many different types of beetles. The similarity in appearance of all the species in this group is due to a similar structure, and similar, or probably often identical, pigments distributed in the same simple manner. That there is a fundamental similarity in the nature of the pigments and the genetical basis which determines its distribution is indicated by the fact that precisely the same type of variation from red to black, through various similar combinations of the two colours, is found in each of the families containing the insects which constitute this group. This is not fully demonstrated by the illustrations, as only representative species have been selected; but an examination of a considerable number of species and individuals has demonstrated this clearly to me. Further, an identical type of variation is sometimes to be observed within a single species, for example, in *Pseudolychnus haemorrhoidalis* Carter, one form is almost pure black (Pl. i., fig. 95) while another, var. *rufipennis* (Pl. i., fig. 91) has pure red elytra and the thorax is red at the sides, and figs. 88 and 89 on Pl. i. illustrate the sexes of an oedemerid, the male having almost pure red elytra, while in the female they are red with a large black central area.

This consideration, that the resemblance to one another of all the species in this group is due to fundamental similarity in structure and colour mechanism, would, at first sight, appear to indicate that we are dealing here, not with a true mimetic group, but with a group of convergent insects. Other considerations, however, place the matter in a very different light. If this type of colouration had arisen quite independently in each species, we should not expect to find any type of association between the insects; for there appears to be no reason why this type of colouration should not occur scattered at random amongst insects which live in different environments, unless the colouration could be considered as a response to common environmental conditions. All the species under consideration are typically flower-visiting forms, and are to be taken together on the same flowers; the greatest difficulty often being experienced in distinguishing mimic form model. The only characters in common between the mimics and models are similar colouration and occurrence in a similar environment in the adult state, and this combination is invariable. Though the life-histories of few of these species have been worked out, it is evident that the early stages of the various mimics and models must be passed in very different environments, for the typical habits of the larvae of the various families represented are as follows: Lampyridae, carnivorous, usually living under rubbish, etc.; Cerambycidae, Curculionidae and Buprestidae, here in the wood of growing trees; Cantharidae, live on eggs and stored food of Hymenoptera and eggs of Orthoptera; Oedemeridae, tunnel in decaying wood. It would seem probable, therefore, that the colouration is, in some manner, a response to the environmental

conditions of the adult. In addition to the red and black models and mimics under consideration, close relatives of each of these types of beetles are to be found in exactly the same situation, at the same time, but the latter differ fundamentally in appearance from the insects belonging to the *Metriorrhynchus* mimetic group. Thus there are two parallel series of related insects, having the same general structure and living in the same environment, but this common environment has not affected the two series of insects in the same manner, though within one series it appears to have brought about uniformity in the appearance of the constituent species. It is necessary to look for some special factor in this environment which can discriminate between these two series of insects; something which could affect one series in a different manner from the other. This cannot be any uniformly operating factor, such as atmospheric conditions or the nature of the food, and the only factor capable of discriminating between insects differing in practically nothing but appearance would seem to be constituted by the natural enemies of the insects; something which can see and discriminate is essential. We are thus led to the conclusion that the red and black mimics belonging to the *Metriorrhynchus* mimetic group have evolved their present appearance definitely in correlation with that of *Metriorrhynchus*, and not independently, in spite of the fundamental similarity of the structure and system of colouration of mimics and models. Actually it is probable that the origin of the colouration was independent in each mimic; its appearance independently in each species being possible owing to the fundamental structural and genetical similarity, but its preservation was due to the fact that it resembled the colouration of *Metriorrhynchus*, and the preservation of characters which appear is of paramount importance in evolution by natural selection. I shall have more to say about this point later, but I must point out the importance of distinguishing clearly between two entirely different processes involved in the process of evolution, viz., the appearance of variations within a species, and the preservation, or otherwise, of such variations.

I have mentioned that close relatives of the insects which form the *Metriorrhynchus* mimetic group are to be found in exactly the same situations. Now, if the natural enemies are to be considered the active part of the environment which brings about the resemblance of mimic to model in the one series of insects, one would expect the natural enemies of the other closely related forms to bring about a similar result in their case. This is found to be so. The red and black type of colouration is dominant amongst lampyrids here, but scarcely less important is the blue-green and orange colouration of such forms as *Telephorus nobilitatus* Er., which is sometimes found in swarms on flowers. The *Metriorrhynchus* mimetic group is closely paralleled by a *Telephorus* group, characterised by a narrow form, orange-yellow thorax and blue-green elytra, often with a yellow band near the tip. Cerambycids, oedemerids, clerids and cantharids are represented in this group, while there are many species of *Stigmodera* (Buprestidae) which appear to have some connection with it, the colouration being somewhat similar, though the form is always much broader.

An examination of the flower-visiting species of the Cerambycidae, one of the families involved in the two mimetic groups under consideration, is particularly instructive. These form a fairly definite group of the Cerambycinae, and in this mimetic species appear to be the rule, their models being of many and various types. The remaining species of the Cerambycidae, which do not visit flowers, never exhibit true deceptive resemblance, with the exception of a few which resemble ants, though a very large percentage exhibits cryptic resemblance. The variety of the mimetic flower-visiting forms and the diversity of their re-

spective models is well shown in the illustrations accompanying this paper (Pl. i., figs. 5, 16, 52, 54, and 73-80, Pl. ii., figs. 1, 4, 12, and 24, Pl. iii., figs. 3, 4 and 7, Pl. v., figs. 1 and 2). It will be seen that each mimetic longicorn resembles some common insect which visits flowers and is therefore to be found in the same situation, and that the models, in spite of their great diversity in appearance, belong to two groups only; the Hymenoptera and the Lampyridae. The fact that the resemblance exhibited is not to any kind of flower-visiting insect, but only to one of these two types, suggests that these insects, the Hymenoptera and Lampyridae, possess some special advantage over other insects; an advantage which may be shared by any insect which happens to resemble them. A further indication of the truth of this suggestion is that the majority of other types of Australian mimetic insects also resemble models belonging to these same two groups. In addition it is known that many hymenopterous insects are distasteful to birds; they possess stings and probably have other unpleasant characteristics. Observations in other countries have shown that many species of lampyrids also appear to have unpleasant characteristics, as they are often rejected by birds. In view of the foregoing series of facts and considerations I am unable to conceive of any other theory to account for the production of mimetic resemblance in the insects under consideration than that it has resulted from natural selection; this selection being exercised by the natural enemies common to mimics and models, which are capable of discrimination on account of appearance and which associate distastefulness with the appearance of the models. Such natural enemies in exercising discrimination between palatable and unpalatable insects on appearance would reject mimics as well as their distasteful models, whether the former were distasteful or not.

There are many other cases in which insects with a very similar appearance are to be found distributed through a number of families in the same order, but in few is there as clear a demonstration of the dependence of the appearance of the mimic on that of the model as in the *Metriorrhynchus* and *Telephorus* mimetic groups already mentioned. It is even probable that in some such apparent mimetic groups there is no dependence of the mimic on the model, so that it may sometimes be necessary to use some non-mimetic explanation to account for the resemblance observed.

In view of the fact that lampyrids so frequently serve as models for other insects it is curious that some species, belonging to the genus *Laius*, should appear to mimic chrysomelids. The resemblance between certain species of *Laius* and species of *Aulacophora* (Chrysomelidae) is very considerable, both in form and colouration. This has every appearance of being a case of true mimetic resemblance and, if so, the chrysomelids must be considered to be the models; for the form is very unusual for lampyrids and is typical for a large group of chrysomelids, and the chrysomelids are far commoner than the lampyrids.

Resemblance between chrysomelids and coccinellids cannot be considered to be very remarkable, for the species belonging to the two families are normally very similar. The general resemblance between these families is evidently fortuitous and is to be considered as simple convergence. There are, however, some cases in which a species of chrysomelid is almost indistinguishable superficially from some species of coccinellid. Such detailed resemblance may be due to the existence of similar tendencies for variation in two unrelated insects with a similar general structure, but it is not improbable that the normal general resemblance between the insects of the two families has served as a basis on which a true mimetic resemblance has been superimposed.

Recently a very remarkable series of examples of resemblance between

tachinids and blow-flies (Calliphoridae) have come under my notice. The resemblance is frequently so close that the two forms can often be distinguished only by a careful examination for the rather obscure family characters. Neither of these two types of insect has very well defined special habitats, so it is impossible to obtain evidence such as I have given in connection with the *Metriorhynchus* mimetic group, in order to show whether the appearance of one form has any relation to that of the other. The two families are so closely related, however, and the normal appearance of typical species is so similar that a mimetic explanation seems unnecessary in order to explain the resemblance. The close relationship, which involves a similar structure and genetical constitution, is probably, in itself, sufficient to account for the production of the same colour patterns, form, etc., in these two families; but this does not preclude the possibility that the preservation of such characters when they appeared was due to their resemblance to those of species belonging to the other family.

Similar considerations apply to the interesting case of the three moths, *Syntomis phepsalotis* Meyr., *Eressa paurospila* Turn. and *Trichocerosia zebрина* Hamp. (Pl. iii., figs. 19-30) the first two species belonging to the Syntomidae and the third to the Aretiidae. All the specimens figured were taken by Mr. G Goldfinch at exactly the same place within a few days of one another. It will be seen that, not only is the resemblance between the three species very considerable, but each species is very variable, and the variations are of the same type in each species. The last point indicates that the moths are not only similar in appearance but that the structural basis of the colouration is very similar in each species; for it is impossible to imagine any type of evolutionary process which could cause the various individuals of a mimetic species to resemble respectively individuals of a long series of very different variants of the model, except by the production and preservation within the mimetic species of a colour mechanism similar to that of the model. Natural selection can only preserve definite characters which appear and cannot produce variability. If, however, a particular range of variability is an attribute of an hereditary factor this may be preserved, but not modified. The existence of a similar range of variation within the three species under consideration, therefore, indicates strongly that the colouration is due to a similar factor, or combination of factors, in each species; for otherwise it would be necessary to consider that different factors in each species accidentally happened to produce the same range and type of variation, which is extremely improbable. Though the insects belong to two distinct families, the Syntomidae and Aretiidae, their structural differences are slight, and the colouration of each may well be simply an expression of the fundamental similarity of the insects, not necessarily involving, or precluding, a mimetic explanation. Such insects may well be truly mimetic, but they are of little or no use in demonstrating the fact of mimetic resemblance. On the other hand they provide considerable evidence in connection with a mechanism which is probably involved in the production of mimetic resemblance in certain forms, as will be shown later.

Within the Hymenoptera a number of apparently mimetic groups can be recognised. For the purposes of this paper the most important of these is the yellow and black banded group which, for convenience, may be termed the *Odynerus* group, as *Odynerus* and related genera occupy a dominant position and are probably to be considered as the models. I have already shown that hymenopterous insects as a whole probably possess distasteful characteristics, for many different species serve as models for other insects. It is evident, therefore, that if the *Odynerus* group, within the Hymenoptera, is to be considered to be mime-

tic, it is almost certainly of the Müllerian type. Yellow and black banded species, similar in appearance to *Odynerus*, occur scattered through most of the super-families of the Hymenoptera; the Vespoidea, Sphecoidea, Apoidea and even Chalcidoidea. Hymenoptera are characteristically flower-frequenting insects, and all forms are to be found together on flowers, so it is again impossible to bring forward evidence for the dependence of the similar forms on one another, such as was used in the case of the *Metriorrhynchus* mimetic group. In each of the yellow and black banded species the colouration appears to have the same structural basis, and may have been produced independently in each species by the operation of similar influences on a similar structure. It is probable, however, that in many species this particular form of colouration has been preserved on account of the resemblance it produced to some common form, such as *Odynerus*. Thus, though the complete pattern which produces the resemblance may owe its origin to the similarity of the general structure and genetical constitution of the mimic to those of the model, it is probable that in many forms the preservation of this pattern is due to natural selection. Such forms would necessarily have to be considered as truly mimetic. Similar considerations apply to the other dominant forms of colouration within the Hymenoptera, such as the large yellow-winged forms and the black and white banded forms.

An examination of the cases of mimetic resemblance described as occurring amongst butterflies in other countries shows that these are somewhat more complex than the examples I have described. The species which serve as models amongst butterflies are confined to a very few well defined groups, and the butterflies which mimic them also mostly belong to a comparatively small number of groups in which mimicry is a relatively common phenomenon. In a group of closely related models, however, the colouration is far from uniform, and each species may have a very distinctive and complex pattern which differs radically from that of all closely related species. The mimics, therefore, cannot have a general resemblance to the average colouration of the group of models, as this would be quite without significance and scarcely recognisable. In a large percentage of the cases of mimetic resemblance in butterflies it is found that mimics and models occur in parallel series. The mimetic butterflies belonging to one group, say a genus, all resemble models belonging to a single group of closely related butterflies. Each mimetic species resembles a particular species belonging to the group of models, and not only differs considerably from the normal type of its own group, but from each of the other closely related mimics. The change from the typical colouration of the mimetic group to that of the complexly coloured model would appear to be so great that one naturally feels that a complex type of evolution must have been involved in the change, and that such complexity could only be considered to have arisen by a series of gradual steps. The possibility of the sudden appearance of the pattern in all its complexity seems incredible. Punnet has dealt with this problem in a masterly manner and has brought forward considerable evidence to show that the mimetic pattern not only may have arisen suddenly, but that this is probable. I cannot go fully into his evidence and considerations here, and must refer those interested to his book, "Mimicry in Butterflies," but I can indicate the main factors involved.

In the first place it must be realised that amongst butterflies mimetic resemblance exists between forms which are much more closely related than are the mimics and models belonging to other groups of insects, with which I have already dealt. In most cases mimics and models belong to a single family, the Nymphalidae, though they commonly belong to different sub-families; but some-

times both mimics and models belong to a single large genus, e.g., *Papilio*. Also, the butterflies form a very homogeneous group in which there is but little variation in structure. There is every probability, therefore, that the genetical constitution, as well as the structure may be very similar in both mimics and models. Another significant point is that great differences normally exist between the colour patterns of the most closely related species in the subfamilies to which the mimics and models belong. It seems probable, therefore, that the genetical basis, of which the colour pattern is an expression, is of a peculiar form in these groups, having potencies for producing radically different colour patterns suddenly. If this were not so, one would expect to find a fairly gradual series of changes in colour pattern through a series of closely related species, and sudden great changes in appearance between neighbouring species should be distinctly rare. If, then, the genetical basis of colouration in two closely related groups be considered to be of this type, and also fundamentally similar owing to close relationship, there is every reason to expect that some at least of the species in the one group should resemble some of the species in the other; the similarity in appearance of these species being simply an expression of the fundamental similarity of the genetical constitutions of the two groups. This conclusion involves the idea that the potencies for suddenly producing widely different colour patterns are of a special type, which permits the production of only a certain definite series of types of colouration. Thus, the groups are not considered to be highly plastic and capable of producing a multitude of different colour patterns within certain very wide limits, but are considered to have a genetical constitution which may contain one or more of a certain limited series of possible factors, any one, or any combination, of which will express itself in a certain definite colour pattern. When the same colour pattern occurs in two or more groups it is considered that this is due to the fact that similar factors, or groups of factors, are operative in each case, and, as the number of possible factors is considered to be very limited, the appearance of parallel series of species with similar colour patterns in two or more groups is accounted for.

That complete and complex colour patterns have a simple genetical basis, such as has just been assumed, is indicated by the manner in which colour patterns are inherited in butterflies with polymorphic females. Breeding experiments have been carried out with several such insects, notably *Papilio polytes* by Fryer in Ceylon, *Papilio dardanus* in Africa and *Papilio memnon* by Jacobsen in Java; and it should be noted that in each of these cases two or more of the female forms are considered to be mimics of different models. The outstanding point brought out in these breeding experiments is that, with any type of cross between different forms, no intergrades between the forms are produced, though all the forms may be represented in the offspring of a single pair. Also, it has been shown that in *P. polytes*, the colour patterns as a whole behave in the manner of Mendelian unit characters, and this is also indicated in the other cases. Had the complex colour patterns been built up by the selection of a series of small variations, each of these variations would be expected to have its own separate genetical basis, and the result of a cross between different forms would be a series of mixtures of the characters which constitute the two colour patterns, and the offspring ought therefore to show a series of intergrades between the two parent forms.

It is probable, therefore, that the resemblance existing between many butterflies, which have long been considered to be mimics and models, is to be accounted for as due to fundamental genetical similarity of a special type, in which a limited series of factors is represented. Any particular combination of these

will give rise to a particular colour pattern, and if the same combination exists in two species of butterflies resemblance will result.

I have noticed that there is a general tendency to consider that Mendelian unit factors can only express themselves in simple morphological changes of the organism in which they appear, and many people seem to experience difficulty in believing that a single factor can be responsible for a complex change. This is probably largely due to the fact that in the best known examples of the inheritance of Mendelian factors, simple morphological characters, such as a simple colour, or a change in form or size, are associated with the factors. There is also a tendency to confuse the factors with the characters which they produce, so that no difficulty is experienced in understanding that a single simple character may be separately inherited, while the concept of the inheritance of a complex series of characters as a unit presents great difficulties. It should be noticed that the primary effect of a factor must be to produce some modification in the normal physiological processes of the organism in which it appears; for preceding a new character there must be a new process to cause its production. It is easy to conceive that a small modification in the physiological processes of an organism may well have far-reaching results. The interaction of a particular modified physiological process with a series of normal processes would be expected to cause a modification in the action of each of these, and the nature of the modification would probably be different in each case. A simple primary modification, therefore, may cause the secondary modification of a number of different processes, and these, in their turn, might cause a considerable change from the normal in the structures which they produce. It will thus be seen that very considerable and complex changes in appearance from the normal may only be the expression of a single simple physiological modification. There should therefore be no difficulty in believing that the complex colour patterns of certain apparently mimetic butterflies may have arisen at a single step, in all their complexity; and that a single factor which produces a simple primary physiological modification may cause the production of similar complex colour patterns in two or more fairly closely related butterflies, in each of which it appears.

It has no doubt been noticed that there is much in common between the case of butterfly mimics and that of the *Metriorrhynchus* mimetic group. The main differences between these groups are that there is a greater diversity in the appearance of the models, and, in most, a closer relationship between mimic and model in butterflies than in the *Metriorrhynchus* group. Similar general considerations apply to each of these groups. In each something is known, or inferred, about the mechanism which underlies the colour pattern; but however perfect the knowledge of this mechanism may be, it cannot explain why a particular colour pattern has persisted. If a complete colour pattern appears as a mutation in a single individual, this individual must have some special advantage over the other individuals of the same species if this pattern is to persist and become the normal pattern of the species. Assuming that the species is in a state of equilibrium with its natural environment, and that the new form possesses no advantage over the normal form, there will be no tendency for this new form to increase in numbers, even if the factor for the new pattern be dominant over that of the old one. When a species is in a state of equilibrium, its numbers remain approximately constant from year to year. Therefore, from each family produced by a pair of insects an average of only one pair will survive and reproduce in each generation. If, then, an individual develops a new pattern, the factor for which is dominant over that of the old one, an average of two individuals in each generation might exhibit this new pattern, though the

probability is that only one would do so. These individuals would be heterozygous for the new factor, for the chances of the mating of two individuals bearing the factor are so remote as to be negligible, even in later generations. On the other hand, if the factor for the new character be recessive there is little probability that the new pattern will ever reappear after the parent generation. Also, with the normal fluctuations in number of the species from generation to generation, it would probably not be long before the variation from the average would reduce the numbers of the new form from two to nil.

It thus follows that, for a new mutation to form a new species or to replace the older form of an existing species, it is necessary that it should possess some special survival value. In the case of the butterflies which are considered to serve as models, we know that a certain series of colour patterns have both been evolved and preserved. What factors operated to their advantage, causing their preservation, we do not know; but there is no reason why the same or similar factors should not have preserved the similar forms which are considered to be mimics, since we consider that both mimics and models possess similar potencies for the production of colour patterns. On the other hand, there is the possibility that the factor operating in favour of the preservation of these forms may be their similarity to particular models which enjoy a certain measure of protection compared with other insects; a protection which may be shared by any insects which happen to resemble them. The fact that mimics and models are usually to be found together, and that apparent mimics of models living in another country are extremely rare, indicates that a mimetic explanation is necessary to account for the preservation of the mimetic forms. If this is not so it is difficult to account for the fact that apparently mimetic forms are not to be found scattered at random over the whole geographical range of the groups to which the mimics belong, quite without reference to the presence or absence of suitable models.

In many mimetic butterflies, therefore, as in the *Metriorrhynchus* mimetic group, fundamental structural and genetical similarity appear to provide the mechanism which produces mimetic forms, while natural selection is the mechanism causing the preservation of the mimetic forms, this operating with definite reference to the models.

Having shown that the resemblances existing between many insects belonging to the same order must be considered to be mimetic, I will now direct attention to the even more remarkable case of resemblances existing between insects belonging to totally different orders. In such cases the structural basis on which the resemblance is built is necessarily quite different in the mimics and models, and it is scarcely credible that such distantly related insects should have a similar genetical constitution. In addition, it will be found that similar appearance is commonly produced in mimic and model in totally different ways. It is therefore obvious that resemblance in such insects cannot be due to an underlying structural or genetical similarity; and consequently this comparatively simple mechanism for the production of complex resemblances cannot possibly be involved in the evolution of mimetic resemblance in the insects now under discussion. Some other mechanism, or mechanisms, must therefore be found to account for the production of the features which build up the resemblance, though it seems probable that the same mechanism operates to preserve the resemblance as before, namely, natural selection.

In the simplest cases of resemblance between insects belonging to different orders, the normal appearance of the insects in the group to which the mimic belongs does not greatly differ from that of the model. In such insects a com-

paratively slight modification of the normal structure may bring about a very close resemblance to the model. The family Mydidae forms a very good example of this. All the flies belonging to this family have a certain general resemblance to wasps. They are all robust, rather elongate, active and strong-flying insects, with unusually long antennae for the sub-order to which they belong, the Brachycera. Even the least wasp-like forms, such as *Miltinus viduatus* Wwd. (Pl. vi., fig. 2), are often very wasp-like in their actions. They are particularly swift fliers, often visit flowers, and when settled are often seen to vibrate their wings rapidly, after the manner of wasps. This is indicated in the photograph by the blurred nature of the distal portions of the wings. On the other hand, when settled on sand, in which situation they are most frequently found, they are commonly quite unmistakably flies. It is possible that *M. viduatus* should be considered as a mimic of the common black and grey-banded psammocharids, but, if so, the resemblance is not very close. As this species shows little more than the common characteristics of the family, however, I think it reasonable to look upon it as a simple representative member of the family.

It is evident that a very perfect mimic of a psammocharid could be built up on such a basis with very little modification; colour alone would be sufficient. A number of such mimetic forms exist and two are illustrated. *Dioclistus aureipennis* Wwd. (Pl. ii., fig. 8) is one of the most perfect wasp mimics I know, the distribution of the brilliant yellow colouration closely approximating to that characteristic of a large and extremely common group of psammocharids, of which *Salix bicolor* Fabr. is probably the commonest. The unusually broad abdomen of this mydoid heightens its resemblance. *Dioclistus gracilis* Macq. (Pl. ii., fig. 10) is also extremely wasp-like, appearing very like certain common thynnids. It is worthy of note that the double row of yellowish spots along the abdomen of this fly consists of almost transparent areas of chitin, through which the tissues show, while the corresponding spots on the abdomen of the thynnid are opaque pigment spots. The few specimens of this insect I have taken were found visiting flowers and in company with thynnids, which they closely resembled in habit as well as appearance.

In the closely related family Asilidae there is a similar, but less obvious, general superficial resemblance to wasps. This family is, of course, very much larger than the Mydidae and contains a much greater variety of forms. It will be shown that many very different types of Hymenoptera serve as models to insects in this family, and it is interesting to note that in each case the model is one which approaches in general appearance to that characteristic of the group of asilids to which the mimic belongs.

Chrysopogon crabroniformis Roder (Pl. ii., fig. 3) is, in many ways, the most perfect example of a mimetic insect I know. The yellow and black markings on the thorax and abdomen correspond exactly to those of the model, *Abispa ephippium* Fabr. (Pl. ii., fig. 2), in superficial, but not in morphological, distribution. The wings are similar in shape, have the same bluish-black tips, bright yellow anterior and smoky-black posterior borders. The legs, also, are similar in colour and size. Only the antennae appear to take no part in the resemblance, these being of the normal small form typical of asilids. This is characteristic of asilid mimics, and it is rather remarkable in view of the astonishing development of the antennae in many of the wasp-mimics belonging to other families of the Brachycera.

Unfortunately I have not observed this insect when alive, but its habits, as described to me, appear to be almost identical with those of the much less perfectly mimetic *Neosarapogon princeps* Macq. (Pl. ii., fig. 14), which I have

observed on a number of occasions. This insect occasionally visits flowers, probably in search of its prey, but usually it is to be found flying rather rapidly in and out amongst shrubs with a curious circling motion, which is almost identical with the habits of the common yellow and black psammocharids, such as *Salix bicolor*. The yellow and black colouration, together with this habit, causes *N. princeps* to exhibit an extremely close resemblance to common wasps which occur in its immediate vicinity.

That *C. crabroniformis* is an almost perfect wasp-mimic in its natural environment is well illustrated by the experience of my friend Dr. I. Mackerras. His particular interest is in Diptera, he has had a great deal of field experience and he has also a very keen eye, so that any dipterous insect which manages to deceive him accomplishes no mean feat. *C. crabroniformis* did accomplish this. Dr. Mackerras had just completed a day's collecting and was about to go home when he saw what he took to be a particularly fine specimen of yellow and black wasp. After the manner of my various entomological friends he thought of my needs and decided to catch the specimen for me. This he did; then he placed the specimen in a killing-bottle and went home. It was not till sometime later, when he emptied his killing-bottle, that he discovered that he had captured his first specimen of *C. crabroniformis*, a prize beyond price in his eyes at the time. He never tires of telling of the thrill he experienced when he made this discovery.

A scarcely less perfect mimic is *Codula vespiformis* King (Pl. i., fig. 3). The model of this fly appears to be the group of common black and orange-banded species of *Odynerus* and related genera. It will be seen from the illustration that this asilid closely resembles its model, both in the colouration and form of the body, though the orange colouration in the mimic is due to pubescence while in the model it is due to the pigmentation of the chitinous body-covering. In addition, it will be noted that the anterior border of each wing is heavily pigmented. This is a very common phenomenon in mimics of diplopterous wasps and, when settled with the wings parallel to the body, these dark borders cause the wings to look very much like the narrow plicately folded wings of diplopterous wasps settled in a similar manner. From an examination of Pl. i. it will be seen that a dark anterior border to the wing is the rule amongst mimics of diplopterous wasps, and is absent from all other types of mimics; a very suggestive phenomenon.

Brachyrhopala limbipennis Macq. (Pl. i., fig. 50) appears to be a general vespoid mimic. It is a very variable species, varying from a fairly uniform pale brown to black with conspicuous yellow marks on the hind tibiae and a very narrow yellow band on the abdomen, as in the specimen illustrated. The highly polished and narrow-waisted body, and the dark bands on the anterior borders of the wings, together with the active and alert habits of the insect, cause it to appear very wasp-like. The paler brownish specimens are not unlike *Polistes*, while the specimen illustrated was extremely similar in appearance to eumenids taken in the same situation. When flying it had the appearance of a black and yellow-banded insect, the yellow marks on the tibiae being confused with the yellow bands on the abdomen of the model. The almost black anterior border of the wings, together with the extremely transparent nature of the posterior border, caused the insect, when settled, to look very like a wasp with folded wings.

Several other species of *Brachyrhopala* appear to be mimetic, making use of other models. *B. fenestrata* Macq. (Pl. i., fig. 24), for example, is a very close mimic of certain species of *Cerceris* (Pl. i., fig. 23).

Cyanonedys leuceura Herm. (Pl. i., fig. 41) has a very unusual appearance for an asilid, and it will be seen from the illustration that its resemblance to the common *Megachile suffusipennis* Ckll. (Pl. i., fig. 40) is particularly close in almost every detail. The resemblance involves both shape and colouration of wings and body, and a characteristic pubescence which gives a furry appearance of both insects. The thick white pubescence at the base of the abdomen is perhaps the most important character involved in the resemblance.

There is quite a large number of other cases in which asilids mimic wasps, a few of which are figured (Pl. i., figs. 11, 21, 35 and 37) but sufficient have been described to indicate the perfection of many such mimics, the great variety in the appearance of the models and that in each case the model fairly closely approaches the normal appearance of the group to which the mimic belongs; the mimetic resemblance being brought about by the superimposition of mimetic characters on a basis which by itself exhibits a certain similarity to the model. The similar appearance of mimic and model is, however, due to a totally different structural development in the two forms.

The closely related family Therevidae also contains a series of mimetic species, though they are not as numerous or as varied in appearance as in the Asilidae. This is only to be expected in a family which is so much smaller and exhibits so much greater uniformity in the structure of its component species. Therevids are all rather elongate, active insects, and it is therefore not surprising that various psammocharids act as models for the mimetic species.

The specimen of *Agapophytus australasiae* Guerin (Pl. i., fig. 45) was taken while it was sipping water at the edge of a pool, where it behaved in a very wasp-like and active manner; and *Prionocnemis connectens* Turn. (Pl. i., fig. 46), its probable psammocharid model, was found amongst weeds at the edge of a slow-running stream. It will be seen that there is a considerable general resemblance in the colouration and form of these two insects. The wings have the same distribution of yellow and dusky marks, the body is similar in shape and colour, as also are the legs, and, perhaps the most remarkable development of all, the antennae of the fly are almost as long as those of its wasp model.

In the species of *Phycus* illustrated (Pl. i., fig. 39) the resemblance is to a black and grey psammocharid with bright yellow antennae, such as the species shown in Pl. i., fig. 38. As in *A. australasiae*, the antennae of *Phycus* are almost as long as those of its model.

In *Ectinorrhynchus superbus* Sch. (Pl. i., fig. 43) and *E. rufipes* Krob. (Pl. i., fig. 44) the resemblance to psammocharid wasps is as close as in the other therevids I have just mentioned, except that in neither species are the antennae longer than in normal non-mimetic therevids.

A black and yellow-banded wasp-like type of colouration appears to be the rule in the Conopidae, though there are many small and inconspicuous species which have little or no resemblance to wasps. In the latter the form is elongate and the abdomen is narrower at its base than towards the tip, so that the appearance of a waist in mimetic species may be regarded as a normal family character and not a mimetic adaptation. The resemblance of many of the species to wasps, however, involves a number of adaptations, such as dark anterior borders to the wings and amazingly long antennae for muscoid flies, as well as a considerable resemblance to eumenid wasps in colouration. In general the distribution of the colour bands on the body is not particularly close to that existing in the Eumenidae, though in general effect the colouration is similar (Pl. i., figs. 19, 29, 30 and 31), but in one species at least (Pl. i., fig. 9) the colouration closely approximates to a definite model. This species has a general black

colouration and a uniformly orange-red abdomen, causing it to appear very like *Odynerus bicolor* Sauss. (Pl. i., fig. 10). Unfortunately systematists appear to have left the Australian Conopidae severely alone.

Though the mimetic resemblance existing in orders in which various species mimic totally different types of models differs only in degree from the type I have just described, it is convenient to make use of such a classification.

Perhaps the best example of this type of mimetic resemblance is afforded by the Cerambycidae, which I have already mentioned in passing. The majority of Cerambycids are cryptically coloured and spend nearly all their time on tree-trunks or branches, and but few visit flowers. Of those which do visit flowers habitually the majority exhibit deceptive colouration, and different species resemble totally different kinds of flower-visiting insects. Also, the model of each mimetic form is a common and conspicuous flower-visiting insect, belonging to one of the groups which are generally considered to be distasteful. These facts alone give strong support to the general theory of mimetic resemblance, and the perfection of the resemblance in most cases strengthens this.

I have already mentioned the Cerambycids which resemble *Metriorrhynchus* (Pl. i., figs. 73-80). Even an examination of the illustrations will indicate that these mimics are by no means closely related, and the various species which mimic *Metriorrhynchus* are placed in several genera which are widely separated in the classification of the Cerambycinae. It seems that this particular form of resemblance has been evolved independently in a number of different forms, which is not surprising if the true explanation for the appearance of this type of colouration is that already put forward; that is, that it is possible owing to the possession of a certain general structural and genetical similarity to *Metriorrhynchus*.

The occurrence of other lampyrid-like forms, such as *Erinus mimula* Pascoe (Pl. iii., fig. 4), which closely resembles *Telephorus nobilitatus* Er. and other lampyrids in form and green and orange colouration, increases the probability of this explanation.

A similar explanation, however, cannot be given in the case of different forms which resemble different types of Hymenoptera, and do so by different methods.

The genera *Hesthesis*, *Tragocerus*, *Agapete* and *Macrones* each resemble hymenopterous insects, usually of different types, and the morphological modifications which produce the resemblance are different in each genus. Therefore, as there is nothing but appearance in common between mimic and model in any of these insects, the structure of the mimic being fundamentally different from that of the model; and as in each genus in which resemblance to some hymenopterous form appears to have been separately developed the structural modifications of the mimic have been of a different type, it is clear that the mimetic pattern must have been both produced and preserved in relation to the appearance of the model. It is perhaps incorrect to say that a mimetic pattern can be produced as a response to the appearance of another insect, as the variations which have taken part in the evolution of the mimetic pattern must have been produced from within the insect, but it is impossible to escape from the conclusion that in the mimetic insects under consideration the resemblance must have been built up in relation to the appearance of the model, and in that sense produced. As there appears to be no possible mechanism by which a complete and complex mimetic pattern could appear at a single step in an insect structurally and genetically different from its model, it can only be concluded that the complex pattern is the result of a series of steps, each of which would make

the resemblance more perfect when it appeared. We know no more in this case than in any other of the processes which produced the variations, but the action of natural selection, through the medium of the natural enemies of the insect, appears to be an adequate mechanism for the preservation of each favourable variation, provided it was large enough to be distinguished by the natural enemies. The problem of how these mimetic forms were produced is thus simply the problem of evolution, as a whole, with the only special character that in this case the operation of natural selection appears to be confined to the medium of the natural enemies which could perceive the variations and exercise discrimination on account of them.

Bearing the foregoing considerations in mind, let us now examine the various types of cerambycid wasp-mimics.

In the genus *Tragocerus* (Pl. ii., figs. 1 and 12) the colour pattern, corresponding to that of the body of the model, is borne on the elytra, and these are curiously modified to serve this purpose. They are joined together along the mid-dorsal line, so that they remain in position over the abdomen when the insect flies. In order that the wings may be extended while the elytra are thus firmly fixed above the abdomen, the side of each elytron is excavated just above the point of origin of the wing, so that the wings can be moved freely without displacing the elytra. The result is that these insects are very wasp-like while flying, though when settled on flowers the resemblance is not convincing. The apparent absence of wings, together with its rather sluggish movements while settled on flowers, causes the beetle to be readily distinguished from a wasp. The wasp-like colouration alone, however, may give this insect some protection from its natural enemies.

Resemblance to wasps is much more perfect in the genus *Hesthesis* (Pl. i., figs. 5, 16, 52 and 54, Pl. ii., figs. 4 and 24, and Pl. v., figs. 1 and 2). In this genus the elytra are reduced to short truncated flaps which do not extend over the abdomen. As a result, the hind wings are exposed, even when the insect is at rest. The colouration is borne principally by the abdomen, and an examination of the figures will show that this varies rather considerably in different species. In most species this produces resemblance to particular types of wasps, while in the remainder it produces a general wasp-like appearance. Specimens of *Hesthesis* are nearly always collected on flowers, and one's first experience of these insects in this situation is apt to be a little disappointing. On flowers *Hesthesis* is commonly sluggish in its movements, like *Tragocerus*, and, though very wasp-like, does not deceive (Pl. v., figs. 1 and 2). This, however, is by no means the invariable habit, and I have frequently seen these insects moving rapidly from flower to flower, often leaving the wings spread out while feeding, after the manner of wasps, and the resemblance to a wasp is then remarkable, as will be appreciated by examining the coloured photograph (Pl. ii., fig. 24). When flying the resemblance is almost complete, and I have observed a specimen flying about in a marshy place which mimicked the movements of a wasp to an almost incredible degree. Agitation was the outstanding characteristic of its movements. It would settle on a grass-stem or other plant for a moment or two, often keeping the wings extended, then it would fly a short distance and settle again, and it kept repeating this process, circling all the time within a comparatively small area, returning again and again over almost the same ground. Had I not had an opportunity of observing it at close quarters I should not have suspected that it was anything but a wasp. I may say that I have heard many accounts of cases of deception by various species of *Hesthesis* from a number of observers, including such a competent coleopterist as Mr. H. J. Carter, so

that, though these insects may not always deceive, they are certainly capable of doing so.

It is interesting to compare the structure of *Agapete* (Pl. iii., fig. 3) with that of *Hesthesis*. Superficially there is a considerable resemblance between the beetles belonging to these two genera. In both the elytra are short and the wings are almost fully exposed, even when the insects are at rest. It appears probable, however, that the two forms have evolved quite independently; for in *Hesthesis* the elytra appear simply to have shortened, while in *Agapete* it appears that reduction in size was due first to a narrowing of the distal part of the elytron, followed later by the disappearance of the greater portion of this narrowed part. An examination of the neighbouring genera indicates the probable steps in this evolution. In *Bimia bicolor* White (Pl. iii., fig. 1) the distal portions of the elytra are somewhat narrowed, while in *Aciptera waterhousei* Pascoe (Pl. iii., fig. 2) they are still more so and it is only necessary for this process to continue still farther in order to produce the type of elytron characteristic of *Agapete* (Pl. iii., fig. 3). *Bimia* does not particularly resemble a wasp but, compared with most beetles, the wings are rather exposed. This might well cause the insect to be occasionally suspected of being a wasp by its natural enemies and, except for the appearance of suitable variations, nothing further is required to cause natural selection to operate in such a manner as to produce forms like *Agapete*. There are few cases in which the probable steps in the evolution of a mimetic form is shown as clearly as in this case, and it illustrates the fact that, in order that a mimetic pattern may be built up by natural selection operating on variations, it is necessary for the insect first to resemble some suitable model sufficiently closely in order to be occasionally mistaken for it. This first step must therefore be purely accidental, but it is probable that quite a vague approximation to the appearance of a suitable model is all that is necessary in order to commence the process. The occurrence of a similar type of reduced elytron in such beetles as *Sitarida* (Cantharidae), which are apparently not wasp mimics, indicates that this type of reduction of the elytron is not necessarily due to selection on account of the appearance of the insect exhibiting it. Necessarily the reduction of the elytron is due to some innate power of the insect of varying in that direction, but it is reasonable to suppose that the variation is preserved by natural selection and in *Agapete* the probable instruments of selection are the natural enemies of the insect.

This is another case in which I have not had the opportunity of viewing the insect in its natural environment. It appears probable, however, that it resembles large braconids, and possibly megalynids, rather than vespid and sphecoïd wasps, which serve as models for *Hesthesis*. The wings have a much softer and more membranous appearance than those of *Hesthesis*, and the colouration is also closer to that of certain braconids.

In the genus *Macrones* (Pl. iii., fig. 7) a very different type of wasp mimic is found. In this genus the models appear to be common ichneumonids, such as *Pamiscus* and *Henicospilus* (Pl. iii., fig. 8), the outstanding characteristics of which are extreme tenuity of body, a thorax noticeably more robust than the abdomen, long antennae, often with white tips, and a "floating" type of flight, progression being slow and direction indeterminate. *Macrones* has all these characteristics and it will be seen from the photographs that length and narrowness are extreme even for a cerambycid, while the elytra are so narrow that they are almost like long spines. The colour in each species is some shade of brown, usually rather pale, which is characteristic of many ichneumonids to be found

visiting flowers, and the tips of the antennae of some of the smaller species are white, a characteristic form of colouration in many ichneumons. When flying these insects are often indistinguishable from ichneumons, the long antennae being most noticeable, appearing like floating threads above a vague cloud formed by the rapidly vibrating transparent wings, while the body is usually inconspicuous.

There are many other flower-visiting cerambycids which possess some resemblance to wasps, such, for example, as *Arideus thoracicus* Don. In these the mimetic resemblance is less perfect and less complex than in the genera I have mentioned, but the general wasp-like effect is unmistakable.

Cerambycid ant-mimics occur in several different genera, and the resemblance is produced in different manners in different species. I have reason to believe that these insects are typically to be found on tree-trunks and branches, in which situations ants would form very suitable models. *Pseudocephalus mirus* Pascoe (Pl. iii., fig. 5) is a mimic of this type and it will be noticed that this species exhibits a most abnormal development of the head and prothorax for a beetle. The head is large, prominent and globular, and the prothorax long and narrow. There is a slight bulbous development of the terminal portions of the elytra, which produces a considerable resemblance to the globular abdomen of an ant, and the sides of the basal portions of the elytra are so coloured that the insect appears to have a waist in this region when on a brown background. These characters, together with the abnormally long legs, cause the insect to have a particularly ant-like appearance. In *Ochyra coarctata* Pascoe (Pl. iii., fig. 6) the resemblance to an ant depends principally on the peculiar, and very considerable, dilatation of the terminal portions of the elytra. In this species, also, the basal portions of the elytra are so coloured as to give the impression that the insect has a narrow waist, when it is on a dark background.

Scarcely less remarkable than the Cerambycids for the variety of their models are the mimetic species belonging to the dipterous family Stratiomyidae. *Syndipnomyia* sp. (Pl. i., fig. 7) is a particularly perfect mimic; brilliant orange bands of pubescence on the abdomen, yellow legs, black costal borders to the wings and extremely long antennae, giving the insect an almost incredibly wasp-like appearance. In *Massicyta picta* Brauer (Pl. i., fig. 28) the resemblance is less striking but is still very perfect. It will be seen from the illustrations that it possesses a considerable resemblance to the thynnid figured (Pl. i., fig. 27), but it is probable that its actual model is a large mimetic group of small hymenopterous insects, consisting of numerous species of solitary bees, and vespoid and sphegoid wasps. The colouration consists of yellow and brown in rather vague bands, there is a distinct waist to the abdomen, the antennae are very long and there is a dark costal border to each wing.

The species of *Ellissoma* illustrated in Pl. ii., fig. 18, is, I think, quite as remarkable as the species of *Syndipnomyia* already referred to. The amazing development of the antennae for a brachycerous fly is perhaps the most remarkable character. White bands on the long antennae of many ichneumons (Pl. ii., fig. 17) are most characteristic, and are often the first thing to attract attention in the field. The antennae are waved rapidly while the ichneumon moves, and the flickering white spots first call attention to it. From experience with other mimetic insects, I feel sure that this stratiomyiid will be found to wave its antennae in a similar manner, though there are unfortunately no records of its habits. In addition to the antennae, however, resemblance to certain ichneumons is shown in other characters. The long legs are banded with

black and yellow-white, the thorax bears a number of bluish-white spots and the wings are hyaline, with a spot on the anterior border resembling the stigma characteristic of many Hymenoptera. The anterior borders of the wings are not dark, the model not being diplopterous. Though I have been unable to figure it, *Ellissoma lauta* White is scarcely less perfect as a mimic than the preceding species, and again the model is different. One of the commonest types of braconid in this country is that with a general black colouration and a large pale pink area on each side of the base of the abdomen, and narrow pink or white lines separate the dorsal segments of the abdomen. *E. lauta* has exactly this colouration and very long black antennae. Pale pink is a most unusual colour for any insect, and the braconids mentioned are the only insects I know which normally exhibit it. That such an unusual colour as pink should be found in a mimetic insect is remarkable in itself, but that it should be of the same shade as that exhibited by the braconids and yet have a different chemical basis is still more remarkable. There can be little doubt, however, but that this is so, as the pink of the stratiomyiid faded almost immediately after death, while that of the braconids persists after many years.

E. lauta is the only stratiomyiid mimic I have seen alive, and unfortunately I only saw this after capture. The student who caught it did not suspect that it was a fly, and both in the net and in the glass-topped box to which the fly was transferred, it had a most wasp-like appearance. It exhibited the characteristically agitated and rapid movements of a wasp, and held the body far from the surface on which it moved. When at rest, however, it had a fairly normal fly-like appearance, the body being held close to the surface on which it rested, and the wings flat on the back and immobile. This appears to be characteristic of flies which mimic Hymenoptera, the wasp-attitudes only being in evidence when the mimic is active.

The family Syrphidae contains some of the best known examples of mimetic insects. The extremely bee-like species belonging to the genus *Volucella* attracted the attention of the earliest workers, and can be considered as classical examples of mimicry. Unfortunately this genus does not occur in Australia, and we have nothing which resembles it, but, on the other hand, amongst our syrphids are some species which show an even more perfect resemblance to other insects.

The resemblance of *Cerioides breviscapa* Saund. (Pl. i, fig. 13), to common species of *Odynerus*, for example, is so perfect that it would be difficult to suggest any improvement, even in detail. The bright yellow bands on the abdomen, and yellow spots on the antero-lateral portions of the thorax, and the general black and dark brown colour of the rest of the body, exactly correspond to the colouration of *Odynerus*. The very narrow waist-like basal portion of the abdomen, together with the sub-spherical terminal portion, forms an almost exact replica of the petiolate abdomen of the model. The wings have the usual dark costal border characteristic of mimics of diplopterous wasps, and the antennae are extremely long for a syrphid, the length being due principally to a very long first segment. In addition, the chitinous covering of the body gives the impression of hardness and strength, this being characteristic of the appearance of wasps, while in the Diptera the body covering usually appears more or less membranous and soft. In habit this insect is amazingly wasp-like and is scarcely distinguishable from the wasps in company with which it is found. The specimen illustrated was taken while sipping water at the edge of a small pool, and it was accompanied by quite a large number of *Odynerus*, of several species. It exhibited the agitated manner characteristic of wasps and in every way conveyed the impression that it was a wasp.

A number of other species of *Cerioides* also resemble *Odynerus* very closely, but in many of these the strong basal constriction of the abdomen is lacking. Also the appearance of long antennae is largely due to a curious column-like process arising from the head capsule, at the end of which the antennae are borne; these in themselves being distinctly longer than is usual (Pl. i., figs. 15, 18 and 32).

The genus *Microdon* contains some equally fine mimetic species, though the majority of the species of this genus are very typical flies, without the remotest resemblance to wasps. *M. variegatus* Walk. is a comparatively common and well known species. It varies rather considerably in appearance, as will be seen from the figures (Pl. i., figs. 20 and 26). The abdomen bears yellow bands on a dark background and is distinctly constricted at the base. It is noteworthy that while in *Cerioides*, as in *Odynerus*, the yellow bands are due to pigment in the chitinous exoskeleton, in *Microdon* they are due to a golden pubescence. The antennae are very long, due in this case principally to an extremely elongated third segment, though the first segment is also unusually long, and the costal border of the wing is rather vaguely pigmented. A comparison of the antennae of the mimetic and non-mimetic species of *Microdon* is instructive. These appear to be very variable structures in this genus, and in the non-mimetic species are surprisingly varied in size and shape, some being very large for a syrphid, but the longest antennae occur in the two mimetic species, *M. variegatus* and *M. waterhousei*.

Like *C. breviscapa*, *M. variegatus* mimics *Odynerus* in habit as perfectly as in superficial structure. This is well shown by the series of flashlight photographs of the living insect (Pl. iv.). These were necessarily taken under laboratory conditions, the insect being inclosed in a special glass box; but the attitudes taken up by the insect under these unnatural conditions were not observed to differ from those of the insect in its natural environment, nor is there any reason to suspect that they would. In fig. 2 the insect is at rest, while in the remaining photographs it is active. This illustrates the fact that when the insect is at rest its attitude is definitely dipterous, while when disturbed it assumes wasp-like attitudes. When one considers the different functional requirements of flies and wasps, it necessarily follows that in habit, as in structure, resemblance can only be due to superficial appearance; the normal fundamental habits must be different. One must distinguish between these fundamental habits of the mimic, evolved principally for purposes of nutrition and reproduction, which cannot differ greatly from those of closely related non-mimetic species, and superficial or mimetic habits, which supplement these. The latter are principally in the nature of special attitudes and manner of movement, which can only be of significance to the mimic in so far as they affect its appearance and increase its resemblance to a wasp; for they serve no useful functional purpose and cannot be an expression of an underlying structural similarity of wasp and mimic, as there is no such similarity.

The photographs illustrate a number of distinct wasp-like characteristics of attitude and behaviour of *M. variegatus*. The insect stands, as it were, on tip-toe, holding the thorax far from the supporting surface, it has a distinct tendency to stand on its head, it often flexes the abdomen so that the tip of this tends to pass under the thorax and the wings are erected somewhat so that they are considerably separated from the abdomen. The walking movements are very rapid and jerky, often being accompanied by rapid vibration of the wings and quick waving motions of the front legs and long antennae. This is well shown in fig. 5, the blurring of the wings, antennae and front legs being due to ex-

tremely rapid movement while the flashlight photograph was being taken. In captivity the behaviour of the disturbed insect was exactly that of a wasp. It hurtled from side to side of the breeding cage, hitting the sides with such force as to produce a distinctly audible dull thud. These hurtling movements were repeated in rapid succession, usually with a short interval intervening during which the insect made a few rapid, jerky walking movements, accompanied by vibrating wings and antennae. Commonly when undisturbed, however, the insect assumed a normal fly attitude, with the body held close to the supporting surface, the legs spread out, and the wings held flat and closely applied to the dorsal surface of the body, and it would remain motionless in this position for considerable periods.

The mimetic habits of *M. variegatus* are no more perfect than those of many of the other insects I have described. It is illustrated, not as a very exceptional case, but because it is the only species of which I have so far had an opportunity of taking photographs of this nature.

A specimen of *M. waterhousei* Ferg. appears much more convincingly wasp-like than one of the preceding species. It has broad bands of brilliant orange pubescence on the abdomen, the wings possess dark anterior borders and the antennae are long; these characters causing the insect to resemble a species of *Odynerus* very closely indeed. The perfect correlation existing between this colouration and form and the mimetic habits of this insect will be appreciated from a description of the manner in which Dr. G. A. Waterhouse captured the type, and at present only known, specimen. He saw what appeared to be a wasp running with rapid jerky movements over the bark of a tree in his garden. It appeared to be a particularly fine wasp of a species he had not previously seen, so he decided to capture it. This he did, and it was only after it had been in the killing bottle for some little time that he began to suspect a deception. Wasps normally succumb to cyanide almost immediately, much more rapidly than most insects. This insect continued to buzz about in the bottle for an unduly long time, which roused Dr. Waterhouse's suspicions. He examined more carefully and was amazed to find that the insect was a syrphid.

Some of the cristalline syrphids show considerable resemblance to other insects. The common *Eristalis tenax*, a fly with an almost world-wide distribution, is referred to in almost every general article on mimicry as a common example. In colour, size and shape it is somewhat like the common hive-bee and it is usually to be found visiting flowers. It is, however, one of the least convincing cases of mimicry I know, and fails to deceive the most casual observer. The resemblance of *Eristalis smaragdi* Walk. (Pl. i., fig. 101) to common species of *Lucilia* and *Chrysomyia* is much more perfect. In shape and colouration, brilliant metallic green with blackish markings, it is an almost exact replica of these blowflies, but a mimetic explanation appears to be superfluous in this case, though it may really apply. The Muscidae and cristalline Syrphidae are similar in shape and sufficiently closely related to have similar potencies for producing certain colours; particularly such colours as metallic green, which occurs in that the appearance produced by this colouration is without significance to the many different families of Diptera. It is not surprising, therefore, that an isolated case should occur in which a species of *Eristalis* resembles some blowfly.

The large subfamily Syrphinae contains principally yellow-banded species. In other characters they have little in common with wasps. It is possible that this type of syrphid may be a general wasp-mimic, the vague resemblance being sufficiently close to cause the insects to be occasionally mistaken for wasps. On the other hand they may exhibit simple warning colouration, as it is possible

that they have some distasteful qualities of their own. A further possibility is that the appearance produced by this colouration is without significance to the insect, it being simply an attribute of the characteristic structure of this group.

The peculiar Australian genus *Pelecorrhynchus* differs from most tabanids in the fact that neither sex sucks blood, and both sexes are commonly to be found visiting flowers or flying in a particularly active manner over marshy places. The colouration is usually brilliant and varies considerably in different species, and in a few cases approximates very closely to that of certain common psammocharids, as in *P. deuqueti* Hardy (Pl. ii., fig. 16) and the undescribed species I have figured (Pl. ii., fig. 22). On flowers these insects may easily be mistaken for wasps, though no special mimetic habits have been observed. It is possible, however, that greater familiarity with these rather scarce insects may reveal such habits, these often not being in evidence when an insect is busy sucking nectar, as has been shown to be the case in *Hesthesis*.

A different type of possible mimetic resemblance is shown by certain more normal tabanids. Several species possess a considerable resemblance to blowflies. Thus *Scaptia violacea* (Pl. i., fig. 99) is metallic blue like many blowflies, such as species of *Chrysomyia*, and *Scaptia* sp. (near *gibbula* Walk. Pl. i., fig. 97) closely resembles the common *Calliphora stygia* Fabr. (Pl. i., fig. 96) in its dull brown colour and golden pubescence. Both species are rather abnormal in shape for tabanids, this approximating very closely to that typical of blowflies. It is possible that the same explanation applies here as has been suggested for the resemblance of *Eristalis smaragdi* to blowflies. That mimicry is involved in the resemblance, however, is indicated by the habits of *Scaptia* sp. (Pl. i., fig. 97). Tabanids and blowflies each have very characteristic habits, and an experienced entomologist can readily distinguish one from the other, either by the sound it makes or its movements when flying. Each produces a different sound and, while tabanids exhibit a certain purposefulness in their manner of settling on an animal, settling as soon as an opportunity is presented, blowflies buzz round in an aimless fussy manner and appear to settle almost by accident. *Scaptia* sp. exhibits exactly this aimless manner of flight and the sound it produces closely resembles the note of a blowfly. Dr. I. M. Mackerras and I have been completely deceived by this insect. On one occasion a number of these tabanids buzzed round us for several minutes before we discovered the deception. It is possible that blowflies enjoy a certain immunity from attack by certain predaceous animals, as observations pointing to this have been made; so that under certain circumstances it might benefit an insect to be mistaken for a blowfly. Dr. Mackerras has suggested another possible explanation. Animals, particularly horses, exhibit great fear of tabanids, and will do all in their power to prevent these insects from settling on them, while blowflies, in small numbers, are practically ignored. The blowfly-like habits of *Scaptia* sp. may therefore make it easier for the insect to obtain a meal of blood, and so the resemblance to a blowfly would give a certain survival value to the insect possessing it.

Several excellent examples of mimetic insects have come under my notice, belonging to groups which do not contain other mimetic forms, as far as I am aware. It is not improbable that other mimetic forms belonging to the same groups may be found in the future, so that these would then be placed in one or other of the groups with which I have already dealt. For the present, however, it is convenient to deal with these as examples of the random occurrence of mimetic forms in non-mimetic groups.

One of the best of these is a bombyliid, the undescribed species of *Systropus* figured (Pl. ii., fig. 5) which exhibits a remarkable resemblance to the common *Scetiphron laetum* Sm. (Pl. ii., fig. 6). Mr. Burns, who captured the insect,

was struck by its remarkable resemblance to *S. laetum* when alive. A long narrow abdomen is characteristic of the genus *Systropus*, giving a suitable basis for the development of a mimetic resemblance to a sphecoid wasp. The perfection in detail of the mimetic pattern superimposed on this favourable normal basis, however, is little less than amazing. The colour markings of thorax, abdomen, legs and antennae are extremely similar to those of the model, and the abdomen, in addition to being long and slender, is dilated at the tip, as in the model, and the antennae are extremely long for a bombyliid.

The cyrtid fly, *Leucopsina odyneroides* Wwd. (Pl. i., fig. 14) is almost as perfect a mimic of *Odynerus* as *Ceriodes breviscapa*. The bright yellow bands on a dark background and narrow constriction of the abdomen, together with the long antennae, dark costal borders of the wings and yellowish legs, make the resemblance almost complete.

One would not expect to find a wasp-mimic in a family of such delicate midge-like flies as the Mycetophilidae, yet one came under my notice under rather startling circumstances. I was collecting in thick brush country when I became annoyed by the persistent attentions of what I took to be a wasp. The insect kept buzzing round my head apparently with intent to sting when opportunity offered. To remove the menace I netted the insect and placed it in a killing bottle as the easiest manner of disposing of it. My astonishment in discovering that this "venomous" insect was a harmless mycetophilid may be imagined. This insect, *Platyura* sp. (Pl. iii., fig. 16), has a dull reddish brown colour with vague yellowish bands on the abdomen, exactly the colouration characteristic of the vespoid genus *Polistes* and related genera. The insect is surprisingly large and robust, and the body covering has an extremely hard and strong appearance for a mycetophilid. The shape, also, as will be seen from the illustration, is very similar to that of *Polistes*. A well marked waist is present, the body is robust and pointed at its posterior extremity, the antennae are prominent and thick, and the wings are strong and very shiny with a pale brown pigmentation. In this case the mimic appears to have departed considerably from the normal structure of the group to which it belongs.

Before dealing with mimetic insects belonging to other orders I must deal in a more comprehensive manner with certain structural developments which take a prominent part in the production of mimetic resemblance in many mimetic flies, though these developments have already been mentioned in connection with the descriptions of the different mimetic species.

One of the most extraordinary features of dipterous wasp-mimics is the common occurrence in such mimics of long antennae, comparable in length with those of their models, in spite of the fact that all these mimics figured and described belong to the Brachycera, with the solitary exception of, *Platyura* sp. One of the outstanding features of the Brachycera is that the antennae are normally very short, and they are usually so small that they are only evident on fairly careful examination. Conspicuously long antennae are exceptional in the extreme in this suborder, yet they appear to be the rule in the mimetic species. It will be seen from an examination of the illustrations that, if the asilids be omitted, practically all the brachycerous wasp-mimics have exceptionally long antennae. The species illustrated were selected entirely without any special reference to this particular character, and I believe that they form a perfectly representative series of mimetic Diptera. Another point of interest is that in those groups of Diptera in which long antennae are the rule, the longest antennae, with the closest resemblance to those of wasps, are developed in those species which show the greatest mimetic resemblance in other characters. This feature

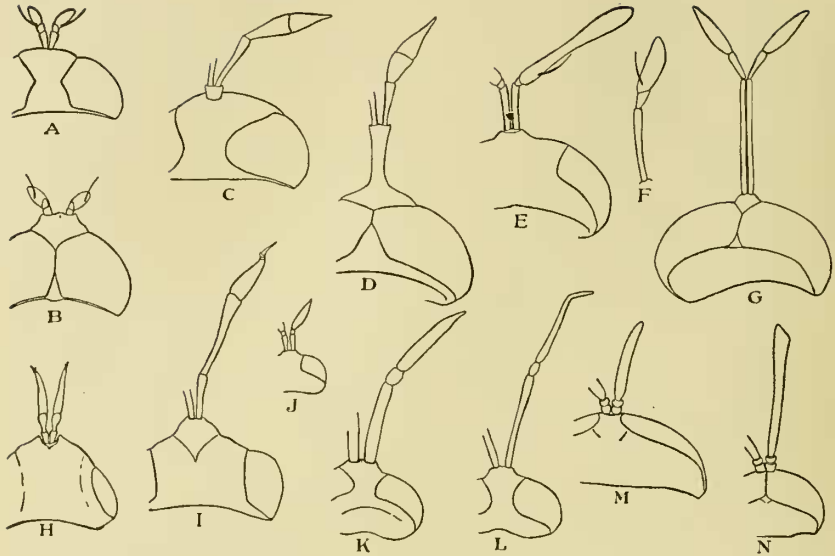
is often very marked, as, for example in the Stratiomyiidae, Therevidae, Conopidae and Syrphidae. It is scarcely credible that the close association of such an abnormal brachycerous character as long antennae with the mimetic species of many different groups of this suborder can be purely accidental, and it would appear probable that long antennae have definitely been produced in many species as a mimetic character.

Long antennae, however, are not entirely confined to wasp-mimics in the Brachycera. There are certain groups within this suborder in which there appears to be a definite tendency towards the production of abnormally long antennae, and it is noticeable that in these same groups there is also a tendency towards the production of mimetic resemblance. Another interesting fact is that though the non-mimetic species of such groups have long antennae, the greatest development of the antennae is to be found in those species which exhibit the most perfect resemblance in other characters, and, between these two extremes, there is often a number of species which show a more or less vague mimetic resemblance, in which the antennae are usually developed to an intermediate degree. It seems probable, therefore, that abnormally long antennae have taken an important part in the production of the primary fortuitous resemblance of many species to wasps, which has served as a basis on which the more perfect mimetic resemblance has later been developed by the action of natural selection. To account for the fact that the most perfectly mimetic species usually have by far the longest antennae it is necessary to consider that a further lengthening of the antennae has been produced by natural selection as a definitely mimetic character, and the colouration of the antennae in many such mimics appears to be almost certainly a mimetic adaptation. Another important point is that, though most brachycerous wasp-mimics have very long antennae, length is produced by different structural modifications in different mimics, sometimes even when these are quite closely related. A brief survey of the mimetic groups of brachycerous Diptera will illustrate the foregoing considerations.

In the Mydidae (Pl. ii., figs. 8 and 10, and Pl. vi., fig. 2) great length of antennae appears to be a normal characteristic of the family, but it is noticeable that the antennae of the more perfectly mimetic species are longer than those of the non-mimetic or slightly mimetic species. In some groups of the Cyrtidae long antennae also appear to be normal and in the very perfectly mimetic *Leucopsina odyneroides* (Text-fig. 1.N., and Pl. i., fig. 14), though the antennae are very long they are equalled in length by those of some species of *Panops*. It should be noticed, however, that the species of *Panops*, such as *P. flavipes*, which have the longest antennae also show some indications of being mimetic. In both the foregoing families the elongation of the antennae is due almost entirely to the great length of the fused series of segments which follow after the second segment. Though the portion of the antennae which follows after the second segment consists actually of a number of more or less fused segments in the Brachycera it will be convenient for present purposes to refer to the whole of this as the "terminal segment," for the fusion between the constituent segments is often so great that it is practically impossible to determine their limits.

The long antennae of the mimetic Therevidae, such as *Agapophytus australasiae* (Text-fig. 1.L., and Pl. i., fig. 45) and *Phycus* sp. (Text-fig. 1.K., and Pl. i., fig. 39) have very long first and terminal segments, which is also characteristic of the related non-mimetic species, though in these the antennae are much shorter (Text-fig. 1.J.).

Long antennae are also characteristic of the subfamily Hermetiinae of the Stratiomyiidae, practically the whole of the elongation being due to the great



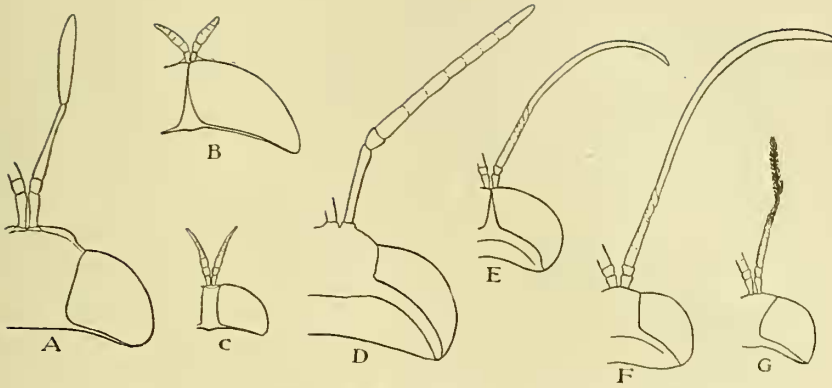
Text-fig. 1. Antennae of Mimetic and related Diptera (x8).

A., B., H. J. and M. non-mimetic, remainder mimetic.

A. *Microdon vittatus* Macq., B. *Syrphus* sp., C. *Cerioides breviscapa* Saund., D. *Cerioides variabilis* Ferg., E. *Microdon variegatus* Walk., F. *Microdon waterhousei* Ferg., G. *Systropus* sp., H. *Conops* sp., I. *Conops* sp., J. *Phycus* sp., K. *Phycus* sp., L. *Agapophytus australasiae* Guer., M. *Panops baudini* Lam., N. *Leucopsina odyneroides* Westw.

A.-F., Syrphidae, G., Bombyliidae, H. and I., Conopidae, J.-L., Therevidae, M. and N., Cyrtidae. (F., after Ferguson).

development of the terminal segment, the constituent segments of which are of very irregular lengths. By far the longest antennae occur in the highly mimetic species such as the remarkable species of *Elissoma* shown in Pl. ii., fig. 18, and Text-fig. 2.F., and *Elissoma lauta* (Text-fig. 2.E.). They are also very long in *Massicyta picta* (Text-fig. 2.G., and Pl. i., fig. 28) and in this species an appearance of thickness is given by the development of a dense pubescence over the terminal portion of the antennae. There is a large number of related species which also have long antennae, built on the same general plan, but most of these appear to be as yet undescribed. Most of these show mimetic resemblance to a greater or less extent, but a knowledge of the habits of the living insects would be necessary in order to decide whether the resemblance is really well developed. The introduced *Hermetia illucens* F. also has long antennae, though they are not relatively as long as in the other species mentioned. A specimen of *H. illucens* does not show any signs of mimetic resemblance, but I have noticed that some of its habits are distinctly wasp-like. It is possible that this species represents



Text-fig. 2. Antennae of Mimetic and other Stratiomyiidae (x8).

B. non-mimetic, A. and C. possibly mimetic in habit, remainder mimetic.

A. *Hermetia illucens* F., B. *Odontomyia decipiens* Guer., C. *Neoeraireta spinigera* Wied., D. *Syndipnomyia* sp., E. *Elissoma lauta* White, F. *Elissoma* sp., G. *Massieya picta* Brauer.

the normal type of this group and its slight resemblance to a wasp would permit of the commencement of the operation of natural selection in the production of mimetic resemblance. *Syndipnomyia* sp. (Text-fig. 2.D., and Pl. i., fig. 7) belongs to a widely separated subfamily, the Clitellarinae, and in this species the first, as well as the terminal, segment is very elongate, and the constituent segments of the terminal segment are uniform and of almost equal length. As far as I am aware, all other types of stratiomyiids have short normal brachycerous antennae (Text-figs. 2.B. and C.).

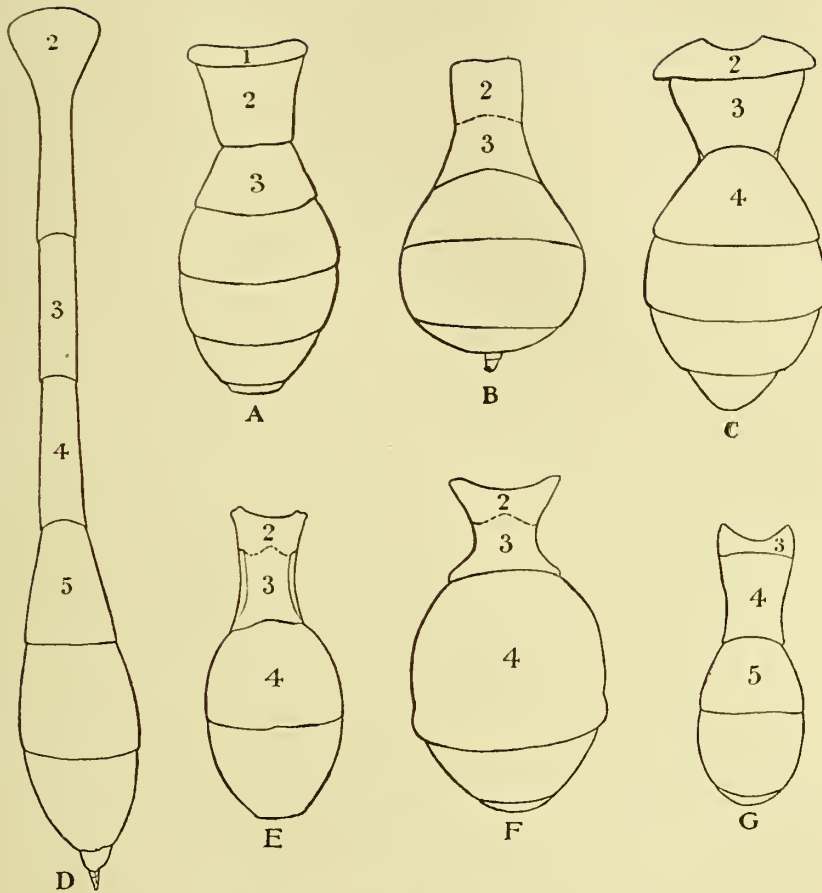
The species of *Systropus* shown in Pl. ii., fig. 5, and Text-fig. 1.G. has conspicuously long antennae, consisting of a very long first segment and moderately long second and terminal segments. This is the only truly mimetic bombyliid I know, and it is also the only bombyliid I know which has very long antennae.

In the Syrphidae long antennae are also found closely associated with those species in which mimetic resemblance is most highly developed. Most, if not all, the species of the Cerioidinae show definite mimetic resemblance and long antennae are the rule in this subfamily. In most species the antennae are borne on the end of a long frontal prominence, which gives the appearance of great length to the antennae which are otherwise quite long (Text-fig. 1.D., and Pl. i., figs. 15, 18 and 32). The length of the antennae of *Cerioides breviscapa* (Text-fig. 1.C., Pl. i., fig. 13) is due to the elongation of the first, second and terminal segments, the frontal process being very short in this species. In the Microdoninae the antennae are very variable structures and are often quite large, even in non-mimetic species, but the longest antennae occur in the two mimetic species. In *Microdon variegatus* (Text-fig. 1.E., Pl. i., figs. 20 and 26, and Pl. iv.) the terminal segment is extremely long, though the first segment is also rather long; while in *M. waterhousei* (Text-fig. 1.F.) the first segment is longest, though the second and terminal segments are also long. In the other subfamilies, such as the Syrphinae and Eristalinae, which do not contain definite wasp-mimics, the antennae are of the normal short type characteristic of the Brachycera.

Most of the Australian Conopidae appear to be more or less mimetic, but it is noticeable that in those species which exhibit mimetic resemblance most clearly the antennae are longest. In the few species which do not appear to be in any way mimetic the antennae are comparatively short, though still rather long for brachycerous insects, the elongation being due principally to the long terminal segment (Text-fig. 1.H.). In the mimetic species this segment is still longer, but the first and second segments are also very long (Text-fig. 1.I., and Pl. i, figs. 9, 19, 29, 30 and 31).

Of almost equal significance to the common occurrence of long antennae in brachycerous wasp-mimics is the almost invariable presence of black anterior borders on the wings of dipterous mimics of diplopterous wasps. It is very suggestive that this particular type of dark anterior border of the wing not only does not seem to occur amongst non-mimetic diptera, but is only found in those mimetic species which resemble diplopterous wasps. It is characteristic of diplopterous wasps, eumenids and vespids, that they fold the wings longitudinally when they are at rest. These folded wings look like narrow dark bars along the sides of the body, and the dark anterior borders of the wings of mimetic diptera have a considerable resemblance to the folded wings of their models when the wings are lying over the body in the position of rest. Such dark anterior borders of the wings occur in mimics of eumenid and vespid models belonging to the families Syrphidae, Asilidae, Stratiomyidae, Conopidae and Tachinidae of the Diptera and in the Cerambycidae of the Coleoptera; this feature in the last family being exhibited by some of the mimetic species of *Hesthesis* (see Pl. i.). There are many non-mimetic species of diptera which have dark anterior borders to the wings, this being particularly noticeable in the Bombyliidae, but these borders do not give the impression of narrow bar-like structures when the wings are placed over the back. In such insects the posterior margin of the dark anterior border is usually either very irregular or gradually shades into the posterior part of the wing.

Another common feature of dipterous wasp-mimics is the possession of a distinct waist to the abdomen just behind the thorax. This is almost a constant feature of wasps, but is extremely rare in non-mimetic Diptera. A well-marked waist occurs in many of the mimetic species belonging to the families Mycetophilidae, Asilidae, Stratiomyidae, Cyrtidae, Bombyliidae, Syrphidae and Conopidae, while in the Mydidae and Tachinidae and in the beetles *Hesthesis* and *Macrones* a waist is present, but less distinct. In the formation of such a waist it is necessary that the basal segments of the abdomen should be constricted, but it is interesting to note that in spite of this limitation there is some variation in the morphological position of the waist in different species. There is a tendency for the dorsal portion of the basal segments of the abdomen to disappear in the Diptera. Though the tergite of the first segment is developed in the Asilidae, it is lacking in most of the other families of the Brachycera, while in some of the Cyclorrhapha the tergite of the second segment also disappears. In *Brachyrhopala fenestrata* (Asilidae, Text-fig. 3.A., and Pl. i, fig. 24) the first segment is very short and the main constriction is between the second and third segments. In *Massicyta picta* (Stratiomyidae, Text-fig. 3.B., and Pl. i, fig. 28) the main constriction is between the thorax and the second segment, the second and third segments taking part in the formation of a waist. In *Leucopsina odyneroides* (Cyrtidae, Text-fig. 3.C., and Pl. i, fig. 14) the second segment is very short and the main constriction is between the third and fourth segments. The very long waist of *Systropus* sp. (Bombyliidae, Text-fig. 3.D., and Pl. ii, fig. 5) consists principally of the long narrow second, third and fourth seg-



Text-fig. 3. Abdomens of Mimetic Diptera (x8).

A. *Brachyrhopala fenestrata* Macq. (Asilidae), B. *Massicyta picta* Brauer. (Stratiomyiidae), C. *Leucopsina odyneroides* Westw. (Cyrtidae), D. *Systropus* sp. (Bombyliidae), E. *Microdon variegatus* Walk. (Syrphidae), F. *Cerioides breviscapa* Saund. (Syrphidae), G. (Tachinidae).

ments. In *Microdon variegatus* (Syrphidae, Text-fig. 3.E., Pl. i., figs. 20 and 26, and Pl. iv.) and *Cerioides breviscapa* (Syrphidae, Text-fig. 3.F., and Pl. i., fig. 13) the main constriction is between the second and third segments, and these two segments are narrow. In the wasp-like tachinid figured (Text-fig. 3.G., and Pl. i., fig. 55) the first apparent segment is probably the third mor-

phological segment, and the main constriction is between segments four and five, segment four being narrow. It appears evident, therefore, that the narrow waists of these mimetic insects must have been produced on account of their appearance, for there is little in common between them structurally.

I will now pass on to consider some other more or less isolated examples of mimetic resemblance.

One would not be impressed with the resemblance between *Trogodendron fasciculatum* Schreib. (Cleridae, Pl. ii., fig. 20) and *Pseudagenia consociata* Turn. (Psammocharidae, Pl. ii., fig. 19) from an examination of the illustrations of these species; yet, under natural conditions, the resemblance is closer than that exhibited by a number of other mimetic insects which appear to be more perfectly mimetic according to the photographs. Large black psammocharids with conspicuous bright yellow antennae, such as *P. consociata*, are very common. They are usually to be seen on the ground or tree-trunks, and their most conspicuous characteristics are rapid movements and a rapid vibration of the antennae. *T. fasciculatum* mimics these habits to perfection. This clerid arrives within the field of vision with almost the velocity of a bullet, gives an impression of commotion when settling and proceeds to move about with rapid, jerky hunting movements, waving its conspicuous bright yellow antennae in exactly the same manner as its model. It will be observed that the resemblance in this case is almost wholly due to mimetic habits, assisted by the conspicuous bright yellow antennae. The general colouration is similar to that of *P. consociata*, but there is little in common between the forms of the two insects. This, however, does not attract attention under natural conditions, the background usually being dark coloured.

In illustrating the *Metriorrhynchus* mimetic group I have included several moths belonging to the genus *Snellenia* (Heliodinidae, Pl. i., figs. 69-72), which I did not mention when dealing with the group. The resemblance to small species of *Metriorrhynchus* is very close. The fore wings are red, though this may be obscured by black on the central area, as in the model. The rest of the insect, including the antennae, is black. An appearance similar to that of the longitudinal ridging of the elytra of the model is produced by darker scales between the main longitudinal veins. The fact that both the pure red and the black and red form of wing colouration may appear in different individuals of the same species indicates that the factors underlying the colouration in mimic and model are similar. The colour in the mimic is borne by scales and in the model by the chitinous covering of the elytra, and the two forms are so distantly related that the factor cannot be considered to be the same in each case nor to have been derived from some common ancestor. The system of colouration is so simple, however, and the colours used of such common occurrence in the Insecta that it is not difficult to believe that similar factors might easily appear in these two very different types of insects which would express themselves in a similar distribution of the same colours.

I have only seen *Snellenia* in its natural environment on two occasions and on each of these it was observed in company with *Metriorrhynchus*. One specimen was seen on the flowers of *Leptospermum*, a very common situation for *Metriorrhynchus*, and others were taken flying in the deep shade of subtropical brush. In the latter situation a small species of *Metriorrhynchus* was very common, and the only hope of securing specimens of *Snellenia* was to capture every specimen of *Metriorrhynchus* seen, and once in a while it would happen that the supposed lampyrid would turn out to be *Snellenia*.

A common form of colouration found in many Australian ants belonging

not only to different genera but to different subfamilies, is a black ground colour and brilliant golden pubescence on the abdomen. A good example of this is *Dolichoderus doriae* Em. (Pl. iii., fig. 12). Such ants are commonly to be found on tree trunks, and in association with them are found the lygaeid bug *Dacrlac tricolor* Sign. (Pl. iii., figs. 11 and 13) and a black spider with golden pubescence on the abdomen. Both the bug and spider resemble the ants in colouration and also in manner of movement. A remarkable phenomenon is the fact that *D. tricolor* resembles the same model in both the larval and adult state, but the resemblance is produced in different ways in the two stages. In the larval bug (Pl. iii., fig. 13) the end of the abdomen is yellowish and convex, closely resembling the golden abdomen of the ant, and the rest of the body is black with brown markings, so arranged that the impression of a waist is conveyed when the insect is on a dark background. The adult, on the other hand, has an oval yellowish mark on the distal end of the hemelytra, shaded in such a manner with darker pigment that this flat area of the hemelytra appears convex and thus closely resembles the abdomen of its model (Pl. iii., fig. 11). As in the larva, the black and brown colouration of the rest of the body is so arranged as to convey the impression of a waist. The photographs do not do justice to this example of mimetic resemblance. It is necessary to place the insects on a dark background in order to appreciate the resemblance fully. Also, the abdomen of the soft-bodied larval specimen has collapsed considerably in drying, so obscuring the characteristic convexity of the end of the abdomen.

The remarkable resemblance to an ant of the larval coreid, *Riptortus* sp., shown in Pl. vii., fig. 2, needs little description, as it is well demonstrated by the photograph. In this case the shape of an ant is mimicked by the actual shape of the larval bug, and not by a special development of its colouration. The larva photographed appears to be in its first or second instar, and at this stage is the same size and colour, pale brown, as a common ant which was found on the same plant. The older and larger larvae are less ant-like, though the resemblance is considerable, and the adult (Pl. vii., fig. 1) does not resemble an ant in any way. It is much too large for such a resemblance to be of any conceivable use.

The mirid bug, *Eucerochoris* sp. (Pl. iii., fig. 15) was taken flying in company with the braconid wasp figured (Pl. iii., fig. 14), the two insects being indistinguishable on the wing. It will be noticed that the antennae are exceptionally long and that in form and size *Eucerochoris* closely corresponds to the braconid, the ample membranous wings being an unusual feature for a mirid. The resemblance in colour is even more striking. The prothorax is bright red, the head and rest of the body being black, except for the narrow white posterior borders of the abdominal segments, a type of colouration characteristic of many of our common braconids. The wings, as well as being ample and membranous, are of a semi-transparent blackish colour, just as are the wings of the braconid. In the Australian Museum there are several closely related species, each of which is unmistakably similar to some common form of braconid. One, for example, differs from the species figured in that the whole of the thorax is of a reddish brown colour, while in another there is a large pink area on the latero-basal regions of the abdomen, both these forms of colouration being noticeable characteristics of many common species of braconids.

What appears to be a very different type of deceptive resemblance from all those I have already described is exhibited by the lycaenid butterfly *Ialmenus evagoras* Don. (Pl. xiv., fig. 2). It will be observed that there is a concentration of the darker colour markings at the posterior extremity of the hind wings and that linear markings radiate from this point over the rest of the wings. Poulton

has put forward the theory that lycaenids which exhibit this type of colouration are definitely mimetic, the butterflies, as it were, mimicking themselves, backwards. The significance of this colouration, he claims, is that when a bird attempts to catch a butterfly it normally attacks the region of the head and thorax and is deceived by the colouration of such "double-ended" butterflies as *I. evagoras* and attacks the posterior end of the hind wings in mistake for the thorax. The result is that the bird simply cuts a small piece out of the hind wings and the butterfly is able to escape, but little inconvenienced by its injury. This theory has been received with considerable scepticism by many entomologists and does not appear to me to be by any means proved. On the other hand, the few observations I have been able to make certainly support the theory. On the one occasion on which I had the opportunity of studying this insect under natural conditions I caught all the butterflies I could in the few minutes at my disposal. I found that most of the older specimens of these had the posterior end of the hind wings considerably damaged, and in many of the specimens the damage appeared to have been caused by something having bitten a piece out of the hind wings. I am not convinced, however, that this would not also be found to be the case in normal butterflies, for if they are attacked when on the wing the attack would almost certainly be commonly from the rear. An examination of the plates illustrating injuries to the wings of South African butterflies given in Marshall's classical work* will show that most of the injuries are to the posterior border of the hind wings, whether the butterfly is "double-ended" or not. It is evident that this matter can only be settled by the careful observation of the manner in which *I. evagoras* and similar butterflies are attacked, and what difference, if any, there is in the nature of the attack on these "double-ended" butterflies and on related butterflies with a normal colour pattern.

The photograph (Pl. xiv., fig. 2) is of a freshly emerged butterfly, and it will be noticed that the butterfly is resting with its head pointing obliquely downwards, which is the reverse of the normal resting attitude of a butterfly. I observed a considerable number of freshly emerged specimens and they were all resting in this attitude, though the older, somewhat abraded, individuals appeared to settle indifferently with the head uppermost or pointing downwards. As the freshly emerged individuals are incapable of strong flight it is possible that this attitude takes a definite part in the mimetic resemblance of this insect.

Summary of evidence for the existence of Mimetic Resemblance and the necessity for the operation of Natural Selection.

In connection with the various types of mimetic resemblance I have described and the numerous examples I have given I have already brought forward a considerable body of evidence to show that mimetic resemblance, that is, resemblance produced as a response to the appearance of the object resembled, certainly does occur amongst insects. I have also shown that natural selection appears to be absolutely essential in order to produce, or at least preserve, mimetic resemblance and that natural selection may operate on any kind of heritable variation, whether small or large. Its operation is by no means confined to the selection of small individual variations, as some writers on the subject of mimicry appear to have assumed. Before giving a detailed account of my views on the question of the

* "Five Years' Observations and Experiments (1896-1901) on the Bionomics of South African Insects, chiefly directed to the Investigation of Mimicry and Warning Colours," by Guy A. K. Marshall.

evolution of mimetic resemblance it will be convenient first to summarise the evidence for the fact of mimetic resemblance and the necessity for natural selection to take part in its production and preservation. It will be necessary to deal separately with cryptic and deceptive resemblance, and I feel that a presentation of the evidence in tabular form will be the most satisfactory way to deal with the subject.

(a) *Cryptic Resemblance.*

1. There is an almost infinite variety of possible backgrounds for insects and of colouration, form and habit amongst insects. If, therefore, cryptic resemblance is simply a fortuitous combination of suitable colouration, form or habit with a suitable background the phenomenon should be extremely rare. Actually it is very common, so that there is little possibility that cryptic resemblance can be fortuitous.

2. The fact that cryptic resemblance in an insect is frequently due to a combination of several very distinct types of factors, such as colouration, form and habit, makes fortuitous resemblance improbable in the extreme.

3. The structural basis underlying resemblance is very different in different insects, i.e., the same end has been attained by several different means. This strongly suggests that resemblance is the actual end-product of some process which is subservient to the production of resemblance, and that it cannot be simply an attribute of some factor common to each insect exhibiting it.

4. Closely related insects in the same oecological environment have different colour patterns, but each of these makes the insect bearing it inconspicuous on its normal background. A similar colouration is therefore not produced in similar insects by the action of the same general environmental conditions. As, however, the type of resemblance produced has in each case a definite relationship to the normal environment of the insect possessing it, it appears necessary that some factor in the environment should be responsible for the production and preservation of this resemblance. The only difference in the environment of such insects is in the appearance of the background on which each is normally found. It is necessary, therefore, that the environmental factor responsible for the production of mimetic resemblance should be one capable of discrimination on account of appearance. Other animals, the natural enemies of cryptic insects, or their prey, in the case of predaceous forms, form the only conceivable discriminating factor of this nature. Only such of these as hunt by sight and attack the stage of the insect exhibiting cryptic resemblance can take any part in the production and preservation of cryptic resemblance.

5. There is every reason to suppose that the natural enemies of insects would overlook a cryptically coloured insect more frequently than a more conspicuous form, and experiments show that this is so. This is all that is necessary to cause the preservation of cryptic characters when they appear. This gives a satisfactory general explanation of the evolution of cryptic resemblance, though it does not account for the production of the original variation or series of variations involved. The latter point, however, is no objection to the theory that natural selection has been involved in the production of cryptic resemblance. In no case do we fully understand what causes the production of a variation, but, in spite of this, natural selection is generally considered to be at least one of the most potent factors in evolution in general.

6. The existence of such an adequate mechanism for the production of cryptic resemblance gives added support to the theory that cryptic resemblance is adaptive and not fortuitous.

7. To summarise. There is little possibility that cryptic resemblance can be fortuitous; it has a definite relationship to the environment of the possessor but cannot be the result of any general environmental influence; the only type of environmental factor which could operate in the production and preservation of cryptic resemblance is one capable of being affected by appearance; the only conceivable factor of this nature is that afforded by other animals, either the natural enemies or prey of the cryptic insects; there is every reason to believe that the behaviour of such enemies or prey would be modified in connection with cryptically coloured insects to the advantage of the latter, and this advantage would cause cryptic insects to have a survival value compared with other insects.

(b) *Deceptive Resemblance.*

1. The same appearance is produced in different ways by the mimics of a single model, sometimes even when the mimics are closely related. It is evident, therefore, that structural similarity is not necessary and that in a large percentage of cases similarity between mimic and model exists in appearance alone.

2. The curiously wasp-like habits and attitudes of many dipterous, coleopterous and hemipterous wasp-mimics can be of no conceivable use to the possessors unless it be on account of their resemblance to the habits and attitudes of wasps.

3. Certain apparently mimetic adaptations occur only in species which would be considered mimetic on account of other characters. The wasp-like habits, already mentioned, of many mimics of wasps do not occur in non-mimetic relatives of the mimics. Very long antennae are common in brachycerous flies which mimic wasps, the elongation of the antennae being produced in different manners, sometimes even in closely related species. This suggests that the antennae do not simply happen to be long but that length has definitely been produced as such, presumably in connection with the other mimetic characters of the insect. Antennae which even approach the length of those common amongst dipterous wasp-mimics are excessively rare amongst non-mimetic flies, and in the two or three such cases which have come under my notice there is reason to believe that when alive the insect may bear a resemblance to a wasp, the resemblance being due principally to habit and attitude. Most fly mimics of dipterous wasps have a dark anterior border to the wing, which, when the insect is at rest, look very much like the folded wings of their models. Not only are darkened anterior borders of this particular type not found amongst non-mimetic flies, but also they are not found in mimics of other types of Hymenoptera. Many different kinds of dipterous wasp-mimics have a narrow waist, always in the same apparent position as in the model but often in different morphological positions in mimic and model and even in different mimics. Mimetic adaptation appears to be the only possible explanation of these facts.

4. In most cases of resemblance between insects, and probably in all those in which the resemblance is truly mimetic, mimic and model occur in exactly the same environment at the same time. If the resemblance were fortuitous there should be no such correlation.

5. Deceptive resemblance is a comparatively rare phenomenon amongst insects, but of the few insects exhibiting it a very large proportion consists of insects each of which shows resemblance to a single model in two or more, and often in very many, independent characters. If resemblance were fortuitous, resemblance in more than one character should be excessively rare, and slightly complex resemblances due to two or three characters should form a very small proportion of the total number of cases of resemblance.

6. If resemblance were due to the operation of the same general environmental factor on mimic and model, it should operate in the same manner on related forms existing in the same environment, this being more probable than its operation in the same manner on two widely distinct forms such as a mimic and its model. Actually we find that in many cases closely related mimics resemble a series of unrelated models which differ from one another greatly in appearance, and which have only one factor in common, namely, that they are all found in the same environment. Therefore the only factor in common between such closely related mimics, other than their common environment, is resemblance to insects, of many types, which are found in the same environment. Mimics resemble their models in appearance alone, and not in structure. Therefore the only kind of environmental factor which could affect the various mimics in such a manner as to produce or preserve their respective resemblances is a factor the operation of which is in some way influenced by the appearance of other insects which exist in the same environment.

7. Deceptive resemblance, then, is not fortuitous, it is not necessarily due to any structural similarity, nor can it have been produced as the direct result of some general environmental influence, and it is evident that it has been produced in some manner as a response to the appearance of a model. The original variation, or variations, which produced the resemblance to another insect must have been due to internal factors in the first place, and the presence of a suitable model could not have influenced in any way either the production or nature of such a variation. It is evident, therefore, that suitable variations must occur amongst insects quite independently of the presence or absence of an appropriate model. As, however, mimic and model are always found together, it is evident that such variations are only preserved in the presence of a suitable model, that is, the variations only have a survival value when the appearance they produce is similar to that of a suitable model which occurs in the same situation as the mimic. The production of suitable variations, therefore, is independent of the presence of an appropriate model, but the preservation of such variations is wholly dependent on this.

8. If, as has been shown to be the case, the preservation of a variation is dependent on the similarity in appearance it produces to that of a suitable model, it is evident that the new variation must have a special survival value compared with that of the old form of the species producing it, and that this special survival value must have been conferred upon it in some manner by the presence and appearance of the model. If a suitable variation, even a complete mimetic resemblance, appears, it must have a special survival value to displace the old form of the species or to produce a new species, for the normal factors which cause the numbers of a species to remain approximately constant in relation to its normal environment would cause an individual exhibiting such a variation to have, on the average, only two descendants in each generation which might carry the factor for the variation, if the variation gave no special survival value to the possessors. The normal variation from this average from year to year would almost certainly cause the complete elimination of such small numbers sooner or later. A mimetic variation, therefore, in order to displace the original form of the species, must have a special survival value due to its similarity in appearance to that of the model, that is, natural selection must operate in its favour.

9. If natural selection is to operate in favour of the new variation on account of its similarity in appearance to that of the model, it is evident that the active agent of natural selection must be one capable of seeing, of discriminating between the appearance of the new variation and the old form of the species; its

operation must in some way be determined by the appearance of both mimic and model; and the appearance of a mimetic variation must cause it to operate less severely on the possessors than on the old form of the species. Other animals which directly affect both mimic and model form the only conceivable active agent of this nature.

10. With minor exceptions, which do not appear to have any connection with the subject under discussion, the significance of other animals to an insect can only be of two types:

- A. They eat the insect.
- B. They are eaten by the insect.

As few mimetic insects are predaceous and the deceptive resemblance of these can seldom be of any conceivable use in enabling the possessor to obtain its prey more successfully, the active agents of natural selection in mimetic insects would appear to consist almost wholly of the natural enemies of the insects.

11. If deceptive resemblance is to be of any advantage to the insect, that is, if the variations producing it have a survival value, it must:

- A. Protect the insect from its enemies; or
- B. Enable the insect to obtain its prey more effectively.

12. It follows from 8 and 11 that mimetic patterns must have been preserved by the appearance of variations deceiving other animals, on account of their similarity to suitable models, causing these to overlook or reject the mimetic forms more frequently than their non-mimetic parent forms, giving them:

- A. Comparative freedom from attack; or
- B. An advantage in catching their prey.

13. It is evident, then, that the models must enjoy a comparative freedom from attack by certain discriminating natural enemies and that this advantage is shared by other insects of similar appearance. If predaceous animals discriminate between suitable and unsuitable food on appearance, the appearance to cause rejection must be associated with the memory of some unsuitability as food of the insect exhibiting it, probably distastefulness. Young birds, for example, will eat anything which moves; discrimination comes later, after experience.

14. Mimics do not resemble any kind of insect but only models belonging to a few well defined groups, which either have known or strongly suspected distasteful characteristics. Widely distinct types of mimic resemble the same model, which, in itself, indicates that the latter must enjoy special advantages, not shared by other insects. It is reasonable, therefore, to believe that the advantage enjoyed by a model is due to a recognition of its distasteful nature by its enemies, recognition being made easy by its conspicuous colouration. As a mimetic form evidently has a special survival value due to its similarity in appearance to its model there can be but little doubt that it shares the advantage conferred on the model by its distasteful nature. The natural enemies, discriminating between suitable and unsuitable food on appearance, mistake the mimic for its distasteful model.

15. Direct experiments designed to show whether distasteful insects are rejected by predators on account of their appearance have been somewhat inconclusive, probably largely on account of the special difficulties of such experiments, but they strongly indicate that this is at least sometimes the case. It is desirable that many more such experiments should be carried out.

16. To summarise. The evidence strongly indicates that natural selection is essential to the preservation of deceptive resemblance; that the active agents of natural selection must be natural enemies of both model and mimic which are capable of discrimination; that the models are regarded as unsuitable food by

such natural enemies and are probably distasteful; and that the special survival value evidently possessed by the mimics is due to the fact that they are confused with their models, owing to their similarity in appearance.

The Nature of Variations selected in the production of Mimetic Resemblance.

As it is necessary that natural selection should have operated in order to preserve mimetic resemblance, the question arises as to what is the nature of the variations on which natural selection has operated. It has already been pointed out that the variations must have arisen in the first place quite independently of their possible use and that only those which gave a special survival value to their possessors could have survived. It is evident, then, that a variation can only be considered to be mimetic after it has commenced to be selected on account of its appearance. The factors governing the first appearance and nature of a particular variation evidently have no direct connection with mimetic resemblance.

All that is necessary in order that natural selection may operate is that a heritable variation should appear causing the insect to resemble some object or organism sufficiently well to enable the possessor to avoid attack by its natural enemies a little more frequently than it would if it did not possess the variation. So long as the variation confers this comparative immunity from attack on the possessor it is immaterial whether the variation is large or small, or quantitative or qualitative. It is well known that animals are capable of producing several different types of heritable variations, and it is unreasonable to suppose that in the production of mimetic resemblance natural selection can only have operated on a single type. Much of the criticism directed against the theory of mimicry has been due to the mistaken insistence of certain of its exponents on the supreme importance of the natural selection of small individual variations in the production of mimetic resemblance.

Two main types of variation are commonly recognised, mutations and individual variations. The conception of the nature of mutations has been modified considerably within the last few years. Previously it was considered that the outstanding characteristic of a mutation was that it was a very large inheritable variation. It was considered to be essentially different from individual variations. Further work, however, showed that size is no criterion of a mutation, for every gradation in size was found from the largest mutations to small mutations indistinguishable from individual variations. Mutationists therefore defined a mutation as any variation which can be inherited, and decided to use the term individual variation only for such small variations as cannot be inherited. In this manner they settled, in their own favour, by the expert manipulation of terminology, the rather sterile controversy as to whether evolution was due to the preservation of mutations or small variations. Actually this definition of a mutation is in every way satisfactory and, indeed, appears to be the only possible one, but it must not be permitted to blind us to the fact that there is a difference in name only between the small mutations we speak of to-day and the individual variations considered by the earlier workers, such as Darwin, to be of paramount importance in evolution. It is scarcely necessary to point out that Darwin and his followers did not consider that small non-heritable variations took any part in evolution.

Having defined what is now meant by "mutation" I shall use this term in subsequent discussions for any type of heritable variation. Previously I have purposely used the more ambiguous term "variation" in order to avoid misunderstanding; for, in spite of the modern views as to what constitutes mutation, there

are still many who are under the impression that a mutation must necessarily be a very large variation. It has been my object to show that any kind of heritable variation, whether large or small, may be selected in the production of mimetic resemblance.

Amongst the numerous forms of mimetic insects, therefore, one would expect that mutations of all degrees of magnitude should have occurred and formed the material on which natural selection could work. One would expect that in some cases the mimetic resemblance should have appeared complete as a single mutation, that in others it was built up by the selection of a series of small or moderate sized mutations and there is no reason why some should not have been built up by the selection of both large and small mutations.

I have already put forward a considerable body of evidence indicating the nature of mutations which must have been selected in order to produce particular cases of mimetic resemblance. It will now be convenient to summarise this.

In the case of many mimetic hutterflies it is evident, as Punnett has shown, that the mimetic pattern must have appeared at first as a single large mutation, or in some cases, as two or three large mutations, no doubt separately selected. This is most clearly demonstrated by the results of breeding experiments carried out on butterflies with polymorphic mimetic females, such as *Papilio polytes* and *P. dardanus*. It is found that the complete colour patterns of the various forms of female are inherited as a whole and behave as Mendelian characters. If the mimetic pattern of each form of female had been built up gradually by the accumulation of a series of small variations, each of these variations ought to be inherited separately and the result of a cross should be that any combination of the numerous small characters, of which each mimetic patterns is built up, should be possible. Instead of each pattern being inherited as a whole there should be every intergrade between the two patterns and the unmodified pattern of either parent form should be of the rarest occurrence. There can be very little doubt, therefore, that in such cases the mimetic pattern must have arisen as a single mutation, complete from the time of its first appearance.

In the var. *romulus* of *P. polytes* it has been shown that two factors are necessary in order that it may appear. One of these is the factor necessary for the production of the other mimetic form, var. *polytes*, while the other is a special factor. The latter only influences the colour pattern of the possessor when it is in combination with the factor for var. *polytes*. It appears necessary to consider, therefore, that var. *romulus* appeared as a single mutation from var. *polytes*, two separate mutations being necessary to produce it from the ancestral form of the species, presumably the male-like var. *cyrus*.

It commonly happens amongst mimetic butterflies that a closely related series of mimics resemble a series of models which are also closely related, though the individual mimics or models may differ considerably in appearance from one another. This suggests that similar potencies for variation exist in the two groups to which the mimics and models belong respectively, for otherwise the mimics would be expected to resemble any kind of suitable model, quite without reference to its relationship to the models of related mimics. When one considers that in structure all butterflies are very similar and that differences of complex colour patterns may have a very simple genetical basis, as has been shown to be the case in hutterflies with polymorphic females, it seems at least probable that similar potencies for variation should occur sometimes in two somewhat widely separated groups, these potencies acting on a similar structure to produce a similar effect. It is necessary that the potencies should be linked together in some manner in order that the same series of colour patterns should occur in the two groups,

otherwise similar colour patterns would be expected to occur scattered at random throughout the butterflies. That some such linkage does occur is indicated by the behaviour of the factors for the various forms of female in *Papilio polytes*. The factor for var. *polytes* together with that for var. *cyrus* determines the colouration of var. *polytes*, and the factor for var. *romulus* together with the other two determines the colouration of var. *romulus*, and is ineffective if this combination does not exist. It seems improbable that the relationship between the various colour patterns existing within a single group of mimics or models should always be of this type, but it is far from improbable that a certain basic similarity should exist between the genetical constitutions of the two groups to which the mimics and models belong respectively, relationship being fairly close and structure almost identical. Given such a basic genetical similarity one would expect that sometimes the same type of genetical variation might occur independently in the two groups, which would be expressed in the adult insects by the appearance of similar types of colouration. It is important to realise that a simple genetical variation may be expressed by a complex modification of somatic characters. The appearance of a complex colour pattern may be determined by a particular factor, but this factor is by no means the only one which takes part in the formation of the pattern. Its function is to modify already existing characters, not to completely displace them. A simile may help to make this point clearer. If a multicoloured picture be examined in a blue light it will have a special appearance which is determined by the blue light. Some parts will remain clear while others are obscured, so that a simple factor, the blue light, produces a complex modification in appearance. The appearance, however, is not wholly due to the blue light, the picture itself is equally essential, and it is a complexity existing in this which determines the apparently complex modification produced by the blue light. It is impossible to say what kind of simple factors might produce such a profound modifying effect on the colour pattern of an insect in which they appeared as mutations, but I would suggest that a factor which produced a slight modification in the normal metabolism of the insect might have such an effect. For example, if the mutation caused the deposition of pigment in the wings to occur at, say, an earlier stage than is normal, it is conceivable that this might cause a modification, both in the nature and distribution of the pigment. That slight changes in the metabolism of an insect can have a profound modifying influence on colour pattern is indicated by the well known fact that simple environmental conditions, such as temperature, humidity and food material, can modify the appearance of an insect, often to a surprising degree, as, for example, in some butterflies which have very distinct seasonal phases. It is evident that this is a secondary effect, the primary effect being some modification of the metabolism of the insect by the environmental factors.

There is another line of evidence which indicates that in many cases of mimicry there must be an underlying genetical similarity between mimic and model which causes each to develop the same appearance. In certain cases, as, for example, the *Metriorrhynchus* mimetic group (Pl. i., figs. 56-95) and the Syntomid group (Pl. iii., figs. 19-30) exactly the same type and degree of variation is found, either between the species contained in the various groups of mimics and models, or within single species, the variability of a particular mimic corresponding closely with that of a single species of model. If the mechanisms underlying the colouration of mimic and model were different there should be no correspondence between the variability of each, and the fact that such correspondence does exist in many cases suggests that in these cases there is an identity, or at least similarity, of mechanism. In the case of a similar range of variation existing

between the different species of mimics and of models it is possible that natural selection might have limited the variation of the mimics to the range of the models, but natural selection could not have operated to cause the variability of a single species of mimic to correspond with that of a particular model. If a mimetic mutation appeared having a variability corresponding with that of the model, natural selection might preserve it, but it is inconceivable that natural selection could either create or even modify a power of variability.

It is well known that in many widely ranging mimetic groups of butterflies the same kind of variation from the normal is to be found in the mimics and models occurring in the same country or district. This is particularly noticeable when the insects occur in a series of very isolated localities, as, for example, on different groups of islands in the Pacific. It is usually claimed that in such cases the models became modified in colouration by the action of some unknown factor and that the mimetic forms developed a similar colouration as a direct effect of natural selection. From what has already been said as to the probable fundamental similarity existing between the colouration of mimic and model in butterflies it is not improbable that both forms have been influenced by the same factors, probably environmental, which would be expected to have a similar result in each case. It is quite possible, however, that natural selection may have played an important part in preserving the resemblances when they appeared.

It appears necessary to consider that a complete mimetic resemblance could occur as a single mutation, or as a very small number of mutations, only if both mimic and model possessed a very similar structure and were sufficiently closely related to have a similar genetical constitution. In all such cases mimic and model would not only look alike but there would be a fundamentally similar mechanism underlying the appearance of each. In cases in which the same appearance is produced in mimic and model in different ways it is obvious that the mimetic resemblance must have been produced in some other manner. This is usually evident where resemblances exist between insects belonging to different orders. The one outstanding exception to this with which I am familiar is the case of the moths belonging to the genus *Snellenia* (Pl. i., figs. 69-72), which not only closely resemble some species of beetle belonging to the genus *Metriorrhynchus* (Pl. i., figs. 56-68), but have a similar range of variation. This may be an exceptional case of similar variability existing in characters which are fundamentally different, but I think that another explanation is more probable. It can scarcely be claimed that a moth and a beetle are fundamentally similar in structure or that they are closely related. The structures affected by the colouration are, however, essentially similar and I consider it probable that the factor which determines the colouration may be of a very simple type which might well occur in very different types of insect. The colouration of each insect consists of plain red front wings, the red sometimes being partially replaced by black, and the whole of the rest of the insect is black. Black is one of the commonest of the pigments which occur amongst insects, red is also very common, and it has been shown that some red pigments, at least, are closely related chemically to the dominant blacks and browns. It is not difficult to believe, therefore, that such a simple distribution of common, and probably closely related, pigments may be determined by some very simple metabolic factor which might well be expected to occur independently in very different types of insect. If the structures affected by this distribution of colour have even a superficial similarity of form and distribution a similar appearance will result, and this is the case in such moths as *Snellenia* and Lampyrid beetles such as *Metriorrhynchus*.

It may be claimed that a mimetic explanation is superfluous to account for

resemblances of the type I have been discussing, as in each case these depend on similar structure and fairly close relationship. The resemblances, however, cannot be due simply to close relationship, as this would necessitate the existence of a series of very different common ancestors of a particular mimetic group and the group to which the models belong, that is a separate ancestral type would be required for each mimic and its model, whereas only a single ancestral type can have existed. The common inheritance by mimics and models from this common ancestor of similar general structure and a similar genetical constitution, carrying potencies for similar types of mutation, is, however, not only possible, but probable. This would account for the appearance sometimes of the same type of colour pattern in the two groups, but I have already shown that it is only possible to account for all the facts of the case by considering that natural selection must have operated to preserve the resemblances when they appeared. Only in this manner is it possible to account for the fact that mimics and models are always found to occur together, as it has been shown that general environmental influences could not have caused this. It is necessary to consider, therefore, that the type of resemblance I have been dealing with is as truly mimetic as if it had been the result of the accumulation of a number of small mutations.

It appears to me that the explanation I have given agrees with the known facts concerning mimicry in butterflies much more closely than the theory that mimetic resemblance has in each case been due to the accumulation of a large number of small favourable mutations. Only in the case of butterflies with polymorphic females has it been possible to bring forward anything in the nature of direct evidence as to whether large mutations or a series of small mutations have been selected in the production of mimetic resemblance. If, however, large mutations must have been selected in such cases, as has been shown, it seems probable that the same process may have been involved in the production of other mimics with which it is impossible to carry out similar experiments, as there appears to be no essential difference between the mimetic patterns of the several forms of a polymorphic butterfly and those of a closely related series of mimetic species. It is evident, then, that the natural selection of small mutations cannot be used as an explanation for the production of certain cases of mimicry in butterflies, and that in many other cases it probably does not apply. There is no reason, however, why this explanation should not be found to apply to some cases of mimicry in butterflies, as it is the only possible explanation of many known cases of mimicry in other types of insect, but adequate evidence of this does not appear to exist at present.

There is still another important consideration which demonstrates that the natural selection of small mutations cannot account for the production of all cases of mimicry in butterflies. In many cases only the female is mimetic, that is, the mimetic pattern is sex-limited.* Sex-limited mutations are of distinctly rare occurrence and it seems incredible that all the small random favourable mutations which are considered to have been selected in building up this mimetic pattern should have been of this rare type. It is surely more probable that a single sex-limited mutation appeared and was selected. It has been claimed that natural selection would operate more effectively on the female than the male, as

* For the purposes of this discussion I am using the term "sex-limited characters" in its literal sense, that is, it signifies characters which can only appear in one sex. These may be sex-controlled or sex-linked, though not all sex-linked characters are of this type. There appears to be no evidence as to which of these categories the sex-limited characters referred to belong.

the preservation of the female is of more importance to the success of the species than that of the male. This theory appears to be due to a curious misconception of the process of natural selection. It appears to have been considered that natural selection operates with a definite end in view, the benefit of the species, and that it is capable of doing anything to attain this end. Actually, of course, it operates without reference to any ultimate object, though it commonly does benefit the species. Natural selection is an evolutionary process, which can only operate by preserving such favourable mutations as appear. It cannot produce, or even modify these. Sex-limitation of characters is a problem of genetics and obviously, therefore, has no connection with natural selection. If a mimetic mutation appeared which was not sex-limited it is immaterial whether natural selection operated in its favour on only one sex or both, in either case the mimetic pattern would be preserved in both, as a mimetic female selected would produce mimetic offspring, of both sexes. On the other hand natural selection could not cause a mutation which was sex-limited to appear in both sexes by any kind of modification of its normal action. It is obvious, therefore, that, far from being a beautiful example of the manner in which natural selection operates for the benefit of the species, as has been claimed, the occurrence of butterflies with mimetic females and non-mimetic males has no direct connection with natural selection, but is purely a genetical problem. The fact that the mimetic pattern as a whole is sex-limited strongly indicates that it is due to a single factor, and it is therefore improbable in the extreme that it should have been built up by the accumulation of small mutations. No doubt, however, the preservation of the mimetic pattern when it appeared was due to natural selection.

In the majority of cases of mimetic resemblance which have come under my notice there is no fundamental similarity between mimic and model. A similar appearance in each has been produced by the modification of different structures in different manners. There is absolutely nothing but appearance in common between mimic and model, and the only possible alternative to a purely mimetic explanation of the resemblance, that is, that appearance has been produced as a response to appearance, is that the resemblance is purely fortuitous, which I have already shown to be practically impossible.

In such cases the mechanism of the resemblance of mimic to model is of a very complex nature. Each of a series of structures in the mimic is modified in such a manner as to produce a resemblance to the model, there being nothing in common between the modifications of these various structures other than their resemblance to some part of the model, or between corresponding parts of mimic and model, these often being developed in very different manners to produce the same appearance, and not infrequently a similar appearance is produced by the development of entirely different parts in mimic and model. A large number of examples of this type of resemblance have already been given, such as wasp-like flies and beetles, and it will not be necessary to refer to these in detail here as I have already demonstrated the extreme complexity of many of these resemblances. It is evident that the series of independent characters which build up a mimetic resemblance of this nature must have had a separate origin and selection, there being no conceivable mechanism by which all could have appeared simultaneously. Natural selection must, therefore, have taken part in the construction of such resemblances, and not simply have preserved them when they appeared. It may be objected that even in these cases natural selection can only have preserved characters which had already appeared. This is so, but natural selection has itself created the resemblance by preserving a series of small suitable characters and rejecting a large number of unsuitable ones. An artist is credited with the

creation of a picture, even though it is known that all the colours he used were in his paint-box before he started.

Though it is evident that such complex mimetic resemblances must have been built up by the selection of a large number of different mutations there is no definite indication of the nature or magnitude of these. In most cases they must have been fairly small, but there is no reason for believing that they must all have been of one type. Any type of heritable variation and any combination of these may have taken part in the construction of a complex mimetic pattern.

It is often objected that if mimetic patterns are built up by the selection of a large number of small mutations it is impossible to understand how the first vague resemblance produced could have a sufficient survival value to be selected; and the same objection applies to the final stages of perfecting an already almost perfect mimetic resemblance. I must leave the detailed consideration of this question to be dealt with later, in connection with the process of natural selection, but I must point out with regard to the first objection that there is evidence that, in some cases at least, the ancestral form of the mimic had, quite accidentally, some resemblance to the insect which later served as the model. For example, it would only be necessary for an apparently non-mimetic species of *Mydaid*, such as *Mitinus viduatus* (Pl. vi., fig. 2), to develop a conspicuous yellow colouration in order to produce a considerable resemblance to certain wasps, as is the case with the fairly closely related *Dioclistis aureipennis* (Pl. ii., fig. 8). Also, an examination of the closest non-mimetic relatives of the many different types of wasp-mimic which occur within the family Asilidae will show that in each case these very definitely exhibit a basis on which the respective mimetic patterns could be built up by comparatively small mutations. As might be expected it appears that in each case the model "chosen" is the one which most closely corresponds to the normal appearance of the group to which the mimic belongs.

It is, of course, evident, that an incipient mimetic pattern must resemble some model sufficiently closely to cause the insect bearing it to be confused sometimes with the model before natural selection can commence to operate in its favour. This first "rough" resemblance must, therefore, be purely fortuitous. When one considers that comparatively few insects are mimetic, that all organisms are capable of considerable variation and of sometimes producing large mutations, and that in any particular environment there is probably quite a number of different insects which could serve as suitable models, it does not seem improbable that some insects should occasionally and accidentally produce a sufficient resemblance to some suitable model to allow natural selection to commence to operate. The small number of known mimetic insects does not appear to me to be by any means too large to be accounted for by such primary fortuitous resemblance. The mutations on which natural selection commences to operate may be very small, if the normal appearance of the species is close to that of the new model, or must be large, if the insect about to become a mimic is very unlike the model. To the former case the objection is raised that if the first small mutation be comparable in size to normal individual variations, it could not give the possessor a sufficient survival value to be selected; it being considered that the survival of the species must have depended on each mutation selected, for otherwise the normal individuals of the species would not have been eliminated. This objection I believe to be due to a misconception of the manner of operation of natural selection, but I must leave consideration of this point to a later stage. I will simply point out that all that is necessary in order that natural selection may operate is that the insect bearing the mutation should have a slightly greater survival value than the normal individuals of the same species. The margin be-

tween being seen and being overlooked must often be very slight, particularly when the insect is near the extreme range of vision of the predator, so that a slight tendency towards cryptic colouration might give the possessors a distinct, though slight, special survival value. The same would apply to a tendency towards deceptive colouration, particularly if, as must often happen, large numbers of non-mimetic and non-distasteful insects occurred together with the incipient mimic. It is at least probable that the predator would attack the obviously palatable insects by preference.

It is generally considered that birds are the most active selective agents in the production of mimetic resemblance and I think it very probable that this is so. It is commonly objected that as birds are so much more experienced as entomologists than we are, and have such superior powers of sight, they would certainly not be deceived by a "mimic" which does not deceive a human entomologist in the field. If this be so, the first vague resemblance of a mimic to its model could be of little use to it. To my mind, far too great an importance has been attached to this objection. I am ready to admit that as a field entomologist an insectivorous bird is vastly superior to me and that its sight is keener, but I do not admit that its power of perception, a mental process, is superior to mine. Experiments have proved that young birds gain experience by the process of trial and error. With some difficulty they learn to associate distastefulness with the appearance of the distasteful object. The mental processes of a bird appear to be of a relatively low type, and it is surely much more reasonable to believe that a bird will associate distastefulness with, say, bright yellow and black stripes than with a complete and detailed mental picture of the whole insect. If this be so the appearance of a simple yellow mark on a non-distasteful species might give it a distinct special survival value. This survival value would naturally be merely relative, and a more perfect resemblance would have a superior survival value and would be selected at the expense of the earlier and vaguer resemblance. In this manner a very perfect resemblance could be built up, provided that the species sometimes produced the right type of mutations. This explanation is dependent on the theory that in order to be selected a mutation need only have a survival value which is relatively superior to that of the normal form of the species. If it be considered that each mutation must have an absolute survival value on which the existence of the species would depend, the explanation would certainly be inadequate; for it would be necessary to consider that the action of the natural enemies of the insect constantly altered during the evolution of the mimetic pattern, and it is difficult to believe that such small mutations as have probably taken part in the production of the mimetic pattern could each have given a sufficiently marked survival value to permit of this explanation. I will shortly bring forward evidence to show that only a relative survival value of the mutations is necessary to account for the production of mimetic resemblance.

I have already pointed out that when the non-mimetic forms of the group to which the mimic belongs differ fundamentally in appearance from the model, it is necessary that the first step in the production of the mimetic pattern must have been in the nature of a very great change from the normal, probably a large mutation, causing the insect to resemble, accidentally, a suitable model. If the new appearance were sufficiently close to that of the model to permit natural selection to commence to operate, the final perfection of the mimetic pattern would be dependent only on time and the appearance of suitable mutations from the new normal of the species. Strong exception has been taken to this explanation on the grounds that a mutation can only be preserved, and not modified, by natural selection; and that therefore the first rough resemblance pro-

duced by a mutation cannot be trimmed into a perfect resemblance. According to our present knowledge of mutations, it is true that their nature cannot be modified in any way by any kind of selection, but it is not necessary to consider that this takes place in the perfection of such a mimetic pattern. Once the primary mutation has been selected it forms a new mean for the species and from this mean mutations of various kinds are bound to occur. Such of these as help to perfect the mimetic resemblance would be preserved. It is the mimetic resemblance which is modified, not the original mutation, and modification takes place by means of the preservation of new mutations, large or small.

There is another means by which the first general resemblance might be brought about, though, as in the previous case, the actual resemblance would be accidental. If we examine any organism we will find that two distinct kinds of structures are present, adaptive and non-adaptive. The adaptive structures may well have been preserved by natural selection, for the development of each would give the possessors a special survival value. Of the remaining structures it is probable that some have definite functions which we have not yet discovered, but there can be little doubt that many structures have no vital importance for the possessors, such, for example, as many of the "ornamentations" of many insects and their eggs. It is obvious that natural selection could not have been directly responsible for the preservation of such non-adaptive structures. The only explanation which can be given for the preservation of such structures is that, having no eliminative quality, they have been preserved along with the adaptive structures with which they occurred. We know no more of the causes which first produced them than we do of the causes which first produced adaptive structures. It appears necessary to consider that all existing organisms have been permitted to survive by the fact that natural selection has operated in their favour, that is, that the perfection of their adaptive structure has so fitted them to their natural environment that they have survived while less perfectly adapted forms have perished. Non-adaptive characters, therefore, must owe their preservation to the fact that they exist in organisms which have been preserved owing to the perfection of their adaptive structures. It seems reasonable to suppose that there must be something in common between the origin of the non-adaptive characters and that of the adaptive characters along with which they are preserved. Non-adaptive characters often show considerable elaboration such as one would expect to result from the continued action of natural selection. As direct selection of such characters is out of the question the most probable explanation seems to be that non-adaptive characters are linked in some manner to certain adaptive characters, so that elaboration produced in the latter by the direct action of natural selection results in an equivalent but dissimilar elaboration of the former. Support is given to this theory by the well known fact that certain factors are quite definitely linked in inheritance. There are two quite different types of linkage; a linkage of two distinct genes, presumably owing to their arrangement in the chromosomes, and the linkage of two or more distinct characters owing to the fact that they are actually only different expressions of a common factor. Though we are apt to think of hereditary factors in terms of the most obvious modification they produce in the structure or appearance of their bearers, it is obvious that the primary influence of the factors must be the modification of the processes of growth and metabolism of the organism, this modification causing the appearance of differences in structure. This being so there is no reason why a single factor should only affect a single structure or portion of a structure, as a slight modification of the normal metabolism may well affect a large number of different structures, and its effect

on different kinds of structures would be expected to be different. Little attention appears to have been given to this problem by geneticists but Morgan has shown that what he terms manifold effects of single factors occur in a number of different mutants of *Drosophila* and similar manifold effects of single factors have been observed in other organisms.* According to these views, therefore, if the progressive elaboration of an adaptive structure be due to the progressive modification of some process of metabolism in a definite direction, this changing metabolism might progressively modify some entirely distinct structure which might reach a considerable degree of development and complexity entirely without the direct influence of natural selection. It is evident, then, that every stage in the evolution of every structure need not, in itself, have a definite survival value. Such an indirect manner of operation of natural selection will permit of the development of non-adaptive structures to a considerable degree of complexity, and it may happen, and probably sometimes does, that such an elaborated structure accidentally serves some definite purpose. It would then be adaptive and its further perfection would be due to the direct action of natural selection. To me it seems not improbable that such highly developed non-adaptive structures may in some cases have formed the basis for selection in the production of mimetic resemblance.

In the preceding discussion I have confined attention principally to deceptive resemblance, but the same processes appear to have been involved in the production of cryptic resemblance, and the same arguments apply. It might conceivably happen that a complete cryptic resemblance should appear as a single mutation, but this would be purely accidental and is improbable. Obviously there can be no underlying genetical similarity between the mimic and its background, so that the explanation which applies, for example, to the close resemblance existing between certain mimetic butterflies and their models, cannot be used for cryptic resemblance. The natural selection of a series of mutations seems the only possible explanation. The mutations selected may be of any size or type, so long as they tend to increase resemblance. There does not appear to be any direct evidence, however, as to the nature of the mutations selected. As to the argument that birds and other predators would not be deceived by resemblances which sometimes fail to deceive even man, I can only reply that a cryptically coloured insect is less likely to be seen than a similar non-cryptic insect, even by birds, and that experiments have proved that this is so. As will be shown, it is only necessary for a slight relative survival value of this nature to operate in order to preserve a mimetic pattern, and that nothing in the nature of absolute immunity is required. Even a vague cryptic resemblance would have such a slight relative survival value.

It may be thought that the evolution of the curiously perfect mimetic habits and attitudes of many insects presents special difficulties, but I do not believe that this is so. Heritable habits must presumably be the expression of special structural peculiarities of the possessors, these probably having some connection with the nervous system. Such habits as give the bearer a special survival value would therefore be selected in the normal manner, their preservation depending on that of the structures of which they are expressions. There appears to be no essential difference between the selection of habits and of appearance. Each is but the expression of some underlying structure, itself the result of some special physiological process determined by the nature of the gene.

* See: Babcock and Clausen, "Genetics in Relation to Agriculture," pp. 133 and 134. and Morgan, "The Theory of the Gene."

The Limitation in Numbers of Animals and its Bearing on the Natural Selection of Mimetic Resemblance.

It is usually considered that the outstanding function of mimetic resemblance is protection. To explain why true mimicry, i.e., deceptive resemblance, is a comparatively rare phenomenon, the theory is put forward that natural selection must have operated more vigorously on the few forms which exhibit it than on other insects, and that the former owe their preservation solely to their great powers of variation. There is absolutely no evidence to support this theory and facts of common observation tell strongly against it. Why, for example, are mimetic insects no more successful than related non-mimetic forms? There are several other important objections to this theory, but I will leave consideration of them till after I have put forward my ideas as to the probable significance of mimetic resemblance.

As butterflies have assumed such an important position in practically all discussions of mimicry it will be convenient to use them to illustrate the considerations I am about to put forward, but practically any kind of insect would serve equally well.

It is considered, then, that the preservation of mimetic species of butterflies has depended on their production of mimetic resemblance. Obviously this can only protect them against enemies, such as birds, which attack the adult insects, and it has been a matter for frequent remark that butterflies are seldom attacked in the adult state. Anyone who has had any experience in breeding butterflies knows that the severest attack is delivered against their earlier stages, particularly the larva. It seems strange, therefore, that a beautiful and apparently complex mechanism for protection should be developed in the adult, to protect it against unimportant enemies, while the larva is unprotected or poorly protected against the most important enemies of the species. If the survival of the species depends on anything it is surely on the efficiency of its protection against its major enemies. It may be objected that efficient protection against the enemies of the earlier stages is impossible, but that these are only capable of destroying the surplus individuals produced in each generation. If this were the case a comparatively small destruction of the adults would bring about the elimination of the species in a few generations, and therefore protection of the adults would be of vital importance to the species. Before accepting such a plausible explanation it is necessary to try to find what factors determine the actual numbers of any particular insect which may exist in its normal environment.

It is well known that the numbers of a particular species existing within any given area will remain approximately the same from year to year unless the conditions change. An exact uniformity of numbers, of course, does not exist, but there is a definite mean around which the numbers fluctuate. The fluctuations may occasionally be very great, but this does not alter the fact that over a long period of years it will be found that the mean remains constant. This must be so, for if any insect had any definite tendency to increase or decrease progressively, the only alternatives, it would in the former case soon overrun the world, and in the latter become extinct. To explain this it is considered that each organism is in a definite state of equilibrium with its environment, but this state of equilibrium does not, in itself, explain what determines the actual number of a particular insect which may exist within a particular area. For example, the numbers of an insect may be considered to be so proportioned to those of its natural enemies that the surplus production of individuals in each

generation is exactly balanced by the numbers which can be destroyed by the natural enemies. This would explain, vaguely, why the numbers of the insect remain constant, that is, how an equilibrium may be established, but it gives no indication of why the equilibrium is established at any particular point. It is this that we want to know; what determines the actual numbers, not simply what causes the numbers to remain approximately constant.

If we examine the occurrence of any insect it will be found that, other conditions being equal, there is a definite relationship between the numbers of the insect and the quantity of food material available. The only manner in which food material could limit the numbers of a species directly is by starvation but, in nature, this is seldom found to happen. Take for example the case of the common wanderer butterfly, *Danaida archippus*. We know that if only two or three plants of milk-weed, its food plant, occur in a particular area we shall find only a few butterflies, while if large areas are covered with milk-weed, large numbers of butterflies will be found. In each case, however, there is a considerable surplus of food plant. The milk-weed could probably support several times as many larvae as it actually does. It appears strange that an increase in the amount of available food plant should cause a corresponding increase in the number of the insects feeding on it when in the first place, before the increase of food occurred, there was already a considerable surplus of food material. Yet this phenomenon can be observed everywhere under natural conditions. Wherever one goes in the field and whatever kind of insect be examined, it will be found that the numbers of insect under observation bear some relationship to the quantity of food material available, though the numbers are seldom directly controlled by the quantity of available food, for there is nearly always an ample surplus of food to support considerably greater numbers of the same species. Apparently the only exception to this is in the case of an exceptionally large fluctuation in numbers, but such plagues of particular species are rare and certainly abnormal, though there is evidence that some, at least, may be periodical in their appearance. It is evident, then, that the quantity of available food material must determine in some indirect manner the numbers of any species which may exist.

It is equally evident that the factors causing the destruction of the surplus numbers of individuals produced in each generation must be the active factors in the limitation of the numbers, and that these factors, therefore, must be influenced in some manner by the availability of food material, causing them to limit the numbers of the insect in some proportion to the quantity of food available.

What then are the active factors tending to destroy insects and so limiting their numbers? The quantity of food available is an obvious possible factor, but it has been shown that it evidently does not operate directly under natural conditions. Unsuitability of food might also have some effect. This would tend to reduce the average number of eggs laid, and might cause the death of certain individuals. As, however, a surplus of individuals would still be produced in each generation there is no reason why the numbers should not increase till limited directly by the amount of available food. Also, under natural conditions unsuitability of food would be an exceptional occurrence due to some change in the environment, such as adverse weather conditions, as each insect is specially adapted to its normal environment. Weather conditions, as is well known, often have a profound influence on the numbers of insects which may exist, and probably form the major factor causing the fluctuations of numbers from year to year. As they operate uniformly, however, at any particular time, they could

not have any special limiting influence governed by the quantity of food material available, and there is nothing in their action from season to season to prevent an insect from increasing in numbers till it consumed all the food material available. As neither food nor weather conditions can produce the observed effect there remain only the natural enemies of the insect, parasites, predators and diseases. Diseases are usually sporadic in their appearance, sometimes causing a very heavy mortality, but more often affecting a species but little. The outbreak of an epidemic often appears to have some connection with weather conditions, such as excessive moisture, and I strongly suspect that the sudden appearance of abnormal numbers of a single species is often the secondary effect of an epidemic disease having destroyed large numbers of some other organism, probably a natural enemy of the species observed. Diseases, then, appear to be too irregular in their action to exercise the stabilising influence on the numbers of insects for which we are trying to account. They appear rather to be one of the major factors causing the fluctuation in numbers which is observed and probably are not infrequently responsible for the largest type of fluctuations which occur, the sudden and apparently inexplicable epidemics of insects which are normally far from common. The action of parasites and predators, on the other hand, appears to be fairly uniform. Though they are subject to fluctuation in numbers like other animals, the fluctuations are normally not great and they appear to exercise a fairly constant influence on their hosts. It is conceivable, therefore, that these may exercise the stabilising influence on the numbers of other insects, the nature of which we wish to determine.

It has already been shown that the factor controlling the numbers of insects must, in some way, be governed by the quantity of food material available for these insects. Is there any manner by which the action of parasites and predators may be governed by the quantity of food material available for their hosts? It appears to me that there is. Parasites and predators have to find their hosts and if a given number of the latter are scattered over a large quantity of their food material they will be more difficult to find than if concentrated on a small quantity, and, therefore, in the former situation each host insect will have a greater chance of being overlooked than in the latter situation, provided, of course, that the number of parasites and predators is the same in the two cases. It follows, then, that the numbers of host insects would increase in each situation till a state of equilibrium was reached in which the proportion of host insects discovered and destroyed by parasites and predators equalled the proportion of the surplus number of individuals produced in each generation, that is, till on the average only one pair of host insects survived from each family in each generation. Further increase would then be impossible. Much larger numbers of insects would be produced in a large area than a small one before this equilibrium was attained, because individuals in the former situation would be more difficult to find.

It will be noticed that this argument entails the idea that the parasites and predators become more and more effective in their action as the numbers of their host increase, and do not simply maintain the same proportion in numbers to their host. This is necessary if the numbers of an insect are to be maintained at a definite level by its natural enemies. If the numbers of an insect increase beyond the normal, it is necessary that the action of the natural enemies should become more severe in order to bring them back to the normal and, on the other hand, if the numbers fall below the normal, the action of the natural enemies must be decreased. A simple proportion existing between the host and its parasites and predators would form a very unstable type of equilibrium which

would be incapable, in itself, of determining the actual numbers of the host which may exist.

If the intensity of the attack delivered by natural enemies be determined by the ease with which they find their host, it is evident that this will provide a mechanism of the required type. If there be larger numbers of the host than is normal within a given area, it is evident that each individual natural enemy should find a larger number than usual. This effect would be intensified in the next generation, for the increased number of hosts attacked would cause an increase in the numbers of the natural enemies, which would still only have to search over the same area and therefore their attack on the host would be intensified, causing further reduction in numbers. This process would continue till the equilibrium was reestablished in which the power of destruction of the natural enemies exactly balanced the power of natural increase of the host. It is obvious that in a similar manner a primary reduction in the number of the host below normal would cause a reduction in the number of parasites in the next generation, in turn causing a decreased attack and an increase in the numbers of the host till the equilibrium was reestablished. The hypothesis that the relative ease with which the host can be found determines the intensity of the attack delivered by its natural enemies therefore gives an adequate explanation as to how the numbers of an insect may be regulated so as to correspond with the abundance of its food without the numbers being actually regulated by this directly. It explains the rather puzzling phenomenon that the numbers of insects in general appear to have some definite relationship to the quantity of their food available, though there is almost invariably an abundant surplus of food which could support large numbers more of the same species. I am unable to find any other factor which could operate in the special manner required to produce this effect and, as the hypothesis I have put forward appears to explain the observed facts in an adequate manner, is at least probable, and I am unable to see any definite objection to it, I feel justified in believing it to be the true explanation of this difficult problem. It at least forms a satisfactory working hypothesis to act as a basis for further work on the subject.

The foregoing considerations apply more particularly to phytophagous insects, though it is probable that they also apply to many insects of other types. The limitation in numbers of most parasitic insects, and probably also of many predators, however, appears to be produced directly by the amount of food available. It is evident that there is not an abundant surplus of food for these insects, for they appear to be the most potent factor in limiting the numbers of other insects and, under natural conditions, normally succeed in destroying all but two of the progeny of any pair of host insects in each generation. The slight excess of food could support only a slightly increased number of parasites and predators temporarily, and could not support any more permanently. Again the actual limiting factor appears to be the "power of discovery" of the parasites and predators. The numbers of these will increase till a point is reached at which they find on the average all but two of the members of each individual family of host insect, and an equilibrium will be established at this point. A further increase in the numbers of parasites or predators would cause a decrease in the numbers of the host, which in turn would cause a subsequent decrease in the numbers of the parasites and predators, so that the equilibrium would soon be reestablished at the original point.

I am well aware that the question of the control of numbers of insects is more complex than I have indicated. The numbers are the result of the interaction of the whole of the environmental factors operating on any particular

insect. Other factors than natural enemies and food supply, however, do not appear to me to enter into the question under consideration, that is, the stabilisation of numbers at a point which has some relationship to the quantity of food material available. Other factors operate uniformly at a given time, without reference to the availability of food, and irregularly at different times and in different places, and so could scarcely be responsible for stabilisation. Such factors would appear to be of importance only in causing fluctuations in numbers from the normal. There is another point which, perhaps, requires explanation. I have been dealing only with the question of the stabilisation of numbers at some definite point and not directly with the factors which determine the actual point at which stabilisation takes place. It is evident that this depends on other factors besides the ease with which the insect can be found by its natural enemies, though this appears to be the final determining factor. The surplus numbers produced by the host in each generation, the efficiency of its concealment, either due to its own appearance or the nature of its normal situation, and the efficiency of its natural enemies in finding it, appear to be the major factors which determine the actual numbers which may exist in any particular situation. If a large surplus of individuals is produced in each generation a correspondingly large proportion must be destroyed to bring about equilibrium, that is, the insect must exist in sufficiently large numbers to cause this severe attack. A small surplus would cause the limitation of the numbers at a low point at which the natural enemies would be relatively ineffective. It is obvious that the more effectively the insect is concealed from its natural enemies the more likely it is to be overlooked, and therefore the greater the number which could exist in a given area before equilibrium could be established. It is equally obvious that the relative efficiency of its natural enemies in finding it will definitely limit the numbers of an insect which may exist. The actual numbers of an insect will be a product of the interaction of these factors, but stabilisation at the point so determined will depend on the relative ease with which the insect may be found should the numbers tend to fluctuate.

It is evident from what has been said that if the numbers of an insect are caused to vary from the normal by any cause there is a definite mechanism which will tend to bring the numbers back to normal. Suppose, then, that the major enemies, on which the numbers of a particular insect depend, attack the larval stage, and that a minor enemy attacks the adult. Does it follow that this increased attack will cause a diminution in the numbers of the insect? At first sight it would appear that the numbers would be reduced in proportion to the increased severity of attack, but a more careful examination will show that this would not be so. The effect of an increased attack on the adults would be to cause less eggs to be laid. There would, therefore, be a decrease in the number of larvae, the food of the natural enemies, causing a decrease in the numbers of parasites and predators and an increased difficulty in finding the larvae. The severity of the attack on the larvae would therefore be lessened so that a larger proportion would reach maturity. Thus the effect of an additional minor attack on the adult stage would be to lessen the effectiveness of the major attack on the larval stage, and the numbers would remain practically unaltered. A curious effect of this equilibrium is that the severer the attack on the adult stage, the larger the proportion of insects which reach maturity. Conversely, if the severity of a minor attack on the adult stage were decreased, there would be a corresponding increase in the severity of the major attack on the earlier stages, and a smaller proportion of the insects would reach maturity.

It is evident, therefore, that the numbers of an insect which may exist

under particular conditions is governed almost entirely by the action of its major enemies, and that a minor enemy only tends to interfere with the action of these and cannot appreciably affect the numbers of its host. An extreme case will, perhaps, demonstrate this most clearly. Suppose that the numbers of an insect are controlled by a single natural enemy and that a new enemy appears which, operating by itself, would be capable of limiting the numbers of the same insect to exactly the same level as the first natural enemy, because its "power of discovery" is the same. The two natural enemies have identical powers for controlling the numbers of the host. Now suppose that the two natural enemies attack the host simultaneously. It is evident that, operating on the usual number of hosts, the food supply of each natural enemy would be reduced to half the normal, owing to the action of the other, and that therefore only half the normal number of each enemy would survive. The combined action of the natural enemies under the new conditions would therefore only equal the action of either enemy acting by itself. This result would be obtained whether the enemies acted together on the same stage of the host or on different stages. In the latter case, however, a difficulty is introduced as to what is meant by equal numbers, as the numbers of the host existing at different stages would be modified. As has already been shown, an increased attack on the adult stage will cause a diminution in the numbers of adults which survive to lay eggs, but a corresponding increase in the number existing in the earlier stages and also actually an increase in the number of adults which emerge. It is evident, however, that the species is equally successful under either condition. This secondary effect of a new natural enemy in causing an increase in the numbers of the insect at stages immediately preceding the one attacked does not affect the subject under consideration, but its importance in connection with the biological control of insects is evident.

So far I have tacitly assumed the action of specific natural enemies only, the numbers of which are automatically controlled by the numbers of the particular host under consideration, the available food of the natural enemies. Many, in fact, probably most, of the natural enemies of insects are not specific in their action, but will attack many kinds of insects, so that their numbers are not directly controlled by the numbers of a particular host. In such cases the diminution in the numbers of a host insect would not cause a corresponding diminution in the numbers of its natural enemies, and it might be considered that this would cause an increased eliminative action to operate against the host, as the same number of natural enemies as before will now concentrate their attention on a reduced number of host insects. Such an effect would, of course, not tend to stabilise the numbers of the host, but would cause further disturbance of the equilibrium. The fact that the numbers of insects do tend to remain stable indicates that some other factor must operate which would cause a decreased severity of attack when the numbers of the host are reduced. Again I believe this to be due to a variation of the relative ease with which an insect can be found which corresponds to its variation in numbers. It is immaterial whether an insect exists in large or small numbers within a particular area in which a definite number of natural enemies is also found. In either case the chance of survival of any particular host insect would be the same, provided the natural enemies searched over the area equally thoroughly, whether the host was rare or common, and therefore there would be no variation in the proportion of the host destroyed dependent on its numbers. The solution of this problem lies, I believe, in the proviso I have made. It is a matter of common observation that the severest attack is delivered by, say, a bird against the insect which is

most abundant. If, for example, a particular species of caterpillar suddenly appears in exceptionally large numbers and becomes very conspicuous, birds are found to concentrate on this caterpillar, neglecting food which is difficult to find and concentrating on that which is easily obtainable. Practically everyone who has lived in the country, whether an entomologist or not, could give examples of this from personal observation. It would appear, therefore, that the increase in numbers of an insect causes an increased activity of its natural enemies against it, whether these be specific or general in their action. The mechanism of the increase in attack with an increase in numbers would appear to be that when an insect is common there is a greater chance that some individual will be seen by a natural enemy than when the species is rare, and, having found one individual, the enemy will remain to search for more. The presence of other individuals in its vicinity therefore lessens the chance of survival of any particular individual of the same species, owing to the fact that the other individuals may attract enemies to its vicinity. It follows, then, that an increase in numbers of an insect will automatically intensify the action of its natural enemies, whether specific or general. This causes an increased proportion of the insect to be destroyed, tending to reduce the numbers to normal, and when this point is reached the factors I have mentioned will operate to maintain an equilibrium.

A good example of the intensification of the attack by natural enemies caused by an abnormal increase in the numbers of an insect has been given to me by Dr. G. A. Waterhouse, an account of which will form an excellent illustration of the point under consideration. The Pierid *Anaphæis java teutonia* Fabr., sometimes known as the "travelling butterfly," does not normally breed in the Sydney district, where its food-plant, *Caparis*, is not native, but it occasionally appears there in large migratory swarms from the north or inland. Dr. Waterhouse has a bush of *Caparis* in his garden and large numbers of butterflies from one of these migratory swarms settled on this bush and laid eggs. Dr. Waterhouse and Dr. E. W. Ferguson together computed that at a conservative estimate there was at least a quarter of a million eggs on this single bush. Assuming that each female laid 100 eggs, probably a fairly accurate estimate, there must have been about 2,500 females and presumably as many males in the portion of the swarm which settled on this bush. The first enemies seen to attack these insects were neuropterous larvae, probably those of *Chrysopa*, which appeared in large numbers and sucked the juices out of many of the eggs and some of the very young larvae. This was followed by an intensive attack by the paper-wasp, *Polistes*, which destroyed large numbers of the larvae. They appeared to concentrate the whole of their energies on these larvae, but before long were seen to be flying round the bush in rather an aimless manner, seldom attacking the larvae. Evidently they had already provided as much food as their own larvae could manage and all that it was necessary for them to do now was to keep these in a state of repletion, so that they could not make further use of the abundant surplus of food provided. Later Tachinids appeared in large numbers and delivered such a heavy attack that it was difficult to find a single larva not bearing at least one Tachinid egg. By this time the whole of the leaves and all the young bark had been removed from the tree and some hundreds of larvae were seen to migrate from the tree, apparently in search of food. This they could not have obtained as another bush of *Caparis* probably did not exist within a radius of several miles. The result of this combined and heavy attack was that not more than 50 adults emerged from the whole brood and many of these were observed to be taken by blue wrens, which attacked the butterflies as soon as they emerged. Thus not more than 50 butterflies, many of

which were immediately destroyed, were produced from a number of eggs estimated at 250,000. If each female lays 100 eggs in the normal state of equilibrium an average of 2% must survive but in this case, owing to the abnormal number of individuals, only an average percentage of 0.02 emerged and few, if any, of these survived to lay eggs. This clearly indicates the proportional increase in the severity of attack brought about by abnormal increase in numbers.

We will now examine the special question of the limitation in numbers of butterflies. Anyone who has had any experience in breeding butterflies will know what an important part is played by parasites in destroying eggs, larvae and pupae; and general observations in the field show that caterpillars are heavily attacked by predators, such as birds and wasps (see Pl. vi., fig. 1). Also, one of the strongest arguments of the opponents of the theory of mimicry is that adult butterflies are seldom seen to be attacked by birds, and that therefore protection from such attack could be of little value to the insect. Again Dr. Waterhouse has provided me with concrete examples to illustrate the action of natural enemies on butterflies. Two batches of eggs, totalling 130 in number, were laid by *Delias aganippe* Don. on a native-cherry tree, *Exocarpus*, in his garden. These were left on the tree and from them only one adult resulted. Later another batch of eggs, estimated at 50 in number, was laid on the tree. These were removed to a large breeding cage of wire gauze, which excluded all the larger parasites and predators, though it was found impossible to completely eliminate spiders, which certainly destroyed some of the larvae. From this batch 26 pupae were obtained and 22 adults emerged. As the two sets of observations were unfortunately not made at exactly the same time, it is impossible to say definitely that the two cases only differed in that in one the insects were exposed to their natural enemies while in the other they were partially protected from them, but this appears to be the only difference of importance as the weather conditions appeared to be in every way favourable in each case. When exposed to natural enemies, then, considerably less than one per cent. survived and when partially protected from them there was a survival of over forty per cent. Everything indicates, therefore, that the major attack is delivered against butterflies when in the earlier stages.

From what has been said it follows that protection from attack in the adult stage can be of little, if any, importance to a species of butterfly; for reduction in the normal slight attack on the adults would only result in a slight decrease in the numbers of the earlier stages and the numbers of adults which emerged, the actual numbers of the species remaining practically unaltered. Therefore if a perfect mimetic pattern appeared suddenly in a non-mimetic species, giving complete immunity from attack, it would not increase the success of the species, which would be just as successful without the mimetic pattern. At first sight this would appear to render natural selection of the mimetic pattern impossible, but actually this is not so.

For the sake of convenience I will consider a perfect mimetic pattern which gives complete immunity from attack to the possessors, and which appears suddenly in a non-mimetic species subject to attack in the adult stage by natural enemies, such as birds, capable of discriminating between the two colour patterns. All the possessors of the mimetic pattern would survive to lay eggs, while a proportion of the non-mimetic individuals would be destroyed by their natural enemies. Therefore the proportion of the mimetic to the non-mimetic individuals would be greater when the insects laid their eggs than it was when the adults emerged. As usual an excess of eggs would be laid and the natural enemies of the earlier stages would eliminate a proportion of these, destroying,

on the average, an equal proportion of the mimetic and non-mimetic stock. As a result, the proportion of mimetic to non-mimetic individuals which would emerge would be the same as that existing between the insects which laid eggs in the previous generation, but greater than that which existed between the adult insects which emerged in the previous generation, and less than that which would later exist between the insects of the same generation when they laid their eggs. The slight selective action of the enemies of the adults is therefore cumulative from generation to generation, while elimination of surplus individuals is brought about by the enemies of the earlier stages operating completely without any selective action. It is evident, therefore, that the mimetic form of the insect would continue to increase at the expense of the non-mimetic so long as it continued to give the possessors a greater survival value than the non-mimetic form, that is, under normal conditions, till it completely replaced it. When, however, the species became completely mimetic and possessed complete immunity from attack by the natural enemies of the adult, it would be no more successful than it would be if it remained non-mimetic. The adults would certainly be free from attack, but less adults would be produced, on account of the increased severity of the attack on the earlier stages. It is therefore evident that the outstanding characteristic of mimicry is not protection, as has usually been assumed; and, on the other hand, the major objection to the theory of mimicry which is so frequently stressed, that is, that in so many cases mimetic animals evidently do not enjoy any special protection, is shown to be no argument against mimicry itself, though it remains the most important objection to the current theory as to the significance of mimicry.

It should be noticed that the foregoing considerations apply equally well to the evolution of Batesian and Müllerian mimicry. All that is necessary is that a character should appear in an incipient mimetic insect which will cause it to be mistaken occasionally by its natural enemies for some other insect which is less liable to attack. The individuals bearing this character would therefore have a slightly greater survival value than the normal individuals of the same species, and the new pattern would gradually replace the old one. The incipient mimic need not therefore be palatable; it need only be less distasteful than its model, other things being equal. If the incipient mimic be less numerous than its model it may be as distasteful, or even more distasteful than the model; for the appearance of the commoner species would be more definitely associated with distastefulness by the natural enemies than that of the rarer species, and this might more than counteract the special protection afforded by the greater distastefulness of the rarer species. On the other hand, a commoner slightly distasteful species might be caused to mimic a rarer very distasteful species because the great distastefulness of the latter more than counterbalances the effects of its rarity. The model, however, must always be the form which is least liable to attack, whether this is due to its special distastefulness or its numerical superiority. There should never be any tendency for the two insects to become mutual mimics and to develop a mimetic pattern intermediate in appearance between their two normal patterns.

As protection cannot be considered to be the outstanding characteristic of mimetic resemblance the question arises as to what is its significance. If we are to think of significance in terms of the teleological concept of ultimate purpose, mimetic resemblance has no significance to the hearers, for it does not benefit them in any way. Though the individuals in the stage which exhibits mimetic resemblance have a greater survival value than similar non-mimetic insects, neither the species nor, on the average, the individual receives any special pro-

tection resulting from mimetic resemblance; for the greater survival value of the individuals in the mimetic stage automatically brings about a correspondingly decreased survival value of the other stages. Mimetic resemblance, therefore, simply serves to fit the possessors more perfectly to their natural environment, without conferring upon them any material advantage.

The theory I have put forward with regard to the significance and probable method of evolution of mimicry in butterflies appears to apply equally well to other examples of mimetic resemblance, whether cryptic or deceptive. There are two points to which I must draw attention, however. It is not necessary that the selective and eliminative agents should always operate on different stages of the insect, though it appears evident that this happens in butterflies and probably also in many other kinds of insects; and it is probable that sometimes a single natural enemy is both the selective agent and also the major factor in controlling the numbers of the insect. I do not think the first point requires any comment as it is evident that the selective agent must operate on the stage which exhibits mimetic resemblance, while the eliminative agent may operate on any stage. With regard to the second point, it is obvious that mimetic resemblance would benefit a species if the selective and eliminative agents were actually the same natural enemy. Numbers would increase to a point at which the increased severity of attack due to increased numbers exactly balanced the value of the increased immunity due to the mimetic resemblance. There is no reason why this should not sometimes occur, but I do not think that it is a common phenomenon. It most certainly does not occur in some cases, as in the butterflies, and it is difficult to understand how, in such cases, each small mutation could have given a special survival value to the possessors; or, if this be granted, how the original non-mimetic form could have survived under what must have been a very intensive attack. It is, however, not difficult to believe that a single large mutation, or a small number of such mutations, might be preserved in this manner.

A Consideration of the More Important Criticisms of the Theory of Mimetic Resemblance.

In the light of the foregoing considerations I will now consider the main objections which have been put forward from time to time, and which are considered by many definitely to disprove that mimicry exists. These may be stated briefly as follows.

1. Why are mimetic insects apparently no more successful than closely related non-mimetic species occurring in the same environment?
2. How did the first rough pattern of an incipient mimetic form give the possessors a survival value if the tiny variations claimed to be selected in the final perfection of an already almost perfect pattern also give a special survival value? It would seem that the selective agent, such as a bird, would at first have to be very easily deceived, while later it would be required to possess very acute powers of discrimination.
3. If birds seldom attack butterflies, how can protection against them be of any importance to the species and so bring about natural selection?
4. Punnett has brought forward evidence which indicates that the proportion existing between the mimetic and non-mimetic females of *Papilio polytes* must have been much the same 150 years ago as it is to-day. If the mimetic form were specially protected its proportion to the non-mimetic form should have altered appreciably.

5. In connection with the same butterfly Punnett has shown that the range of the models does not correspond exactly with that of the mimie, but that the proportion existing between the mimetic and non-mimetic females remains apparently the same wherever the species is found in India and Ceylon.

6. Though in nearly all cases mimics are less common than their models there are some instances in which the mimie is commoner than the insect which apparently serves as its model. It is considered that a mimie must be rarer than its model if it is to receive any protection from its resemblance.

The first objection is well illustrated by Buxton's observations on the colours of desert animals. He points out that two main types of colouration occur amongst desert animals, sand colour, which has usually been considered as a particularly clear example of "protective colouration," and black. These two types of colouration are exhibited by animals inhabiting exactly the same situation and sometimes occur in quite closely related animals. The black species appear to be in every way as successful as the "protectively coloured" pale brown species, in spite of the fact that the former often move about freely and habitually in broad daylight. Also, the habits of many of the sand coloured species are such that their colour can be of very little use in concealing them as some spend almost all of their time underground, and others only come out at night. It is quite evident that any explanation which depends upon a necessity for a definite protective value of the sand colouration to account for its production and preservation will not explain the observed facts, and Buxton has tentatively put forward the theory that sand colour, and also black, may be due to some special physiological requirements common to many desert animals; that is, that the colour is simply the expression of some underlying physiological condition of the animal induced by the special environmental conditions of the desert and that the colour, in itself, is of no significance. This theory appears to me to be satisfactory in part, but it does not give an adequate explanation of the perfection of the cryptic colouration exhibited by many forms; the rather complex "counter shading," for example, which causes many bulky animals to appear flat and to be inconspicuous on a plain surface. Such colouration shows a very definite adaptation of appearance to the animal's environment, and some explanation appears to be necessary to account for this adaptation. It is evidently necessary that there should be some mechanism, by which adaptation can be evolved, which does not involve any necessity for the actual survival of the species to depend on the special protection afforded by each mutation. Such a mechanism I have already described, and I believe that this gives an adequate explanation of the observed facts concerning desert animals. What is the major factor controlling the numbers of desert animals I do not know, but it is evident from Buxton's observations that predaceous animals capable of discrimination do not constitute this factor. If, however, they exercise any selective influence, even though it be very slight, this will be cumulative and will be capable of producing a complex form of adaptive colouration, provided that the right type of mutations occur, but the mutations selected, and even the finally perfected cryptic colouration, will not in any way modify the degree of success of the species.

One further point must be mentioned. In this case, as in all others, it is necessary that the colouration of the animal should first resemble that of the background sufficiently to permit the commencement of natural selection, the primary resemblance thus being purely fortuitous. Pale brown is a common colour amongst animals, and it is not improbable that the special environmental conditions of the desert may tend to cause the appearance of this colour by some modification of the normal physiology of the animal. This alone may be the

cause of the colouration of some forms which do not show adaptation in detail, and it may have formed the basis on which natural selection operated in the production of the more perfectly adapted forms. In a similar manner black may have been induced by the altered physiological conditions of other animals; and if this black colouration, or the processes underlying it, gave the possessors even a slight advantage relative to the normal individuals of the same species, it would eventually become the normal colouration of the species. As before, this change would be brought about without any alteration in the success of the species being necessary. The advantage given by black would probably not be due to its appearance, but to some other property of the pigment, or the processes underlying its production. For example, its function is not improbably the protection of the delicate underlying tissues from the intense light characteristic of desert regions. In some animals such protection from intense light may be of more importance than protection from predaceous animals, which would cause the production of black rather than sand colour, but in neither case would the protection afforded be of vital importance to the species.

The second objection to the theory of mimicry I have put forward is very clearly stated by Punnett in his book, "Mimicry in Butterflies," in the following passage (pp. 139-140). "Even if birds are the postulated enemies it must be further shown that they exercise the postulated discrimination. It is required of them that they should do two things. In the first place they must confuse an incipient or "rough" mimic with a model sufficiently often to give it an advantage over those which have not varied in the direction of the model. In other words, they must be easily taken in. Secondly, they are expected to bring about those marvellously close resemblances that sometimes occur by confusing the exact mimicking pattern with the model, while at the same time eliminating those which vary ever so little from it. In other words, they must be endowed with most remarkably acute powers of discrimination. Clearly one cannot ask the same enemy to play both parts. If, therefore, birds help to bring about the resemblance we must suppose that it is done by different species—that there are some which do the rough work, others which do the smoothing, and others again which put on the final polish and keep it up to the mark. This is, of course, a possibility, but before it can be accepted as a probability some evidence must be forthcoming in its favour." It is evident that the difficulty here is not to explain why birds should less frequently attack a more perfect than a less perfect mimic, but why, in the early stages of the production of a mimetic pattern, they should eliminate very imperfect forms and pass over slightly more perfect forms, and later eliminate forms whose mimetic patterns are almost, but not quite, perfect, and which are very much more perfect than those of the individuals which were previously passed over. The difficulty is due to the belief that the active principle of natural selection is the elimination of the less fit individuals, whereas, according to the views I have put forward, it is "the survival of the fittest"—a Darwinian concept which appears to have been strangely misunderstood in recent years. Thus, in his "Origin of Species," Darwin says: "As natural selection acts solely by the preservation of profitable modifications, each new form will tend in a fully stocked country to take the place of, and finally to exterminate, its own less-favoured forms with which it comes into competition." Thus he lays stress on the preservation of the fit, and not the elimination of the less fit, this elimination being a secondary result of the success of the fit. In recent years, and particularly in connection with the subject of mimicry, it appears to have been assumed that the only possible mechanism for natural selection is the exact reverse to that described by Darwin in the above passage. It has been assumed

that the fit can only survive and replace the less fit by the active elimination of the latter, and this idea has caused a number of apparently insuperable difficulties to arise, such as the one under consideration, in connection with the operation of natural selection in particular cases; difficulties which are due solely to a concentration on one possible manner of operation of natural selection. In one sense, of course, the idea of the survival of the fittest automatically entails that of the elimination of the less fit; but one is only the secondary effect of the other, and it is of the utmost importance to realise which is primary, that is, the active principle of natural selection. At first sight it would appear that the simple survival of the fittest could not in itself bring about natural selection, without a corresponding active elimination of the less fit. I have already shown, however, that it can. The survival of the fittest automatically brings about an overstocking of the environment in which they occur. This causes an intensification of the action of the normal eliminative factors which reduce the numbers to normal by an impartial destruction of fit and less fit, but the proportion of fit to less fit individuals will increase from generation to generation, owing to the cumulative action of the selective factor which gives the fit a slight survival value relative to the less fit. The last point is most important. It is not necessary that each variation should give the possessors an absolute survival value, without which they would perish; it is only necessary that each variation should give the possessors a slightly greater relative survival value than the other individuals in which the variation does not appear. Elimination of the less fit, therefore, is a direct result of the relatively greater success of the fit and would only occur in the presence of the fit.

It is evident, therefore, that the objection under consideration is not an objection to the theory of mimicry, but to a current theory as to the manner of operation of natural selection. If birds discriminate on appearance they could bring about the selection of all the stages in the production of a mimetic pattern, without modifying the nature of their discrimination, and without there being any necessity for the operation at different times of a series of different birds with different powers of discrimination. All that is necessary is that butterflies with a more perfect mimetic pattern should be slightly less frequently attacked than those with a less perfect mimetic pattern, and there can be but little doubt that birds are capable of exercising the simple type of discrimination required to bring this about.

It is often considered that some form of orthogenesis is required in order to explain the final perfection of the mimetic pattern of certain insects. The leaf-hutterfly, *Kallima*, is usually taken as an example to illustrate this. It is claimed that natural selection could operate to bring about a general resemblance to a leaf, but that once the hutterfly was sufficiently like a leaf to deceive its enemies, natural selection could take no further part in perfecting the resemblance. Fine details, such as the marks which look like mould spots and transparent areas of membrane which look like holes, are considered to be inexplicable as the result of natural selection. Personally I can see little force in this argument. These details are simple derivatives of structures which are not only to be found in closely related non-mimetic forms, but occur practically throughout the Nymphalidae. The "mould spots" are evidently derived from the "ocelli" which are so common on hutterflies' wings, the long mark looking like the mid-rib of a leaf has its counterpart in large numbers of nymphalids, and the smaller marks which look like leaf veins are evidently only a development of marks with a similar distribution in many related non-mimetic forms. The normal system of colouration of the Nymphalidae, therefore, has

formed the basis for the evolution of the mimetic pattern in *Kallima*, and the selection of a series of simple variations from the normal is sufficient to account for the particularly perfect resemblance of this insect to a leaf. The idea that natural selection gave an inadequate explanation of this case was evidently due to the difficulty already considered; that is, it was considered that each variation must have given an absolute survival value to the possessors, so that when the insect had received the "protection" of the earlier types of pattern, further favourable variations could not give the insect a further survival value, and therefore these could not have been selected. It is evident, however, that if it is only necessary that new variations should have a slightly greater relative survival value than the normal form of the insect, new favourable variations could be selected indefinitely till complete immunity from attack is conferred upon the insect by the perfection of its resemblance. There is no evidence that this point has yet been reached by *Kallima* and certainly there is none to show that this point was reached by the insect long before the present perfection of its mimetic pattern was produced, as is postulated by those who believe that orthogenesis must have taken part in the production of this pattern. There is a further objection to this rather nebulous theory of orthogenesis. One could understand that orthogenesis might occur if it were simply the expression of the progressive development of something within the insect. A progressive increase in size, either actual or relative, or the intensification of a colour, might be explicable as the result of the progressive development of some process within the insect, but I fail to see how any conceivable type of orthogenesis could direct a progressive development towards a goal set by some factor which has no direct influence whatever on the insect. I cannot see how the appearance of a leaf could possibly direct an orthogenetic process in *Kallima* to bring about resemblance. If the leaf does not direct this process, and it be considered to be necessary that orthogenesis must have brought about the resemblance, then the resemblance must be fortuitous and orthogenesis, though responsible for the colour pattern of the insect, would not actually have produced the resemblance, as such.

As to the objection that birds seldom attack butterflies, this is but another of the difficulties manufactured by the theory that natural selection can only operate by the direct elimination of the less perfect forms. On the theory that the more perfect forms need only have a slightly greater relative survival value than the normal forms in order to be selected, this difficulty ceases to exist. Only an occasional attack by birds, provided they discriminate between mimetic and non-mimetic forms, will give the more perfectly mimetic forms a relatively greater survival value, so that in this manner a complete mimetic pattern may be built up. Protection from birds is no "object" of mimetic resemblance. Mimetic resemblance is simply a more perfect adaptation of the insect to its environment, brought about by the selective action of certain of its natural enemies, but the adaptation is not of vital importance to the species.

Papilio polytes has three types of female in India and Ceylon. Two are mimetic, apparently mimicking two other species of *Papilio*, while the third is non-mimetic and is similar in appearance to the male. Punnett brings forward evidence which indicates that the proportion existing between the mimetic and non-mimetic females must have been much the same 150 years ago as it is today. If the mimetic forms have any survival value over the non-mimetic form, there ought to have been an appreciable change in this proportion in such a long period. The fact that there has been no such change indicates that the mimetic forms have no greater survival value than the non-mimetic forms. If this be so, how can one account for the production and preservation of the mimetic forms?

The following consideration appears to me to give an adequate explanation. It is considered that birds associate the colour of a distasteful insect with its distasteful characteristics, and that a mimic of such an insect receives special freedom from attack owing to the fact that it is often mistaken for the distasteful model. Suppose, then, that such a mimetic form suddenly appears in a previously non-mimetic species. Birds will definitely associate its appearance with distastefulness, as all the insects of that appearance previously taken by the birds would be distasteful models. The mimic would therefore have a greater relative survival value than the normal non-mimetic form of the species, which it would progressively displace. When, however, the numbers of the new mimetic form approached those of the model the special survival value of the mimic would be decreased, for birds would almost as frequently associate palatability as distastefulness with the appearance common to mimic and model; for they would catch nearly as many mimics as models. The progressively decreasing special survival value of the mimetic pattern might therefore reach a point where it was no greater than the survival value of the non-mimetic form, at which point the relative proportions of the two forms would remain constant. In *Papilio polytes* the mimetic forms are actually nearly as common as their models, and, judging by the appearance of the forms of this species, I should say that the nature of the equilibrium existing between these forms is probably as follows. The mimetic forms are more conspicuous, but have a slight special survival value owing to their resemblance to their models, while the non-mimetic form is slightly less conspicuous, which probably gives it a slight special survival value. I should judge that the equilibrium has been established at a point where the eliminative value of the conspicuous colouration, together with the slight survival value of the mimetic resemblance of the mimetic forms, just equals the slight special survival value of the less conspicuous colouration of the non-mimetic form. Some of the former therefore are destroyed because they are more conspicuous, while some survive, which would not otherwise have done so, because they are confused with the model; while some of the latter escape detection because they are less conspicuous, and others are destroyed which would have escaped had they been mimetic. When the proportion destroyed of each form is the same, owing to the interaction of these factors, a position of stability is reached in which there would be no tendency for one form to increase at the expense of the other. It is easy to see that if a second mimetic form arose it would eventually be brought into a similar state of equilibrium with the other forms. The answer to this difficulty, therefore, is that the mimetic forms have lost their original special survival value as a direct consequence of their increase in numbers and they now have no greater survival value than the non-mimetic form.

Before dealing with the objection based on the slight lack of conformity between the distribution of *Papilio polytes* and its models I must briefly indicate the nature of the mimetic resemblance exhibited by this insect. There are three forms of female. One is almost identical in appearance with the male, the second, var. *polytes*, which is conveniently referred to as the A. form, resembles *Papilio aristolochiae* and the third, var. *romulus*, known as the H. form, resembles *Papilio hector*. The two mimetic forms resemble their respective models in form and general system of colouration, but the resemblance is by no means perfect. In particular the red is not as brilliant as in the models, nor is it as extensive in its distribution. Also, the two mimetic forms are not very dissimilar, and I strongly suspect that each may be considered as a general mimic of the type of butterfly represented by the two insects considered to be models, rather than as a specific mimic of a single model, though not improbably the mimetic resemblance

may be of an intermediate type between these two extremes. This would mean that either type of mimic might receive a special survival value in the presence of either model. I have already shown that there is reason to believe that birds, and other discriminating natural enemies, are more likely to associate the general appearance of an insect with distastefulness than the whole of the details which together make up that appearance.

As far as I can make out from the information given by Punnett the distribution of *P. polytes* and its models is as follows. *P. aristolochiae* has a very wide range and is found over the whole range of distribution of *P. polytes*, while *P. hector* has a more restricted range and there are some districts in which *P. polytes* occurs where *P. hector* is absent. According to the considerations I have given, in such districts the H. form of *P. polytes* may retain its special survival value owing to the presence of *P. aristolochiae*; but this, by itself, is scarcely sufficient to account for the fact that the proportion existing between the three forms of female is the same in such districts as in others in which both models exist. Districts from which *P. hector* is absent, however, are only on the fringe of the distribution of this insect. One would therefore expect that a certain amount of interbreeding should occur between individuals of *P. polytes* occurring just within the limits of distribution of *P. hector* and other individuals occurring beyond these limits. This would tend to retain the same proportion between the three forms of *P. polytes*, both within and beyond the limits of the distribution of *P. hector*. The effects of such chance interbreeding would, of course, be very slight, but they would only have to counteract a very slight tendency for the proportion of the forms to change. A slight decrease in the survival value of the H. forms, owing to the absence of its specific model, would be largely counteracted by the presence of its other possible model; and this, operated upon by a selective agent which seldom attacks the butterflies and probably does not exercise a very marked discrimination, is required to have its effects nullified by the slight stabilising influence exercised by occasional interbreeding with insects from an area in which both models occur. It does not appear to me that this is in any way beyond the limits of probability, and I certainly do not consider that any difference in the proportion of the forms to one another brought about by such conditions should be evident from a casual observation of the insects in the two areas. Before such arguments can be considered as evidence against the theory of mimicry, therefore, it will be necessary to produce much more definite data, based on careful statistical studies carried out in the different areas, or cases will have to be found in which the two types of area are completely isolated.

According to the theory that the success of a mimetic species depends wholly on the perfection of its resemblance to its model it is evident that the mimic could not exist in larger numbers than its model, for this would indicate that it had a superior survival value to its model, which could not possibly be conferred upon it by its resemblance, however perfect. Unless the resemblance be of extreme perfection it is difficult to understand how the numbers of a mimic could even closely approach those of its model. Cases are recorded, however, in which the mimic is considerably commoner than the insect considered to be its model, though these are very exceptional. Such cases can easily be explained if it be granted that the numbers of the mimic are governed by some other factor than the one which selects the resemblance, and there can be but little doubt that this is so. If a mimetic form appears which has a relatively superior survival value to that of the normal non-mimetic form, due to its resemblance to some suitable model, it will progressively displace the non-mimetic form till its survival value has been reduced to that of the latter, or till the whole of the individuals of the

species become mimetic. The mimetic form will still retain a special survival value due to its resemblance, even after its numbers have become greater than those of its model, though this will be greatly reduced. Very occasionally a bird, for example, would reject a mimetic form because it happened to have taken one or more of the distasteful model previously, but this would be a rare occurrence if the model were less common than the mimic. Still, a slight special survival value would be retained on account of the mimetic pattern, and the mimetic form would continue to displace the non-mimetic unless the non-mimetic form had some special survival value of its own which would allow an equilibrium to be produced eventually between the mimetic and non-mimetic forms. Failing this the mimetic form would ultimately completely displace the non-mimetic, even though the species existed in much larger numbers than the model.

This being so it would naturally be asked why it is a general rule that mimics are less common than their models, and usually comparatively rare. This I believe to be due to the fact that in order to form an effective model an insect must be fairly common, as discriminating enemies could only gain sufficient experience in order to associate appearance definitely with distastefulness in the case of common insects. On the other hand the average species of insect is not common, reference to any systematic collection will demonstrate this. Since, therefore, only common insects can serve as effective models while any kind of insect may become a mimic, and since most insects are not common, it follows that in most cases mimics should be scarce and models common.

In dealing with the various objections put forward to the theory of mimicry I have found it convenient to make frequent reference to the work of Punnett, as the problem appears to me to be stated more clearly in his valuable book, "Mimicry in Butterflies," than elsewhere. In order to avoid any possible misunderstanding I shall take this opportunity of stating that, far from wishing to belittle his work, I consider that it has constituted one of the greatest advances in our knowledge of this subject. He has clearly elucidated one of the most difficult problems concerning the mechanism of the production of mimetic resemblance and he has not hesitated to state clearly difficulties for which he had no adequate explanation. It is the very clarity and excellence of his work which has caused me to refer to him rather than to other authors.

Before concluding I must point out that the considerations I have given apply only to cases of true mimetic resemblance, and not necessarily to all cases of resemblance which appear to be mimetic. Amongst the large number of apparently mimetic insects there are not improbably a few in which the resemblance is purely adventitious. Also similarity in appearance may have been brought about in some cases by other factors, such as environmental conditions. I have already shown that common environmental conditions cannot have brought about resemblance in many forms, but in some others they may have done so. For example, I believe that the "mimicry rings" consisting of several species of *Euploea* which are found on various groups of islands in the Pacific are of this nature. The primary resemblance, no doubt, is simply due to close relationship, while the fact that all the species in one group of islands are similar in appearance, but differ in appearance from those in other groups of islands, is more reasonably explained as due to the action of common environmental factors operating on a series of insects with closely similar bodily structure, than as due to the direct operation of natural selection through the medium of discriminating enemies.

Summary.

The conclusions to be drawn from the evidence and considerations I have now placed before you may be briefly summarised as follows.

Of the actual fact of mimicry there can be no doubt, as there is an abundance of evidence to show that in a large number of cases of resemblance appearance can only have been produced as a response to the appearance of something else. Only the theory of natural selection will account for the preservation of all kinds of mimetic resemblance, and it is essential to the production of many kinds. The material used by natural selection is any kind of heritable variation, so that in some cases there is evidence that the complete mimetic pattern has been produced at a single step, when mimic and model are closely related, while in others the mimetic resemblance can only be considered to have arisen by the selection of a large number of smaller mutations. Natural selection has not operated by the direct elimination of the less perfectly mimetic forms, but by the special preservation of the more perfect, elimination being due to a non-selective factor. The numbers of a species are not controlled by the selective agent, but, in most cases at least, by some other agent which is non-selective; the former thus perfects mimetic resemblance by discriminating in its favour, and the latter controls the numbers of the species by a system of proportional elimination, which is regulated by the actual number of individuals existing within a particular environment in such a manner that it tends to counteract any fluctuation in the numbers from the normal. The success of a species, therefore, does not depend on its relative freedom from attack by the selective agent, but on its power of avoiding attack by the non-selective eliminative agent. It follows, then, that an adequate mechanism exists for the preservation and perfection of mimetic resemblance, causing the insect to become more and more perfectly adapted to its environment, but that the success of the species is in no way affected by this adaptation, even in its most perfect form.

If the species does not benefit from the possession of mimetic resemblance it is evident that the outstanding characteristic of such resemblance cannot be protection, as has usually been supposed. In a very special sense mimetic resemblance does, however, give protection to the possessors. An insect exhibiting mimetic resemblance is slightly less liable to attack than a closely related non-mimetic insect, but this is only a protection from the particular enemy which acts as selective agent; and the very fact of this special protection, tending as it does to cause an increase in numbers, in turn causes an increase in the severity of the attack delivered by those enemies which control the numbers of the species. Therefore neither the species nor the individual, on the average, enjoys any protection due to the possession of mimetic resemblance. Mimetic resemblance therefore simply fits an insect more perfectly to its normal environment; and in order to explain its production there is no need for any teleological concept of ultimate purpose.

The theory of the production of mimetic resemblance I have outlined appears to apply to practically all cases of true mimetic resemblance, but the possibility must not be overlooked that in a few cases the same factor may have operated both in the selection of mutations and in the limitation of the numbers of the insects. It must also be noticed that what appears to be mimetic resemblance may sometimes be produced by very different types of factors which produce similar appearance independently in two or more unrelated insects, the resulting resemblance being actually fortuitous.

Conclusion.

I am well aware that the theory I have put forward will be repugnant to many enthusiastic supporters of the theory of mimicry. The beautiful perfection of adaptation shown in many mimetic forms naturally predisposes one to consider that it must have a definite purpose, for a desire to find purpose in all things appears to be an inherent human failing. It is this very assumption of purpose which has obscured the obvious conclusions to be drawn from the known facts concerning mimetic resemblance, and this is by no means the first time that a conviction of ultimate purpose has interfered with the progress of science. Yet a simple consideration of facts with which all are familiar from personal observation will show that mimetic insects cannot have any advantage over non-mimetic insects in their normal environment. It is well known that in an undisturbed environment the numbers of any organism will remain approximately constant from year to year so that therefore, on the average, only two individuals will survive from each family in each generation. The remainder must be destroyed or the numbers of the species will progressively increase, which is impossible. It may be considered that the mimetic resemblance does give the possessors an advantage, but that this is counteracted by the more intensive eliminative action of some other factor. This, in point of fact, appears actually to be the case, but it does not alter the fact that mimetic insects can have no advantage over non-mimetic. "Purpose" and "advantage," therefore, can have no place in the true explanation of mimetic resemblance.

To my mind a mechanism which can cause the progressive perfection of the adaptation of an organism to its environment by preserving each more perfect mutation as it appears, without threatening the existence of the species should such mutation not appear, is much more worthy of our admiration than a mechanism which operates by the direct destruction of less perfect forms and constantly threatens the species with extinction. The latter mechanism exhibits a crudity such as one would not expect to find in Nature. Far more important than this, however, is the fact that a theory, simple in the extreme and based on obvious deductions from well known facts concerning the limitation in numbers of animals, when applied to the known facts concerning mimetic resemblance was found to explain them all, including those which have hitherto been considered as insuperable objections to the theory of natural selection, and did so without any recourse to supplementary and problematical hypotheses such as a special severity of the operation of natural selection on mimetic forms, orthogenesis towards some goal determined by some external object, a progressive modification of the habits of the selective agent or a constant change of selective agents during evolution. The singularly complete conformity of the theory with the known facts leads me to believe that this theory gives the true explanation of the evolution and significance of mimetic resemblance. It will be necessary, however, for the theory to explain such new facts as come to light, and it is to be hoped that every effort will be made to collect as many of these as possible in order that the theory may be proved or disproved; the ultimate object being to gain a complete understanding of the problem, which in itself would involve the solution of the greater problem of evolution.

Evidence is principally required in two directions. First, the nature of the mutations which are selected in the production of mimetic resemblance. As has been shown, we already know something of this, but this is principally by inference. More work of a purely experimental nature is required, though it is unfortunately evident that there are few forms suitable for such experimental work.

Careful search, however, should be made for suitable species. Secondly, we still have a very inadequate knowledge of the nature of the discriminating enemies which are responsible for selection. Careful observation in the field is required to determine what animals act as selective agents under natural conditions, and experiments on the same animals are required in order to determine the nature and extent of the discrimination exhibited by these animals. The collection of further cases of mimetic resemblance is of subsidiary importance, though of considerable interest. Such cases, however, as bring to light new facts may be of the greatest importance, but such facts are more likely to be found by the intensive examination of a few cases than by the enthusiastic collection of all insects which can be considered by any stretch of the imagination to show some form of mimetic resemblance.

In conclusion I should like to make a plea for the more intensive study of purely biological problems in Australia. We have special advantages for the study of such problems which few other countries possess and which will not be available to future generations in this country. Even within easy access from such a populous centre as Sydney there are hundreds of square miles of country still in practically its primeval condition, and this gives us unique opportunities for studying organisms in relation to their normal environment. I feel strongly that every possible use should be made of these opportunities while they remain, even if that has to be partly at the expense of taxonomic work. I do not wish to belittle the importance of taxonomic work. The long series of species mentioned and illustrated in this address which I have been unable to get identified clearly demonstrates the urgent necessity for further taxonomic work, as a large number of these are known to be undescribed species and probably a considerable proportion of the remainder are also undescribed. Still, I feel that the biological side of the subject is receiving less than its fair share of attention, and I hope that this address may stimulate some others to take up purely biological work who would not otherwise have done so.

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The identification of the species to which I have referred, belonging as they do to many different orders, has been no mean task, and it would have been impossible for me to do this myself. It therefore gives me pleasure to acknowledge my indebtedness to the following entomologists for the trouble they have taken in the identification of specimens; to Dr. I. M. Mackerras, of the Department of Public Health, Sydney, for the identification of a long series of Diptera; to Mr. G. H. Hardy, of the Queensland Museum, Brisbane, who assisted Dr. Mackerras in the identification of some of the more troublesome species of Diptera; to Mr. H. Hacker, of the Queensland Museum, Brisbane, for the identification of the Hymenoptera; to Mr. A. M. Lea, Entomologist of the South Australian Museum,

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I should also like to acknowledge my indebtedness to the Trustees of the National Park. Their public spirited action in setting aside two cottages, at Gundamain and Waterfall, in the National Park, for the use of those who wish to study animals and plants in the field is deserving of the highest commendation and has been of material assistance to me. Many of my observations were made, and some of the photographs reproduced were taken while I was making use of one or other of the cottages.

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Explanation of Plates.

- Pl. i., Pl. ii., figs. 1 to 22, and Pl. iii., photographs of pinned specimens.
Pl. ii., figs. 23 and 24, and Pls. iv.-xiv., photographs of living insects.
Except in Pl. x., figs. 1 and 2, and Pl. xii., fig. 2, all the photographs shown in Pl. ii., figs. 22 and 23, and Pls. v.-xiv. were taken of insects just as they were

found in their natural environment, without interfering with them in any way. In the three exceptions mentioned the insects, in order to be photographed, were placed in situations as nearly as possible identical with those from which they were collected. No photograph has been retouched.

For the sake of brevity in the lists of species the orders are represented by the following letters:—

D.—Diptera, H.—Hymenoptera, C.—Coleoptera, L.—Lepidoptera, R.—Hemiptera (Rhynchota), N.—Neuroptera, O.—Orthoptera.

Plate I.—All Figures are Natural Size.

1. *Paralastor* sp. (H. Eumenidae).
2. *Hylaeoides concinna* Fabr. (H. Hylaeidae).
3. *Codula vespiformis* King (D. Asilidae).
4. *Leucospis* sp. (H. Chalcididae).
5. *Hesthesis variegatus* Fab. (C. Cerambycidae).
6. *Crabro tridentatus* Sm. (H. Crabronidae).
7. *Syndipnomyia* sp. (D. Stratiomyiidae).
8. *Paralastor* sp. (H. Eumenidae).
9. *Conops* sp. (D. Conopidae).
10. *Odynerus bicolor* Sauss. (H. Eumenidae).
11. *Laphria* sp. (D. Asilidae).
12. *Paralastor* sp. (H. Eumenidae).
13. *Cerioides breviscapa* Saund. (D. Syrphidae).
14. *Leucopsina odyneroides* Westw. (D. Cyrtidae).
15. *Cerioides variabilis* Ferg. (D. Syrphidae).
16. *Hesthesis* sp. (C. Cerambycidae).
17. *Odynerus* sp. (H. Eumenidae).
18. *Cerioides ornatus* Ferg. (D. Syrphidae).
19. *Conops* sp. (D. Conopidae).
20. *Microdon variegatus* Walk. (D. Syrphidae).
21. *Chrysopogon* sp. near *fasciatus* Ricardo (D. Asilidae).
22. *Odynerus* sp. (H. Eumenidae).
23. *Cerceris australis* Sauss. (H. Philanthidae).
24. *Brachyrhopala fenestrata* Macq. (D. Asilidae).
25. *Cerceris opposita* Sm. (H. Philanthidae).
26. *Microdon variegatus* Walk. (D. Syrphidae).
27. (H. Thynnidae).
28. *Massicyta picta* Brauer (D. Stratiomyiidae).
29. *Conops* sp. (D. Conopidae).
30. *Conops* sp. (D. Conopidae).
31. *Conops* sp. (D. Conopidae).
32. *Cerioides opuntiae* Ferg. (D. Syrphidae).
33. *Odynerus* sp. (H. Eumenidae).
34. (H. Braconidae).
35. *Brachyrhopala pulchella* Macq. (D. Asilidae).
36. *Plecia fulvicollis* Fab. (D. Bibionidae).
37. *Brachyrhopala* sp. (D. Asilidae).
38. (H. Psammocharidae).
39. *Phycus* sp. (D. Therevidae).
40. *Megachile suffusipennis* Ckll. (H. Megachilidae).
41. *Cyanonedys leucura* Herm. (D. Asilidae).
42. *Calopompilus raplor* Sm. (H. Psammocharidae).

43. *Ectinorrhynchus superbus* Sch. (D. Therevidae).
44. *Ectinorrhynchus* sp. ? *rufipes* Krob. (D. Therevidae).
45. *Agapophytus* sp. ? *australasiae* Guer. (D. Therevidae).
46. *Prionocnemis connectens* Turn. (H. Psammocharidae).
47. *Miscothyris* sp. (H. Larridae).
48. *Elimus* sp. (H. Eumenidae).
49. *Odynerus* sp. (H. Eumenidae).
50. *Brachyrhopala limbipennis* Macq. (D. Asilidae).
51. *Arpactus frenchii* Sm. (H. Arpactidae).
52. *Hestesis* sp. ? *cingulata* Kirby (C. Cerambycidae).
53. *Arpactus bellicosus* Sm. (H. Arpactidae).
54. *Hestesis* sp. ? *cingulata* Kirby (C. Cerambycidae).
55. (D. Tachinidae).
- 56-58. *Metriorrhynchus rhipidius* Macl. (C. Lampyridae).
- 59-61. *Metriorrhynchus irregularis* Waterh. (C. Lampyridae).
62. *Metriorrhynchus rufipennis* Fabr. (C. Lampyridae).
63. *Metriorrhynchus marginipennis* Lea (C. Lampyridae).
64. *Metriorrhynchus heterodoxus* Lea (C. Lampyridae).
65. *Metriorrhynchus marginipennis* Lea (C. Lampyridae).
66. *Trichalus ampliatus* Waterh. (C. Lampyridae).
67. *Metriorrhynchus eremitus* Fabr. (C. Lampyridae).
68. *Metriorrhynchus cryptoleucus* Lea (C. Lampyridae).
- 69-71. *Snellenia hylaea* Turn. (L. Heliodinidae).
72. *Snellenia lineata* Walk. (L. Heliodinidae).
- 73 and 74. *Eroschema poweri* Pasc. (C. Cerambycidae).
75. *Pterostenus suturalis* Oliv. (C. Cerambycidae).
76. *Chaodalis macleayi* Pasc. (C. Cerambycidae).
77. *Pterostenus suturalis* Oliv. (C. Cerambycidae).
78. *Tritocosmia roei* Hope (C. Cerambycidae).
79. *Eroschema* sp. (C. Cerambycidae).
80. *Eroschema atricolle* Pasc. (C. Cerambycidae).
81. *Rhinotia haemoptera* Kirby (C. Cureulionidae).
82. *Stigmodera rufipennis* Kirby (C. Buprestidae).
83. *Stigmodera nasata* Saund. (C. Buprestidae).
84. *Stigmodera erythroptera* Boisd. (C. Buprestidae).
85. *Stigmodera praetermissa* Carter (C. Buprestidae).
86. *Palaestra assimilis* Hope (C. Cantharidae).
87. *Palaestra rubripennis* Cast. (C. Cantharidae).
- 88 and 89. *Pseudolychus haemopterus* Guer. (C. Oedemeridae).
- 90-95. *Pseudolychus haemorrhoidalis* Fabr. (C. Oedemeridae).
96. *Calliphora stygia* Fabr. (D. Museidae).
97. *Scaptia* sp., near *gibbula* Walk. (D. Tabanidae).
98. *Onesia* sp. (D. Museidae).
99. *Scaptia violacea* Walk. (D. Tabanidae).
100. *Pycnosoma rufacies* Macq. (D. Museidae).
101. *Erystalis smaragdi* Walk. (D. Syrphidae).

Plate II.—Figures 1 to 22 are Natural Size.

1. *Tragocerus formosus* Pasc. (C. Cerambycidae).
2. *Abispa ephippium* Fabr. (H. Eumenidae).
3. *Chrysopogon crabroniformis* Roder (D. Asilidae).

4. *Hesthesis ferrugineus* Boisd. (C. Cerambycidae).
5. *Systropus* sp. (D. Bombyliidae).
6. *Sceliphron laetum* Sm. (H. Sphecidae).
7. *Cryptocheilus fulvidorsalis* Turn. (H. Psammocharidae).
8. *Diochlistus aureipennis* Westw. (D. Mydidae).
9. *Lesticothynnus frauenfeldianus* Sauss. (H. Thynnidae).
10. *Diochlistus gracilis* Macq. (D. Mydidae).
11. *Eveirus lateritius* Shuck. (H. Exeiridae).
12. *Tragocerus spencei* Hope. (C. Cerambycidae).
13. *Cryptocheilus fulvidorsalis* Turn. (H. Psammocharidae).
14. *Neosarapogon princeps* Macq. (D. Asilidae).
15. *Calopompilus ornatipennis* Sm. (H. Psammocharidae).
16. *Pelecorrhynchus deuqueti* Hardy (D. Tabanidae).
17. *Suvatta* sp. (H. Ichneumonidae).
18. *Elissoma* sp. (D. Stratiomyidae).
19. *Pseudagenia consociata* Turn. (H. Psammocharidae).
20. *Trogodendron fasciculatum* Schreib. (C. Cleridae).
21. (H. Psammocharidae).
22. *Pelecorrhynchus* sp. (D. Tabanidae).
23. *Tenodera australasiae* Leach (O. Mantidae) in its natural environment and eating a larval tettigoniid. $\times \frac{1}{2}$.
24. *Hesthesis variegatus* Fab. (C. Cerambycidae) about to fly from flower of *Leptospermum*. $\times 1\frac{1}{2}$.

Plate III.

1. *Bimia bicolor* White (C. Cerambycidae). $\times 1$ 1-3.
2. *Aciptera waterhousei* Pasc. (C. Cerambycidae). $\times 1$ 1-3.
3. *Agapete carissima* Newm. (C. Cerambycidae). $\times 1$ 1-3.
4. *Erinus mimula* Pasc. (C. Cerambycidae). $\times 2\frac{1}{2}$.
5. *Pseudocephalus mirus* Pasc. (C. Cerambycidae). $\times 2\frac{1}{2}$.
6. *Ochyra coarctata* Pasc. (C. Cerambycidae). $\times 2\frac{1}{2}$.
7. *Macrones capito* Pasc. (C. Cerambycidae). $\times 1\frac{1}{2}$.
8. *Henicospilus* sp. (H. Ichneumonidae). $\times 1\frac{1}{2}$.
9. *Mantispa* sp., near *australasiae* Guer. (N. Mantispidae). $\times 1\frac{1}{2}$.
10. *Paroxyphilus* sp. (O. Mantidae). $\times 1\frac{1}{2}$.
- 9 and 10 illustrate simple convergence.
11. *Daerlae tricolor* Sign. (R. Lygaeidae). $\times 2\frac{1}{2}$.
12. *Dolichoderus doriae* Em. (H. Formicidae). $\times 2\frac{1}{2}$.
13. Larval *Daerlae tricolor* Sign. (R. Lygaeidae). $\times 2\frac{1}{2}$.
14. (H. Braconidae). $\times 2\frac{1}{2}$.
15. *Eucecoris* sp., near *basifer* Walk. (R. Miridae). $\times 2\frac{1}{2}$.
16. *Platyura* sp. (D. Mycetophilidae). $\times 1\frac{1}{2}$.
- 17 and 18. *Systoechus vetustus* Walk. (D. Bombyliidae), in 17 viewed from in front, in 18 the same specimen is viewed from behind. $\times 1$.
- 19-22. *Syntomis phepsalotis* Meyr. (L. Syntomidae). $\times 1$.
- 23-26. *Eressa paurospila* Turn. (L. Syntomidae). $\times 1$.
- 27-30. *Trichocerosia zebrina* Hamps. (L. Arctiidae). $\times 1$.

Plates IV.-XIV.

For explanation see the Plates.